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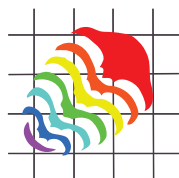
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Hidden subsurface garden on own faeces – the trace fossil *Tubulichnium rectum* (Fischer-Ooster, 1858) from the Cretaceous-Palaeogene deep-sea sediments

Alfred Uchman and Andreas Wetzel

ABSTRACT

Tubulichnium rectum (Fischer-Ooster, 1858) is an oblique to horizontal, unbranched, blind ending tube having margins densely lined with ellipsoidal muddy pellets. It occurs in fine sandy to muddy, siliciclastic and marly deep-sea sediments mostly from Turonian to Eocene times. It was probably produced by “worm”-like organisms, which fed on organic-rich sediment deposited seasonally or episodically on the sea floor. The faecal pellets were stored in the deep parts of the burrow within the anoxic zone beyond the depth that other burrowers usually penetrate. During periods of food shortage, the pellets were utilized as a supplementary nutrition source. Such behaviour in constructing and using a cache is interpreted as an adaptation to increased competition for food in the deep sea after the Cenomanian.

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INTRODUCTION

Trace fossils record variable strategies of feeding by their producers, which include systematic utilization of deposits in horizontal, vertical, or oblique directions, random sediment reworking, filter feeding, predation, chemo(sym)biosis, farming, etc. (for a review see Seilacher, 2007; Vallon et al., 2016). Owing to seasonal oligotrophy or general

oligotrophy, efficiency of these strategies is challenging in the deep-sea, where supply of organic matter is, on average, rather low and commonly strongly fluctuating (e.g., Lutz et al., 2007; Arndt et al., 2013). Under such conditions, competition between organisms forces them to develop nutritional strategies most of which are still poorly known. Theoretically one strategy is to ingest as

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FIGURE 1. Location maps: **1**, a part of Europe with main localities of the material studied and indication of the main study area in the Polish Carpathians; **2**, the main study area in the Polish Carpathians with indication of several localities of the material studied or reported occurrences of *Tubulichnium rectum*.

much as possible during times of food abundance and utilize one's own, possibly fermented, faeces as a new food resource during times of nutritional misery.

A good example of this strategy is represented by the trace fossil that was described originally as *Halymenites* von Sternberg, 1833 and later as *Tubulichnium* Książkiewicz, 1977 or *Ophiomorpha* Lundgren, 1891. However, morphology, ethological function, and environmental meaning of this trace fossil are still poorly understood. It is the purpose of this paper to: (1) provide an ichnotaxonomic revision of this trace fossil on the basis of the original material, (2) investigate the morphology and occurrences on the basis of newly sampled additional material from the Polish Carpathians, and (3) propose a new ethological model of the discussed trace in connection with neoichnological data from the modern deep sea.

MATERIAL AND METHODS

Material

The specimens analysed derive from many localities (Figure 1.1). However, the specimens for morphological studies were collected mostly from the Ropianka Formation (Campanian–Paleocene) of the Magura Nappe in the Polish Flysch Carpathians in the Słupniczanka River section at Słupnice and Zamieście (Figure 1.2). This formation con-

sists of turbiditic sandstones, siltstones, mudstones, and marls. The discussed trace fossil was observed mainly in thin- to medium-bedded turbiditic sediments, which occur in three thrust sheets; these sediments are interbedded with isolated packages of thick sandstone and rarely pebbly mudstone beds (Uchman, 2008b). Additional observations were made in the Rhenodanubian Flysch of the Alps in Austria and Germany (Uchman, 1999), and the Pagliaro Formation (Paleocene) in the Ligurian Domain of the Northern Apennines (Uchman 2007a). All of these deposits consist of deep-sea turbiditic sediments. A list of the occurrences of the discussed trace fossils known by the authors is given in Table 1, together with the relevant literature.

The original material of *Halymenites* Fischer-Ooster, 1858 is preserved in marl. It was collected from the Gurnigel Nappe in the Fribourgian Alps (Switzerland). The Gurnigel Nappe is composed mainly of siliciclastic turbiditic deposits and only subordinately of marls with intercalated turbidites. The marly deposits are Maastrichtian in age, while siliciclastics accumulated during the Palaeogene (van Stuijvenberg, 1979). The marly beds are restricted within the type region mentioned by Fischer-Ooster (Seeliggraben) to a rather small area (roughly at Swiss coordinates 601'060/176'450; Schweizerische Geologische Kommission, 1961).

TABLE 1. Occurrences of *Tubulichnium rectum* (Fischer-Ooster, 1858). * – reserve inclusion in *T. rectum*; ** – probably not *T. rectum*.

Formation and general location	Localities	Age	Facies	References
Al Ayn Formation, Oman		Upper Triassic	Deep-sea turbiditic sandstones and shales	Wetzel et al. (2007)
Globotruncana Marl, Pieniny Klippen Belt, Carpathians, Poland	Sromowce Wyżne	Turonian	Deep-sea, pelagic and hemipelagic sediments	Książkiewicz (1977)
Zementmergelserie, Rhenodanubian Flysch, Bavarian Alps, Germany	Kalkgraben quarry, Arzbach Stream, Steinbach near Benediktbeuern, Halbammer Valley	Turonian–Maastrichtian	Turbiditic limestones, marlstones and mudstones	Uchman (1999)
Sromowce Beds, Pieniny Klippen Belt, Carpathians, Poland	Sromowce Wyżne	Coniacian–Maastrichtian	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977)
Holovnia Marl, Skole Nappe Carpathians, Poland	Krzeczkowa – old quarry	Coniacian–Santonian	Deep-sea marls	This study
Ropianka Formation (Inoceranian Beds), Skole Nappe, Carpathians, Poland, Ukraine	Poland: Wara, Wołódz, Kuźmina, Bachów, Huwniki, Kalwaria Paclawska (the steram Sopotnik), Wola Romanowa. Ukraine: Dora (Yaremche)	Coniacian–Paleocene	Deep-sea turbiditic sandstones and marls	Książkiewicz (1977); this study
Kropivnik Furoid Marls, Skole Nappe, Carpathians, Poland	Wiar section	Campanian–lower Maastrichtian	Deep-sea marls	Leszczyński (2004)
Tuscan Apennines, Italy	Alberese	Campanian–Eocene	Deep-sea marls	Reis (1909); Abel (1935); Seilacher (1959)
Monte Antola Formation, Ligurian Domain, Northern Apennines, Italy	Vagge, Molino Vecchio, Val Gardenella, Monte Colletto, Candini, Roiale	Late Campanian – Maastrichtian	Deep-sea turbiditic marls, sandstones and shales	Uchman (2007b, 2009)
Northpenninic Flysch, Alps, E Switzerland	Fähnernspitz Mt.	Upper Cretaceous	Deep-sea turbiditic marls, sandstones and shales	Fischer-Ooster (1858)
Ropianka Formation, Magura Nappe, Carpathians, Poland	Złatna, Mordarka, Biczycze, Wola Brzezińska, Wola Krogulecka, Siary, Uście Gorlickie, Koninki, Stara Wieś, Lubomierz, Słopnice	Maastrichtian–Paleocene	Deep-sea turbiditic sandstones, shales, locally marls	Książkiewicz (1977); Uchman (1991c, 1998); this study
“Zumaya Flysch”, Basque Country, Spain	No data	Upper Cretaceous – lower Eocene	Deep-sea turbiditic limestones, marls, sandstones and shales	Cummings and Hodgson (2011)*
Upper Istebna Beds, Silesian Nappe, Carpathians, Poland	Kamesznica (the stream Janoska)	Paleocene	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977)
Kanina Beds, Magura Nappe, Carpathians, Poland	Lubomierz	Paleocene	Deep-sea turbiditic marls and shales	Cieszkowski et al. (1992)
Itzurun Formation, Basque Country, Spain	Zumaya section	Paleocene	Deep-sea turbiditic Limestones, marls, sandstones and shales	Giannetti (2010)

TABLE 1 (continued).

