

Corkscrew-like horizontal trace fossils with a focus on a new ichnospecies of *Helicodromites* from the Oligocene Molare Formation of NW Italy

Alfred UCHMAN^{1,} * and Bruno RATTAZZI²

- ¹ Jagiellonian University, Faculty of Geography and Geology, Institute of Geological Sciences, Gronostajowa 3a; 30-387 Kraków, Poland; ORCID: 0000-0002-0591-777X
- ² Bruno Rattazzi, Museo Paleontologico di Crocefieschi, Via alla Chiesa 12, 16010 Crocefieschi (Genova), Italy

Uchman, A., Rattazzi, B., 2023. Corkscrew-like horizontal trace fossils with a focus on a new ichnospecies of *Helicodromites* from the Oligocene Molare Formation of NW Italy. Geological Quarterly, 67: 22, doi: 10.7306/gq.1692

Associate Editor: Anna Wysocka

Horizontal helical trace fossils constitute a characteristic burrow architectural design, but their ichnotaxonomy requires some clarification. In this paper, we review and revise this taxonomy on the basis of collections and data from the literature. *Helicorhaphe* is included in *Helicodromites* because its type ichnospecies displays the same morphological principles. A new ichnospecies of *Helicodromites* is distinguished from Oligocene offshore fan delta deposits in NW Italy. All ichnospecies of *Helicodromites* is distinguished from formeters that allow their distinction. All were probably produced by capitellid polychaetes in a deep tier within the sediment. They were generally stationary burrows, whose tracemakers benefited from feeding on microbes without significant sediment reworking.

Key words: ichnology, ichnotaxonomy, new ichnospecies, Piemonte Tertiary Basin, Paleogene.

INTRODUCTION

Simple corkscrew (helical) cylindrical trace fossils are very distinctive in their morphology. In the marine realm, vertical forms include the relatively large *Gyrolithes* Saporta, 1884 (e.g., Uchman and Hanken, 2013) as well as the small *Lapispira bispiralis* Lange, 1932 which has double helical turns (Lanés et al., 2007). Horizontal forms include a few ichnogenera whose representatives are known from the lower Paleozoic but became more common since the Cretaceous. Data on them are dispersed through the literature, and the criteria for distinguishing them (ichnotaxobases) are not always clear. The discovery of a new horizontal helical trace fossil in the Oligocene of NW Italy, and access to important collections, has provided an opportunity for their review, including some ichnotaxonomical clarifications that have already been signalled (Uchman, 2010), and that is the aim of this paper.

The horizontal helical trace fossils considered in this paper include *Helicolithus* Azpeitia-Moros, 1933, *Helicodromites* Berger, 1957, *Helicorhaphe* Książkiewicz, 1970, *Helicoichnus* Yang in Yang et al., 1982 and *Parahelicorhaphe* Yang in Yang et al., 1982, *Avetoichnus* Uchman and Rattazzi, 2011, and *Augerinoichnus* Minter et al., 2008. Thus far, *Helicolithus* and Helicorhaphe have been ascribed to uniramous meandering graphoglyptids, and *Helicodromites* and *Augerinoichnus* to horizontal helical burrows, according to their trace fossil architectural designs (Buatois et al., 2017). Most of them are so far monospecific, except for *Helicolithus* and *Helicorhaphe*. *Helicoichnus* and *Parahelicorhaphe* are known only from single occurrences.

The function of the helical course of the horizontal burrows remains unclear, even if their tracemakers can be interpreted with a higher level of confidence. Increasing knowledge on this matter is summarized in the discussion.

GEOLOGICAL SETTING

The new trace fossil occurs at a few localities in the Oligocene Molare Formation, which is part of the Tertiary Piedmont Basin (TPB) succession (Eocene to upper Miocene) (Fig. 1). The basin is located on the suture zone between the Northern Apennines and the Western Alps (e.g., Gelati et al., 1993, 1998; Mutti et al., 1995) and was affected by anticlockwise rotation of the Corsica–Sardinia block, which resulted in backthrusting northwards in the Ligurian Alps (Capponi et al., 2009). Transtensional synsedimentary tectonics involving the basin basement influenced sedimentation in the lower part of the succession (Gelati et al., 1993; Mutti et al., 1995; Mutti et al., 2002; Ghibaudo et al., 2014).