Formation and general location	Localities	Age	Facies	References
Pagliaro Formation, Ligurian Domain, Northern Apennines, Italy	Pallavicino, Celio, Salata, Cabella Ligure, Fubbiano, Borassi	Paleocene	Deep-sea turbiditic sandstones, marls and shales	Uchman (2007a); this study
Greifenstein Sandstone, Wienerwald, Rhenodanubian Flysch, Austria	Hof bei Karsten, Schleifsteinbruch	Eocene	Deep-sea turbiditic sandstones and shales	Abel (1935); Uchman (1999); Kern (1978)
Variegated Shale, Magura Nappe, Carpathians, Poland	Wola Brzezińska	Upper Paleocene–Upper Eocene	Deep-sea shales with turbiditic sandstones	Książkiewicz (1977)
Szczawnica Formation, Magura Nappe, Carpathians, Poland	Hałuszowa, Krościenko-Łąkcica, Szczawnica, Szlachtowa, Łomnica, Wierchomla Mała, Łosie, Jamne, Jaszcze, Rzyczanów	Upper Paleocene–Lower Eocene	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977); Uchman (1991c, 1992a, 2008a); Wetzel and Uchman (1998); this study
Gurnigel Flysch, Fribourgian Alps, Switzerland	Seeliggraben n. Gurnigelbad, Zollhaus	Upper Paleocene	Deep-sea, pelagic and hemipelagic sediments	Fischer-Ooster (1858); Crimes et al. (1981), Uchman (1998, figure 26B, C)
Flysch del Grivó, Julian Prealps, NE Italy	Clapp, Vernasso	Upper Paleocene–Lower Eocene	Deep-sea turbiditic sandstones and shales	Tunis and Uchman (1993, 1996)
Beloveža Formation, Magura Nappe, Carpathians, Poland	Sidzina, Zbludza	Lower–Middle Eocene	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977); this study
Hieroglyphic Beds, Magura Nappe, Carpathians, Poland	Rajcza (?)	Eocene	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977)
Hieroglyphic Beds, Dukla Nappe, Carpathians, Poland	Daliowa	Eocene	Deep-sea turbiditic sandstones and shales	Książkiewicz (1977)
Piwniczna Sandstone Member of the Magura Formation, Carpathians, Poland	Tylmanowa-Baszta	Lower Eocene	Deep-sea Turbiditic sandstones and shales	This study
Bisericani Formation, Marginal Folds Unit, Eastern Carpathians, Romania	Mt. Geamana, Valea Corbu	Upper Eocene	Marls	Krejci-Graf (1936)
Numidian Flysch, Atlas, Tunisia	Meloula-Tabarka	Upper Oligocene	Thin-bedded turbidites interbedded with light green mudstones	Riahi et al. (2014)*
Middle Bhuvan molasse sediments of Mizoram, Northeast India	No data	Miocene	Intertidal to subtidal clastics	Rajkumar et al. (2012)**

Methods

Organic matter and carbonate content was measured for 11 samples using LECO RC612 equipment. The samples were stepwise heated to (1) 110 °C, (2) 450 °C, and (3) 1100 °C and the cor-

responding loss in weight was recorded. During step (1), water evaporates, during step (2) organic matter is burnt, and during step (3) carbonate decays.

SYSTEMATIC ICHNOLOGY

Ichnogenus *TUBULICHNIUM* Książkiewicz, 1977

Type ichnospecies. *Tubulichnium incertum* Książkiewicz, 1977.

Emended diagnosis. Oblique to horizontal, unbranched, straight or slightly winding, blind ending, filled, or originally almost void but preserved collapsed tube, which may be slightly swollen and stacked in the middle part. It is lined with small, elongate mud pellets.

Remarks. The original diagnosis of the ichnogenus *Tubulichnium* by Książkiewicz (1977, p. 142) stating: "Void subhorizontal and horizontal tubes with lined walls" is too broad. It does not refer to pellets, which are considered the diagnostic feature. The presence of pellets is mentioned in the diagnosis of the ichnospecies *Tubulichnium incertum* Książkiewicz, 1977. Therefore, the ichnogenus diagnosis is emended.

Tubulichnium rectum (Fischer-Ooster, 1858) comb. nov.

Figures 2.1-6, 3.1-7, 4.1-11, 5.1-8

- *v. 1858 *Halymenites rectus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 2. [also in Uchman, 1998, fig. 25B.]
- non v. 1858 *Halymenites flexuosus* F.O. – Fischer-Ooster, 55, pl. 13, fig. 1. [(Transferred to Halymenidium Schimper by Schimper in Schimper and Schenk, 1879, p. 37, p. 37)]
- partim v. 1858 *Halymenites minor* F.O. – Fischer-Ooster, 56, 65, pl. 13, fig. 1. [Redrawn in Uchman, 1998, fig. 25C] (non 65, pl. 16, fig. 2). [(Transferred to Halymenidium Schimper by Schimper in Schimper and Schenk, 1879, p. 37)]
- v. 1858 *Halymenites incrassatus* F.O. – Fischer-Ooster, p. 65, pl. 16, fig. 3. [also in Uchman, 1998, fig. 25A]
- non v. 1858 *Halymenites dubius* F.O. – Fischer-Ooster, 66, pl. 12, fig. 4.
- ? 1863 *Halymenites rectus*, *H. flexuosus* und *H. minor* F. O. – Ettingshausen, p. 461. [Not illustrated]
- 1909 *Granularia* cf. *arcuata* Schimp. – Reis, pl. 17, figs. 2–4. [Specimen in fig. 2 also in Häntzschel, 1975, p. W65, fig. 40.3a, under the same name]
- 1935 agglutinierte Wohnröhre – Abel, figs. 395, 396.
- 1936 Großer Fukoid – Krejci-Graf, 312, fig. 5.
- non 1942 Agglutinierende Polychäten (Terebelinen) – Papp, figs. 1-3.

- 1959 Mit ellipsodischen Kotpillen austapezierter Gang – Seilacher, tab. 3.52.
- v. 1977 *Tubulichnium incertum* n. ichnosp. – Książkiewicz, p. 143, pl. 11, figs. 14, 15. [For fig. 15 see also Uchman, 2008c, text-fig. 29]
- 1978 ?*Granularia* – Kern, 255, fig. 10A.
- partim 1981 *Granularia* sp. – Crimes et al., p. 969, pl. 2, fig. 5 (non pl. 4, fig. 4).
- v. 1991a *Tubulichnium incertum* – Uchman, p. 289, fig. 2A.
- v. 1991c *Tubulichnium incertum* Książk. – Uchman, 209. [Not illustrated]
- v. 1992 *Tubulichnium incertum* – Cieszkowski et al., p. 94. [Not illustrated]
- v. 1992a *Tubulichnium incertum* – Uchman, p. 55 [Not illustrated].
- v. 1993 *Tubulichnium incertum* Książkiewicz – Tunis and Uchman, p. 87. [Not illustrated]
- v. 1996 *Tubulichnium incertum* Książkiewicz – Tunis and Uchman, p. 177, fig. 3J.
- v. 1998 *Ophiomorpha rectus* (Fischer-Ooster, 1858) – Uchman, 126, figs. 25, 26.
- v. 1998 "*Tubulichnium incertum*" Książkiewicz – Wetzel and Uchman, p. 537, fig. 5.
- v. 1999 *Ophiomorpha recta* (Fischer-Ooster, 1858) – Uchman, 104, pl. 11, figs. 1, 2.
- 2004 *Ophiomorpha rectus* (Fischer-Ooster, 1858) – Leszczyński, p. 45, fig. 20.
- v. 2007a *Ophiomorpha recta* (Fischer-Ooster, 1858) – Uchman, 224, pl. 2, fig. 1.
- v. 2007b *Ophiomorpha recta* (Fischer-Ooster, 1858) – Uchman, 989, figs. 4B-C, 5B.
- v. 2007 *Ophiomorpha recta* – Wetzel et al., p. 573, fig. 7.
- 2007 *Muensteria* – Seilacher, pl. 72.
- v. 2008a *Ophiomorpha recta* – Uchman, 121, fig. B6.2.C.
- v. 2009 *Ophiomorpha recta* (Fischer-Ooster, 1858) – Uchman, 50, fig. 46.
- 2010 *Ophiomorpha rectus* – Giannetti, 110. [Not illustrated]
- ? 2011 *Ophiomorpha recta* – Cummings and Hodgson, 173, pl. 1A.
- non? 2012 *Ophiomorpha rectus* Fischer-Ooster, 1858 – Rajkumar et al., p. 71, fig. 2K.
- v. ? 2014 "*Ophiomorpha*" *recta* (Fischer-Ooster, 1858) – Riahi et al., p. 161, fig. 7D, E.
- non 2014 *Ophiomorpha* cf. *recta* – Knaust et al., p. 2237, fig. 12D.
- v. 2017b "*Ophiomorpha*" *recta* (Fischer-Ooster) – Uchman and Rattazzi, fig. 8C.

Diagnosis. Oblique to horizontal, unbranched, straight or slightly winding, blind ending, commonly

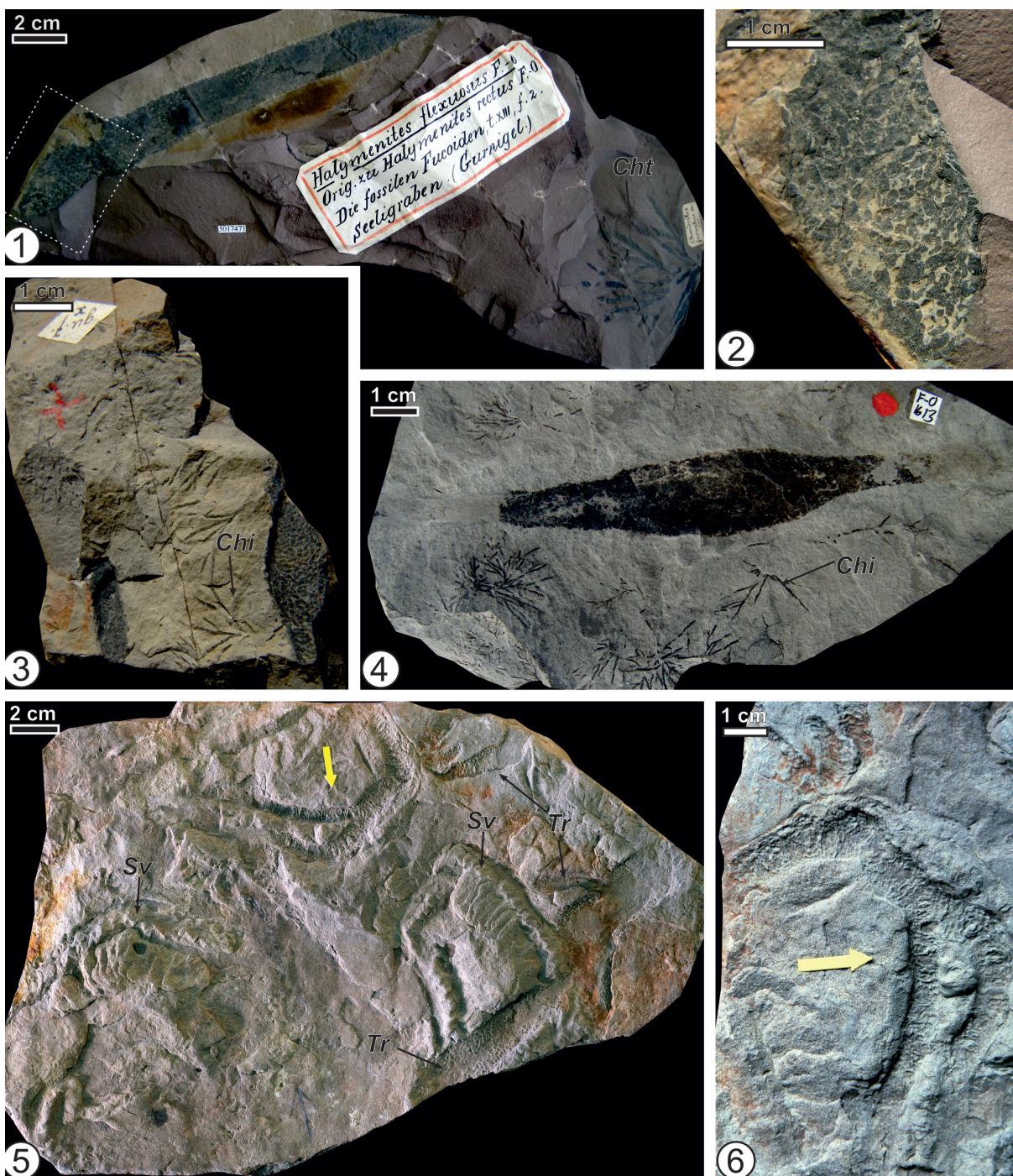


FIGURE 2. Holotype of *Tubulichnium rectum* (Fischer-Ooster, 1858) and some other key specimens described by Fischer-Ooster (1858) and Książkiewicz (1977), which are housed in the Naturhistorisches Museum der Burgergemeinde Bern (NMBE) in Switzerland and in the Nature Education Centre of the Jagiellonian University – Museum of Geology, Kraków, Poland, respectively: **1**, holotype, originally *Halymenites rectus* Fischer-Ooster and *Chondrites targionii* (Cht), Gurnigel Flysch (Maastrichtian), Seeligraben near Gurnigelbad (Switzerland), specimen NMBE 5017471. Detail illustrated in **2** marked by the quadrangle; **2**, detail of **1**; **3**, original of *Halymenites minor* Fischer-Ooster, 1858 and *Chondrites intricatus* (Chi) from Gurnigel Flysch (Maastrichtian), Seeligraben near Gurnigelbad (Switzerland), specimen NMBE 5017474; **4**, original of *Halymenites incrassatus* Fischer-Ooster, 1858, Fährnenspitz, Upper Cretaceous, E Switzerland, specimen NMBE 5017470; **5**, holotype of *Tubulichnium incertum* Książkiewicz, 1977 (yellow arrow), other specimen of the same ichnotaxon (Tr) and *Scolicia vertebralis* (Sv); Ropianka Formation (Inoceranian Beds), Upper Cretaceous-Paleocene, Bachów, Skole Nappe, specimen UJTF 938; **6**, detail of **5** showing the holotype.