^{*} Corresponding author: e-mail: alfred.uchman@uj.edu.pl

Received: March 4, 2023; accepted: May 12, 2023; first published online: July 5, 2023

The Molare Formation (Franceschetti, 1967) is a 40-600 m thick basal unit of the Langhe Sub-basin succession in the western part of the TPB (e.g., Gelati, 1971; Gnaccolini, 1978; Turco et al., 1994). It lies unconformably on the basement which is formed of crystalline (mostly ophiolitic and metamorphic rocks of the Voltri Group) and sedimentary rocks of the Northern Apennines and the Western Alps (e.g., Lorenz, 1984; Barbieri et al., 2003; Maino et al., 2013). The lithological composition of the Molare Formation is laterally very variable (Gnaccolini, 1974; Rossi et al., 2009). Usually, its lower part is built dominantly of fluvial polymictic conglomerates and alluvial fan breccias, which fill incised valleys and tectonic depressions. These are absent on palaeotopografic elevations. Up-section, they are replaced by receding fan delta conglomerates (Gnaccolini, 1978; Mutti et al., 1995; Gelati et al., 1996; Gelati and Gnaccolini, 2003; Dallagiovanna et al., in press; Gelati et al., in press). Their clasts are dominated by metamorphic and ophiolithic rocks (Capponi et al., 2009), but limestone clasts are present in places. They are massive or thick bedded (Gelati, 1971; Gelati et al., in press), and their composition is laterally variable (Gnaccolini, 1974).

Shallow marine, poorly sorted, polymictic sandstones and finer-grained deposits replace the conglomerates up-section. Their deposition was at least partly influenced by tides and storms (Mutti et al., 1996; Gelati et al., 1998; Di Giulio et al., 2019). They contain many ophiolitic grains and clasts. Sandstone beds are usually discontinuous, in some cases amalgamated, up to 1 m thick, with normal or reverse graded bedding, parallel or cross lamination, or HCS, and bioturbation structures at the top (Di Giulio et al., 2019; Dallagiovanna et al., in press; Gelati et al., in press). Finer-grained grey sandstones, sandy marls and siltstones contain various fossils, including bryozoans, bivalves (e.g., Cardium, Chlamys, Lucina, Meretrix, Pecten, Pectunculus), gastropods (Cerithium, Turritella), echinoids (Echinolampas), macroforaminifers (Amphistegina, Heterostegina, Nummulites, Operculina), microforaminifers, tropical and subtropical flora (Laurus, Cinnamonum, Castanopsis), plant detritus and coralline algae, and brachiopods (Erymnaria, Gryphus, Terebratulina, Megathyris; see Bitner et al., 2020). Small coral and algal reefs, up to 12 m thick, are present on some palaeohighs (Fravega et al., 1994; Vannuci et al., 1997; Quaranta et al., 2009).

Locally, deposits of the Molare Formation form three backstepping, fining-up units (Molare 1, 2, 3) separated by discontinuities (Turco et al., 1994), which are a record of transgressive-regressive pulses (Gelati et al., 1998; Rossi et al., 2009) within a generally transgressive succession (Lorenz, 1979) of one depositional sequence (Gnaccolini et al., 1998). The succession records general deepening up to upper slope facies of unit Molare 3, which includes the Rigoroso Marl (Turco et al., 1994).

The Molare Formation was deposited during the transgression from N–NE to S–SW (Lorenz, 1979, 1984). Hence, according to Barbieri et al. (2003), the Molare Formation in the eastern part of its range is older (lower Oligocene) than in the western part (upper Oligocene). Favrega et al. (1994) and Turco et al. (1994) regarded the Molare Formation to extend to the lower Chattian. The earliest Chattian *Paragloborotalia opima opima* Zone (probably the upper part of the IFP21b Zone) is documented in the eastern part, and the late early to late Chattian *Globigerina ciperoensis* Zone (IFP22) in the western sector at the top of the Molare Formation (Dallagiovanna et al., in press). However, pelitic deposits at the top of the formation contain foraminifers of the early late Rupelian P20 Zone (Gnaccolini et al., 1998). Furthermore, the nannoplankton zones NP21b to NP22 (early Rupelian) to the lowest part of the NP23 Zone (middle Rupelian) are present in the Roccaverano-Merana area (Ghibaudo et al., 2014). In the architectural framework of the TPB filling by Rossi and Craig (2016), the upper Molare Formation extends to the lower Miocene, but no biostratigraphic data were provided.

The Molare Formation passes gradually into or is separated by an erosional surface from the overlying Rocchetta Formation, which is 100–550 m thick. Their contact is progressively younger from NE to SW (e.g., Gelati et al., 1993; Fravega et al., 1994; Vannucci et al., 1997). The Rocchetta Formation is composed mostly of mudstones interbedded with sandstones or, more rarely, with limestones. They are pelagic and turbiditic deposits and prodelta marls (Gelati, 1968; Artoni et al., 1999) dated to the Rupelian–Chattian in the eastern part of this formation and the Chattian–Aquitanian in the western part (Gelati, 1968; Gelati et al., 1993; d'Atri et al., 1997).