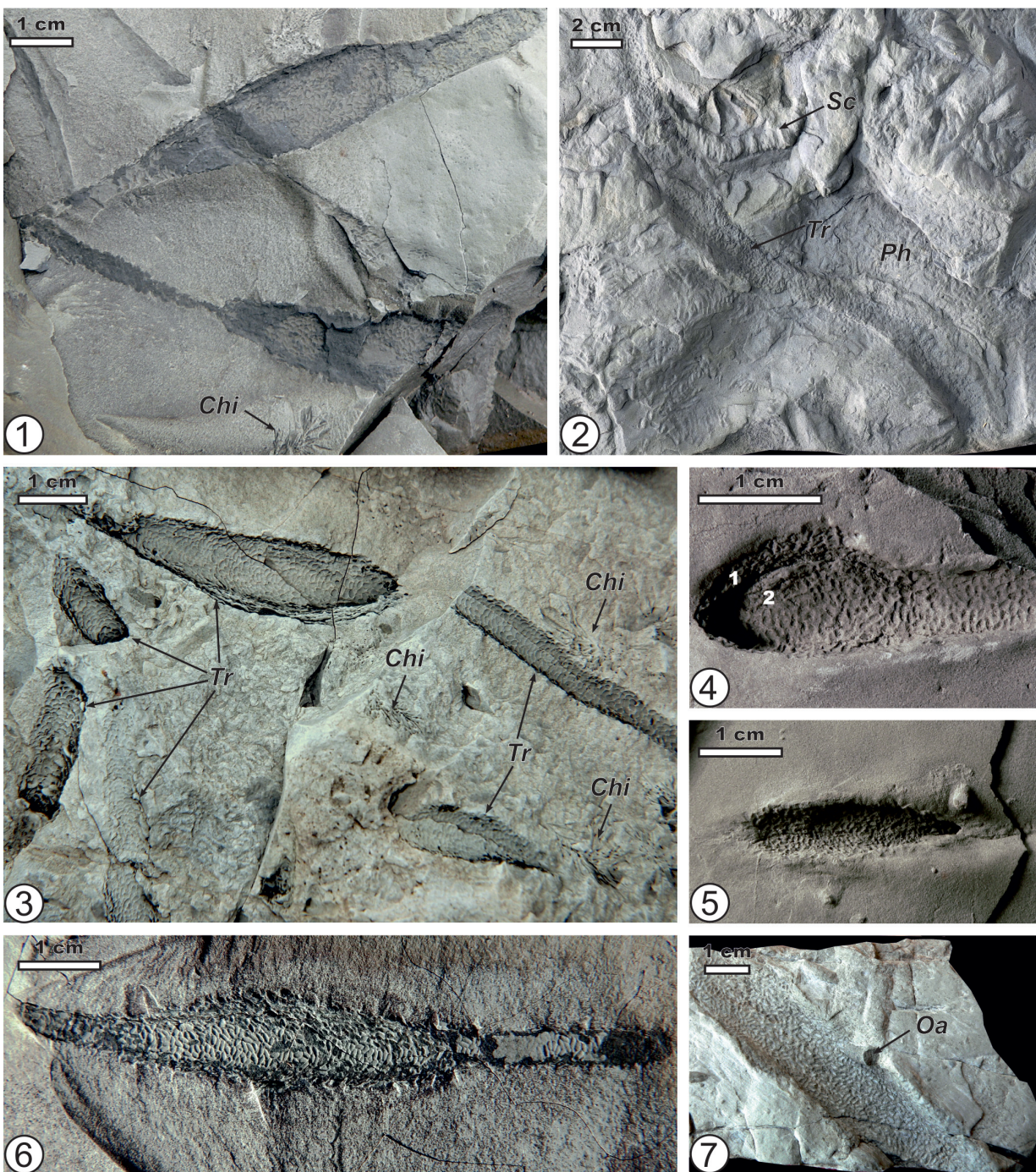


FIGURE 3. *Tubulichnium rectum* (Fischer-Ooster, 1858) on upper bedding surfaces from different formations: **1**, on the upper surface of turbiditic marl with *Chondrites intricatus* (*Chi*), Pagliaro Formation (Paleocene), Cabella Ligure, Northern Apennines, Italy, field photograph; **2**, curved example of *T. rectum* (*Tr*), *Scolicia* isp. (*Sc*) and *Phycosiphon incertum* (*Ph*), Ropianka Formation (Upper Cretaceous), Wara, Skole Nappe, Carpathians, Poland, UJTF 1426, Książkiewicz collection; **3**, several specimens of *T. rectum* (*Tr*), some cross cut by *Chondrites intricatus* (*Chi*), Pagliaro Formation (Paleocene), Cabella Ligure, Northern Apennines, Italy, field photograph; **4**, specimen with two (1, 2) superimposed pellet pavements. Inoceramian Beds (Upper Cretaceous-Paleocene), Słopnice, INGUJ144P190a; **5**, specimens with elevated edges and collapsed roof, Inoceramian Beds (Upper Cretaceous-Paleocene), Słopnice, INGUJ144P140; **6**, example of spindle-shaped burrow enlargement, Pagliaro Formation (Paleocene), Cabella Ligure, Northern Apennines, Italy, field photograph; **7**, *T. rectum* cut by *Ophiomorpha annulata* (*Oa*), Inoceramian Beds (Upper Cretaceous-Paleocene), Słopnice, INGUJ143P66.

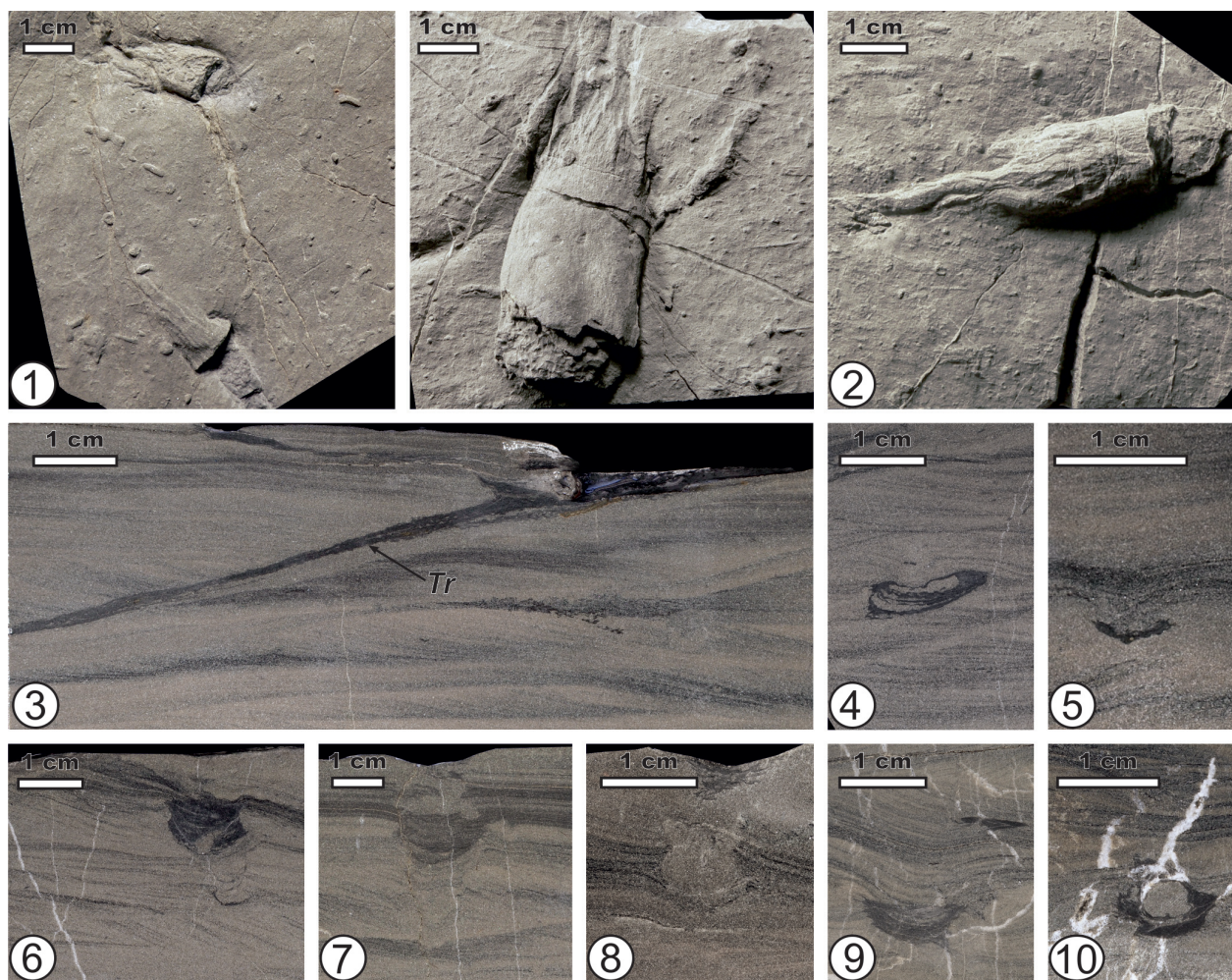


FIGURE 4. *Tubulichnium rectum* (Fischer-Ooster, 1858) on the lower bedding surfaces (1-3) of and in longitudinal (4) and transverse (5-10) cross-sections of turbiditic sandstones from the Inoceranian Beds (Upper-Cretaceous-Paleocene) at Słopnice: **1**, note external and internal parts INGUJ144P176; **2**, note sandy mantle covering the pelleted part, INGUJ144P193a, **3**, note wrinkles on the mantle, INGUJ144P187a; **4**, longitudinal cross section (*Tr*), INGUJ144P193; **5-10**, transverse sections, E – INGUJ144P182d, F – INGUJ144P180, G – INGUJ144P192b, H – INGUJ144P170a, I – INGUJ144P190, J – INGUJ144P192c, K – INGUJ144P192.

originally almost void but preserved collapsed tube, which may be slightly swollen in the middle part. It is lined with small, elongated muddy pellets.

Holotype. Specimen NMBE 5017471, Naturhistorisches Museum der Burgergemeinde Bern (Switzerland), labelled as “*Halymenites flexuosus* F.O. Die fossilen Fucoiden, t. XIII, f. 2, Orig. zu *Halymenites flexuosus* F.O. Seeligraben (Gurnigel.),” illustrated by Fischer-Ooster (1858, p. 55, plate 13, figure 2). Figure 2.1-2 in this paper.

Other specimens. Naturhistorisches Museum der Burgergemeinde Bern (Switzerland): 1) specimen NMBE 5017470 – original of *Halymenites incrassatus* Fischer-Ooster, 1858, Fährnerspitz, E Switzerland (Figure 2.4); 2) specimen NMBE 5017474 – original of *Halymenites minor* Fischer-Ooster,

1858, Seeligraben, Gurnigelbad, Switzerland (Figure 2.3).

Institute of Geological Sciences, Jagiellonian University, Kraków, Poland: 1) 28 specimens from the Słopnice section, the Inoceranian Beds, Magura Nappe, Carpathians, Poland (INGUJ143P42, 66, 74, INGUJ144P170-180, 182-195); 2) one slab from the old quarry at Krzeczowa, Holownia Marl, Skole Nappe, Carpathians, Poland (INGUJ193P140); 3) one specimen from the Szczawnica Formation at Łąkcica (INGUJ144P99), three specimens from the same formation at Jamne (INGUJ143P84, 86, 87) and one from Jaszcze (INGUJ143P85); 4) one specimen from the Piwniczna Sandstone Member of the Magura Formation (Lower Eocene) at Tylmanowa-

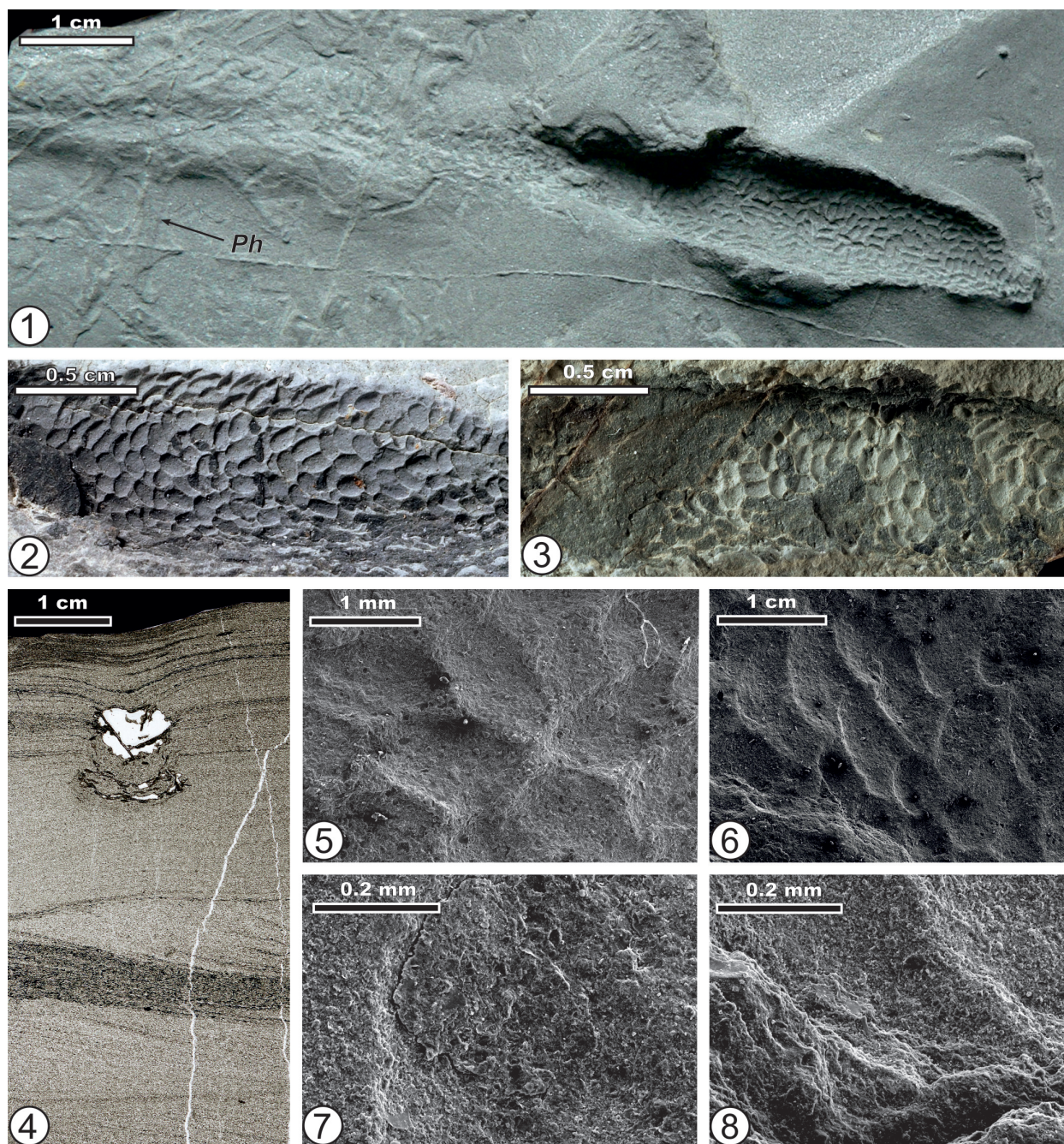


FIGURE 5. Macroscopic and microscopic and SEM observations of *Tubulichnium rectum* (Fischer-Ooster, 1858) occurring in turbiditic sandstones of the Inoceranian Beds (Upper Cretaceous–Paleocene), Słopnice, Poland (1, 4–8) and turbiditic marls of the Pagliaro Formation (Paleocene), Italy (2, 3): **1**, specimen with elevated edges and bent down roof as seen on upper bedding surface (INGUJ144P195); **2, 3**, depressions of pellets in the burrow margin after pellets have been partly or completely removed (INGUJ196P36 and 38); **4**, photomicrograph of transverse cross-section; note deformed laminae above the collapsed burrow; **5, 6**, burrow margin showing depressions of pellets that have been removed by weathering; **7**, part of split pellets in place consisting of clay minerals and siliciclastic silt grains; **8**, outer part of a split pellet showing platy minerals oriented $\pm$ parallel to surface.

Baszta (INGUJ144P140); 5) 10 specimens from the Pagliaro Formation (Paleocene) at Cabella Ligure, Northern Apennines, Italy (INGUJ149P11b, 13; INGUJ149P35-41) and Celio (INGUJ149P42); 6) three specimens from the Gurnigel Flysch, Paleocene, from Seeligraben (INGUJ154P100, 102) and from the Zollhaus Quarry (INGUJ154P101).

The Nature Education Centre of the Jagielloonian University (CEP) – Museum of Geology, six slabs in the Książkiewicz collection: 1) Skole Nappe, Inoceramian (Ropianka Beds) at Bachów (UJ TF 938 – the holotype of *Tubulichnium incertum* Książkiewicz, 1977; Figure 2.5-6) and Wara (UJ TF 1426 – Figure 3.2; UJ TF 1434); 2) Magura Nappe, Inoceramian (Ropianka Beds) at Wola Brzezińska (UJ TF 1026) and Berest (UJ TF 856, 1844).

Crocefischi Museo, Crocefieschi N of Genova, Italy: three specimens 5008, 5214, 6444 from the Pagliaro Formation (Paleocene) at Salata.

Naturhistorisches Museum in Vienna, Austria, two specimens (without numbers): 1) one specimen from the Greifenstein Sandstone, Greifenstein quarry, Wienerwald, Rhenodanubian Flysch, Austria (collected in 1908); 2) one specimen from the Inoceramian Beds, Skole (Skyba) Nappe, Dora (Yaremche), Ukraine.

The Bavarian Natural History Collections (Staatliche Naturwissenschaftliche Sammlungen Bayerns, SNSB): one specimen PIW1993X221, Flysch del Grivó (Paleocene-Eocene) at Clapp, Friuli, Italy.

Description. Inclined to horizontal, strongly flattened, blind ending tubes, observed usually in the upper part of sandy beds. The tubes are 2–22 mm wide, in maximum 215 mm long. Usually, only a short segment of the trace is observed because the remaining part is plunging into the bed. The width of the tube changes along its course exhibiting usually one spindle-shaped swelling in the middle (Figures 2.4, 3.1, 3.6). Two swellings are very rare. The swellings are up to 6.5–15 mm, rarely up to 29 mm, wide. The holotype is 172 mm long and 14–20.5 mm wide, but is limited by the edges of the slab.

Most of the tubes are straight. Curved tubes are rare (Figures 2.5-6, 3.2). The interior tube margin is covered with small, elongate mud pellets, which are 0.7–2 mm long and 0.7–1 mm wide. When the pellets are removed or weathered, the burrow margin shows scalloped depressions, which are elliptical, half-elliptical, or crescent in outline, 0.5–1.2 mm long, and up to 0.8 mm wide

(Figure 5.1-3, 5.5-8). If the pellets are densely packed, the depressions tend to form an irregular, elongated meshwork, with straight or slightly curved bordering crests. The pellets are composed of clay and fine silt grains and most of them are less than 10 µm in size. Close to the surface of the pellets, mineral flakes can be parallel or subparallel to the pellet surface.

In transverse cross-section, the burrow geometry shows some variability (Figures 4.5-11, 5.4). It can be irregularly elliptical, sub-angular, trapezoid, wedge-shaped, or bent-down bar-like in outline. Width is usually larger than height, but inverse cases may occur. Occasionally if the height of the burrow exceeds its width, the lower part is narrower than the middle and upper part. The lower part of the burrow fill is usually muddy and the upper enriched in sand. In many transverse cross-sections, spreite-like lamination is present, usually bending down in the central part. The laminae can be underlined by a muddy or sandy film. Terminations of the laminae are uneven, occasionally splitting. Therefore, in cross-section the tube sides appear in many cases uneven. Rarely, the mantle is sandy (Figure 4.9). In some cases, a sandy core wrapped partly, or rarely completely, by a muddy mantle is seen (Figure 4.11).

The burrows are horizontal or nearly horizontal for most of their course, or they dip into the beds at a more or less constant angle ranging from 15° to 27° (Figure 4.4). Some burrows pierce a bed and occur on the lower side as inclined tubes with a sandy mantle, which can be covered by longitudinal wrinkles (Figure 4.1-3). Laminae within the bed are slightly bent down at the sides of the burrow for a distance of 1–3 mm. The laminae above the burrow are commonly bent down probably due to collapse of the causative tube after abandonment (Figures 4.6, 4.10, 5.1). Edges of some burrows are elevated (Figure 5.1).

Remarks. *Tubulichnium rectum* occurs in very fine and fine-grained calcareous sandstone, sandy marl, or marl beds of variable thickness. They are of turbiditic origin and interbedded with pelagic/hemipelagic, calcareous, or non-calcareous mudstones (Figure 6).

Tubulichnium rectum co-occurs in the same bed with *Scolicia vertebralis* Książkiewicz and *Phycosiphon incertum* Fischer-Ooster (see Książkiewicz, 1977, p. 143), *Chondrites intricatus* (Brongniart), *C. targionii* (Brongniart), *C. affinis* (Sternberg), *Lophoctenium ramosum* (Toula), *Nereites irregularis* (Schafhäutl), *Zoophycos* isp., *Ophiomorpha annulata* (Książkiewicz), *Planolites*

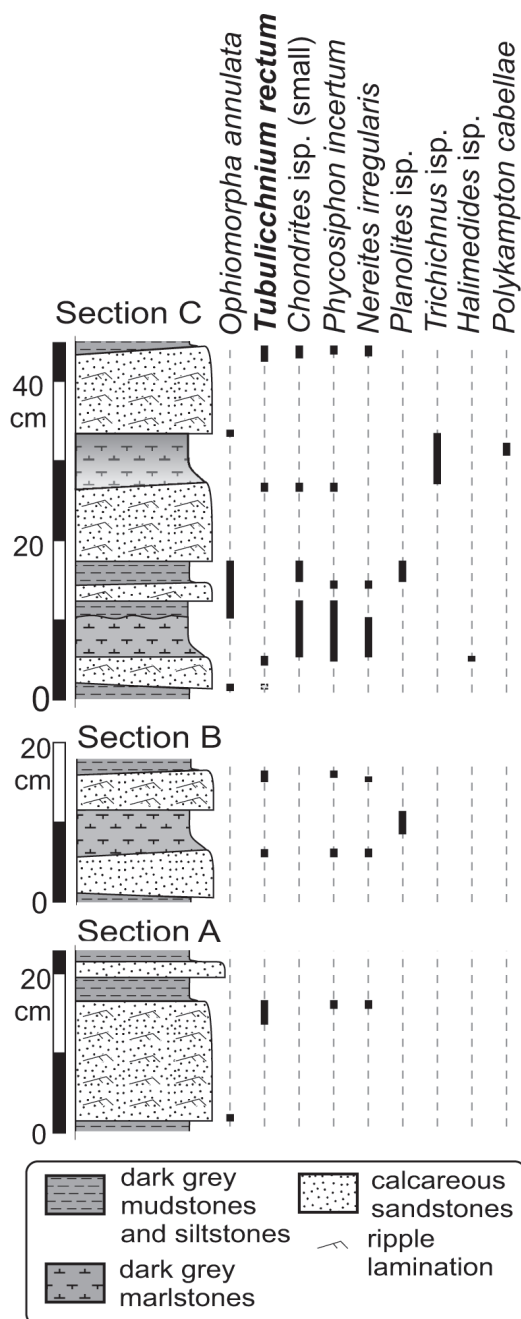


FIGURE 6. Short sections showing position of *Tubulichnium rectum* and associated trace fossils in strata of the Ropianka Formation (Inoceranian Beds) at Słopnice, Magura Nappe, Carpathians, Poland. GPS coordinates: section A: 49°42.982'N, 020°20.448'E; section B: 49°42.974'N, 20°20.453'E, section C: 49°42.610'N, 20°20.687'E.

isp., *Taenidium* isp., *Trichichnus* isp., *Polykampton cabellae* Uchman and Rattazzi, *Phycosiphon geniculatum* (von Sternberg), "*Rhizocorallium*" *hamatum* (Fischer-Ooster), *Acanthorhapha* isp. and *Megagraption* isp. Some specimens are cross cut

by *O. annulata*, *C. intricatus*, *Ph. incertum*, and some unidentified tubular burrows. In some beds, *T. rectum* penetrates *S. vertebralis*, *N. irregularis*, *C. intricatus*, and *C. targionii*.

DISCUSSION

Ichnotaxonomic Problems

Originally, the presented trace fossil was described as an alga under the genus *Halymenites* von Sternberg, 1833. As the first species, Fischer-Ooster (1858) established *Halymenites rectus* Fischer-Ooster, 1858, which should be considered as the type ichnospecies by page priority. Furthermore, Fischer-Ooster (1858) distinguished *Halymenites flexuosus*, *H. minor*, *H. incrassatus*, and *H. dubius*. The latter was described in the same publication as *Chondrites dubius* (p. 54), but transferred to *Halymenites* on page 65. This trace fossil shows branches and is dissimilar to the *Halymenites* ichnospecies. The original diagnosis of *Halymenites rectus* by Fischer-Ooster (1858, p. 55) states: "*Halymenites fronde plana recta simplici latitudinem fere pollicarem attingente, sporangis ovatis lineam metientibus replete.*" It can be translated as: "*Halymenites* with foliage [being] plane, straight, simple, [so] dense that nearly touching at the long side, filled up with ovate sporangia having a line in the length." Very likely the whole tube was interpreted by Fischer-Ooster as foliage (at another place he describes it as a stem), whereas the pellets were interpreted to represent sporangia.

Schimper in Schimper and Schenk (1879, p. 37) stated that *Halymenites* Sternberg, 1833 is a very problematic genus. Therefore, he erected a new genus *Halymenidium* in which he included, according to the order in the text, *Halymenites flexuosus* Fischer-Ooster, 1858, *Halymenites minor* Fischer-Ooster, 1858, *Halymenites lumbricoides* Heer, 1865 and *Phymatoderma diervallii* Watelet, 1866. Indeed, the original species of *Halymenites* published by von Sternberg, 1833 are Jurassic plants from Solnhofen in Germany (Häntzschel, 1962) and cannot be used for ichnotaxonomic purposes (Uchman, 1998). *Halymenidium* Schimper, however, is also problematic, because the aforementioned taxa included in *Halymenidium* represent different ichnogenera, including the first taxon accounted by Schimper, i.e., *Halymenites flexuosus* Fischer-Ooster, 1858. The original material of *H. flexuosus* is not present among the other ichnospecies of *Halymenites* in the Museum in Bern (U. Menkveld-Gfeller, 2016, personal communication). Judging from the drawing by Fischer-Ooster, 1858

(plate 13, figure 1), this trace fossil is composed of a stem and side branches containing small pellets arranged perpendicular to the stem and branches. It resembles better *Phymatoderma* Brongniart, 1849 than the discussed trace fossil (for *Phymatoderma* see Fu, 1991). *Phymatoderma dinevalli* Watelet, 1866, the other species included in *Halymenidium* by Schimper, is in fact a synonym of *Ophiomorpha nodosa* Lundgren, 1891 (Häntzschel, 1952). *Halymenites lumbricoides* Heer, 1865 was included in *Alcyonidiopsis longobardiae* Massalongo, 1856 by Chamberlain (1977). Therefore, *Halymenidium* Schimper is not recommended for further use (Uchman, 1998).

Häntzschel (1952) noticed that *Halymenidium rectum* (Fischer-Ooster) and *H. incrassatum* (Fischer-Ooster) differ from *Ophiomorpha* Lundgren, 1891 by the straight course and smaller diameter and thus, they cannot be synonymized. However, Häntzschel (1962, p. 206) included *Halymenidium* Schimper in *Ophiomorpha* with a question mark. Also Vialov (1966) included reservedly *Halymenites rectus* Fischer-Ooster, 1858, *H. incrassatus* Fischer-Ooster, 1858 and *H. flexuosus* Fischer-Ooster, 1858 in *Ophiomorpha*. This suggestion was adopted by Uchman (1998), who emphasized the pelletal lining as the principle morphological feature and proposed a new combination; *Ophiomorpha rectus* (Fischer-Ooster, 1858) corrected by Uchman (1999, 2007b) as *Ophiomorpha recta* (Fischer-Ooster, 1858). After studying numerous specimens of this trace fossil, the assignment to *Ophiomorpha* should be considered as unfortunate, because: 1) *Ophiomorpha*, typified by *O. nodosa* Lundgren, 1891 (for this ichnogenus and ichnospecies see Frey et al., 1978, 1984) is a branched burrow, whereas *O. recta* is unbranched, and 2) *O. nodosa* shows a constructed wall composed of relatively large pellets, circular in outline and built of muddy sandstone, whereas *O. recta* does not have a constructed wall, only a local mantle that may be present, and its pellets are relatively small, elliptical in outline, and consist of mud.

The discussed trace fossil was also described by Reis (1909) as *Granularia* Pomel, 1849 (the same Häntzschel, 1975), but *Granularia* is not recommended for further use (Uchman, 1995). Seilacher (2007) illustrated the trace fossil as *Muensteria* Sternberg, 1833, but also this ichnogenus is not recommended for further use (Mikuláš and Uchman, 1996).

For the discussed trace fossil, Książkiewicz (1977) erected a new ichnogenus and ichnospecies *Tubulichnium incertum* Książkiewicz, 1977.

Due to taxonomic situation outline above, *Tubulichnium* is considered as the valid, proper ichnogenus name, but the ichnospecies name should be taken from *Halymenites rectus* Fischer-Ooster, 1858. Therefore, the new combination *Tubulichnium rectum* (Fischer-Ooster, 1858) is proposed. The holotype of *Tubulichnium incertum* Książkiewicz, 1977 is a rather atypical example of *T. rectum*, because it is represented by two curved overlapping burrows (Figure 2.5-6). Nevertheless, on the same slab, a straight, but less complete, burrow is present. Moreover, other specimens in the Książkiewicz collections, labelled as *Tubulichnium incertum*, are typical *T. rectum*. Therefore, there are no doubts that M. Książkiewicz considered all of them as belonging to the same ichnotaxon.

Cummings and Hodgson (2011, figure 1A) recorded “*Ophiomorpha recta*” in fringe, fan fringe–basin floor, basin floor transition and lobe-off axis facies in Palaeogene flysch of northern Spain, but the only illustration of this trace fossil is a hypichnial full relief, which makes inclusion into *Tubulichnium rectum* problematic (see the synonymy list).

Tubotomaculum García-Ramos et al., 2014, typified by *T. mediterranensis* García-Ramos et al., 2014, from the Upper Cretaceous–Miocene deep-sea deposits of the Mediterranean region displays the same basic morphological pattern: unbranched form, spindle widening, elongate pellets present in the external parts, and a teichichnoidal shift of the causative tube. This shift is more extensive than in *Tubulichnium rectum* and *Tubotomaculum* is typically mineralized. Nevertheless, the differences should be considered as insignificant at the ichnogenus level and, therefore, *Tubotomaculum* García-Ramos et al., 2014 should be considered as a junior synonym of *Tubulichnium* Książkiewicz, 1977, with conservation of *T. mediterranensis* as a separate ichnospecies.

Ophiomorpha puerilis Gibert et al., 2006 is a simple, cylindrical, mostly vertical burrow, 1.6–3.3 mm in diameter, associated with *Ophiomorpha nodosa* Lundgren, 1891. It displays a wall built of subcylindrical pellets. Because of the pellets and unbranched morphology, this trace fossil resembles *Tubulichnium*, but it displays a constructed wall, similar to *Ophiomorpha nodosa*. Moreover, its vertical orientation and close association with *Ophiomorpha* strongly suggest their taxonomic separation.

Trace Maker and Ethological Interpretation

Originally, *Halymenites rectus* (now *Tubulichnium rectum*) was regarded as a fucoid alga (Fischer-Ooster, 1858). Reis (1909) reinterpreted it as worm burrow. Abel (1935) interpreted *Tubulichnium rectum* (his “agglutinierte Wohnröhre”) as a dwelling trace of a tubiculous worm. Książkiewicz (1977, p. 19, 144) considered it as a post-depositional “feeding burrow which could serve as temporary or permanent shelter” produced by crustaceans. Also Crimes et al. (1981) regarded that such burrows (their *Granularia*) are produced by crustaceans. Uchman (1991, 1992b) considered *Tubulichnium rectum* (*Halymenites* in the cited publications) as an opportunistic trace fossil. Wetzel and Uchman (1998) noticed its deep-tier position and connection to the sea floor.

The unbranched pattern, the swellings and the constriction of the tunnel at both ends suggests a soft-bodied “worm”-like organism, which was able to change the width of its body. Furthermore, the pellets pressed into the lining, deformed laminae around the lower part of the burrow and within the external part of the filling suggest that the trace maker was able to compress the sediment. The spreite-like basal part documents a long occupation of the burrow, with sediment that was occasionally introduced into the burrow being compressed at the base of the tube.

The ellipsoidal muddy pellets, usually less than a millimetre long, are very similar to those found in *Rhizocorallium*, *Zoophycos*, *Phymatoderma*, and *Ophiomorpha puerilis* (Izumi, 2013; Knaust, 2013; Uchman and Rattazzi, 2017a; Netto et al., 2017). If isolated, they are usually described as *Coprulus oblongus* Mayer, 1952 and referred to the ichnofamily Coprulidae (see Knaust, 2008). Knaust (2013) noticed in his revision of *Rhizocorallium* that such pellets suggest a common producer, possibly a polychaete. Indeed, most ellipsoidal pellets are produced by polychaetes (e.g., Kraeuter and Haven, 1970; Kulkarni and Panchang, 2015). However, echinurans can produce similar pellets (Popkov, 1992; Biseswar, 2005), as well as enteropneusts (Thomas, 1972) and sipunculids (Jumars et al., 1990). In addition, some sipunculids may construct a cache while shifting the causative tube in its deepest part vertically (Jumars et al., 1990, figure 1). Therefore, a closer determination of the “worm” producers is not possible.

Tubulichnium rectum occupies a relatively deep tier. In the Ropianka Formation, it crosses up to 6.5 cm thick sandstone beds and in the Pagliaro Formation it penetrates 3–5 cm deep from the top

of thick marl beds. In the latter case, *Chondrites* and *Trichichnus* are produced deeper in the sediment, similar to *Ophiomorpha annulata* in the Ropianka Formation (Figure 6). In cases that *Tubulichnium rectum* cross-cuts *Chondrites*, it is interpreted to have been produced in a late phase of colonization of a freshly accumulated turbidite, according to the model of sequential colonization by Wetzel and Uchman (2001). After deposition, content of oxygen in pore water and food in the turbidite decreases within a few years and thus, horizontal sediment reworking becomes an inappropriate nutritional strategy.

The pelleted filling of *Tubulichnium rectum* resulted from an active transfer of organic-rich material into a relatively deep tier. Compared to the host sediment containing $1.1 \pm 0.1\%$ organic carbon and the overlying dark mud ($0.7 \pm 0.1\%$ C_{org}), the pelleted burrow fill is enriched in organic matter ($1.5 \pm 0.1\%$ C_{org}). Furthermore, the carbonate content of the pelleted fill ($20 \pm 1\%$) is higher than that of the (hemi)pelagic dark mud ($12 \pm 2\%$). The carbonate content of the turbiditic sandstones ($26 \pm 4\%$) is of detrital origin and hence, not considered here. The enrichment of organic matter and carbonate within the pelleted fill implies that organic material and carbonate shells accumulating on the sea floor during bloom times were transferred into a burrow before organic and carbonate content decreased after bloom times due to oxidation of organic matter (e.g., Aller, 1994). The outlined scenario is supported by observations in the modern South China Sea; during blooms, not only large amounts of organic matter, but also carbonate shells, accumulate on the sea floor and both become degraded during non-bloom times (e.g., Wetzel, 2008, figure 9). Burrows of endobenthic organisms that ingest material deposited during bloom times contain carbonate shells even in settings below Calcite Compensation Depth (CCD), because carbonate dissolution is hindered within the burrows (Wetzel and Unverricht, 2013).

After feeding on nutritional mud on the surface, especially after the arrival of fresh organic matter, the trace maker packed organic-rich muddy pellets into its burrow within the oxygen-deficient host sediment at a depth beyond the range that shallowly burrowing sediment-feeders usually penetrate. During times of starvation, the burrow producer could feed on such sequestered material. Because of oxygen deficiency, organic matter was not subjected to rapid decomposition and was available as a food source for some time even if it was microbially fermented (e.g., Arndt et al., 2013).

In fact, the burrow represented a sort of a nutritional cache, similar to the cache model of *Zoophycos* (Bromley, 1991). The food from the pellets can also be exploited indirectly, probably by solutions and ectoenzymes. There is no evidence of direct and repeated reworking, but the burrow was inhabitation by the producer for a long time. Microbial activity within the burrow fill is likely (e.g., Kristensen, 2000), but not easy to prove, as no microbial structures were observed.

Such a feeding strategy as proposed for *Tubulichnium rectum* is a good response to seasonal oligotrophy on the deep-sea floor, where nutritional quality of freshly-deposited organic matter deteriorates quickly by oxygenation and microbial decomposition. Modern examples from the South China Sea point to an intensive use of seasonally supplied organic-rich sediments sequestered in burrows as a food source (Wetzel, 2008). Such a strategy fits well to the new ethological category, sequestrichnia, as proposed by Uchman and Wetzel (2016). The success of the outlined nutritional strategy is illustrated by the relatively high density of *T. rectum* in some beds. For the top bed in section C (Figure 6), it reaches about 50 burrows/m².

Environmental Significance and Stratigraphic Range

Tubulichnium rectum specimens have been reported to occur in Triassic to Paleogene, mainly turbiditic, occasionally calcareous sediments (Table 1). In clastic turbiditic deposits, *T. rectum* occurs mostly in thin- and medium-bedded, very fine or fine-grained calcareous strata, which commonly show cross bedding. Rarely, *T. rectum* was encountered at the top of up to 150 cm thick sandstone beds. In the Pagliaro Formation, *T. rectum* occurs at the top of up to 40 cm thick marls, which form the upper part of turbiditic sandstone-marl couplets. The marls are covered by dark grey, non-calcareous (hemi)pelagic mudstones. Similarly, in the Ropianka Formation, the overlying non-turbiditic mudstones can be free of carbonate. Consequently, accumulation of these deposits below the local CCD is highly likely. The producer of *T. rectum* appears to prefer distal depositional lobe, interlobe, fan fringe, and basin plain turbiditic facies as established in classic sand-rich deep-sea fan models (e.g., Mutti, 1992; Stow et al., 1996). The trace producer tolerated different substrates varying from fine sand to marly mud.

The associated trace fossils are typical of the *Nereites* ichnofacies, in particular the *Paleodictyon*

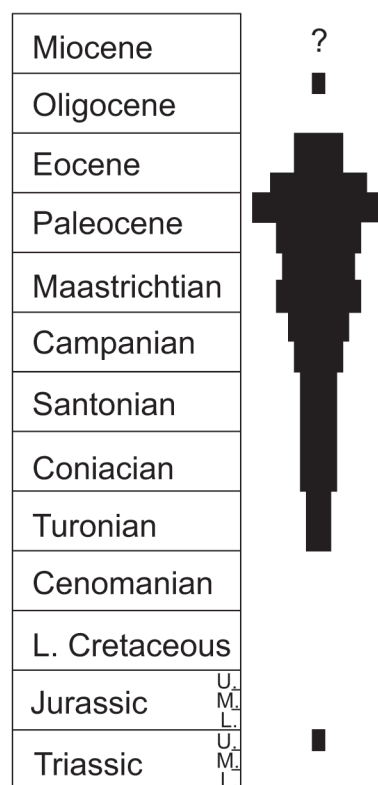


FIGURE 7. Stratigraphic range of *Tubulichnium rectum* (Fischer-Ooster, 1858) and number of formations per stage in which it occurs.

or *Nereites* subichnofacies, which may contain graphoglyptids or dominating *Nereites* and *Phycosiphon*, respectively (for details see Uchman and Wetzel, 2012). The occurrence of *T. rectum* in the *Zoophycos* ichnofacies appears to be possible, but any evidence is lacking so far.

An isolated Triassic occurrence is noted by Wetzel et al. (2007), which is related to an unusual high-diversity trace-fossil association. The trace fossil producers there were minimally affected by the severe ecologic conditions following the Permian-Triassic mass extinction (Wetzel et al., 2007). *Tubulichnium rectum* ranges continuously from the Turonian to Eocene (e.g., Książkiewicz, 1977; see also Figure 7 and Table 1). *Tubulichnium rectum* is more frequently recorded in Campanian to the middle Eocene strata, with an acme in the upper Paleocene. The isolated occurrence in the upper Oligocene (Riahi et al., 2012) is questionable; the burrows therein are mineralized and fit better to *T. mediterraneensis* (García-Ramos et al., 2014). The Miocene occurrence (Rajkumar et al., 2012) is doubtful because it is poorly documented and occurs in shallow-marine sediments with shallow-marine trace fossils.

The increase in abundance of *T. rectum* during the Cretaceous could be related to a response of burrowing organisms to both increasing organic matter delivery to the deep-sea following the evolution of calcareous algae (e.g., Erba, 2006) and increasing competition for benthic food in the deep sea by shallow as well as deep-burrowing organisms (e.g., Uchman, 2004; Buatois et al., 2016). The declining of abundance during the Oligocene can be related to climatic changes (cooling) and follows general declining trace-fossil diversity in the deep sea (Uchman, 2004).

CONCLUSIONS

Tubulichnium rectum (Fischer-Ooster, 1858) is the proper name for simple, pellet-lined burrows produced by “worm”-like organisms in deep-sea turbiditic sandstones and marls, mostly from Late Cretaceous to Eocene times. The trace makers ingested organic-rich mud deposited seasonally or episodically on the sea floor and stored faecal pellets in a deep tier beyond the depth range of other burrowers. The pellets are suggested to have been utilized as a food source during starvation times. Such behaviour represents a response to increased competition for food in the deep sea after the Cenomanian. *Tubulichnium rectum* is typical of the *Paleodictyon* and *Nereites* subichnofacies of the *Nereites* ichnofacies, mostly in distal parts of turbiditic depositional systems.

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