The new trace fossil was found at a few sections close together in the western part of the Langhe Subbasin in the upper part of the Molare Formation (Fig. 1 and Table 1). It occurs in siltstone intercalations in marly mudstones, which are sparsely interbedded with thin beds of sandy siltstones and sandstones. Most specimens derive from the Lesche and the Spigno Borroti sections. In the Lesche section, which is 19.09 m thick, they occur in a natural escarpment in a partly wooded area (Fig. 2A). The section is dominated by pale grey marly mudstones intercalated with sparse beds of siltstone and very fine, partly parallel- or ripple-laminated sandstones (Fig. 3). The helical trace fossil occurs in a bed 15–20 m thick of totally bioturbated siltstone. In the upper part of the section, a tempestite bed is present with intraclasts, nummulites, and ophiolitic grains at the base. The Spigno-Borrotti section (Fig. 2B) is ~10 m thick. It comprises grey siltstone with yellow pillar-like enclaves, perhaps resulting from weathering. These deposits contain crustacean burrows (1-2 cm in diameter), the bivalve Pholodomya in life position, other bivalves, gastropods and plant remains, including fruits. The helical trace fossil occurs in the yellow enclaves. These sections represent the upper part of the Molare Formation, which is probably upper Rupelian in age.

ICHNOTAXONOMY

Ichnogenus Helicodromites Berger, 1957

Type ichnospecies. – Helicodromites mobilis Berger, 1957.

D i a g n o s i s. – Horizontal, non-meandering helical, cylindrical burrow (modified from Berger, 1957).

R e m a r k s. – The type ichnospecies of *Helicodromites* Berger, 1957, *H. mobilis* Berger, 1957, was diagnosed in German by Berger (1957) as "Wagrecht verlaufende, nich mäandrirende, spiralige Lebensspur", which can be translated as a horizontal, non-meandering, spiraling trace of life. This diagnosis was repeated by Kappel (2003). Häntzschel (1975: W67) described *Helicodromites* based on *H. mobilis* Berger, which reads: "Smooth screw-shaped burrows, horizontal; diameter of tunnels about 2 mm; interval between spiral turns about 5 mm." In this "diagnosis", morphometric parameters are used, but size is not recommended as an ichnotaxobase, especially at the ichnogenus level (Bertling et al., 2006, 2022). However, a combination of size parameters (as in Häntzschel's description), may reflect some morphological aspects (i.e., proportions can be considered as an expression of shape) and can be used



Fig. 1. Geological maps

A – study region in the Tertiary Piedmont Basin with location of the sections studied (based on Gelati et al., 1996, with some changes); ABM – NW Apennines–Basso Monferrato–Collina di Torino wedge; SV – Sestri–Voltaggio line; B – location of the study region on the map of Italy

at the ichnospecies level. As the surface of the trace fossil described in this paper does not need to be completely smooth, this reference would be too restrictive. The non-meandering course invoked by Berger (1957) is important, because *Helicolithus* Azpeitia Moros, 1933, typified by *H. sampelayoi* Azpeitia Moros, 1933, is a meandering helical trace fossil, with a change of direction of helical coiling (dextral vs. sinistral) at the turns of its meanders, and the distinction between *Helicodromites* and *Helicolithus* is worth maintaining. *Helicolithus* belongs to graphoglyptids, and probably the helical turns of burrow in *H. sampelayoi* were connected to the seafloor by regular shafts (Seilacher, 1977). Another graphoglyptid, *Spirocosmorhaphe* Seilacher, 1989, is an even more complex burrow.

Among horizontal helical trace fossils, *Avetoichnus* Uchman and Rattazzi, 2011 has a central core enveloped by a helical tunnel (Uchman and Rattazzi, 2011; Monaco et al., 2012). *Helicorhaphe* Książkiewicz, 1970 typified by *H. tortilis* Książkiewicz, 1970, is a very small, simple, horizontal helical

Table 1

Localities, their location and specimens of Helicodromites helix isp. nov. from them

Locality/GPS coordinates	Outcrop	Associated trace fossils	Specimens
Spigno Borroti, from N44°32'24.44", E008°20'52.39", to N44°32'29.44", E008°20'56.89"	A roadcut of a local road. A few metres-thick section of mudstones and siltstones with a few intercalations of fine muddy sandstone.	?Thalassinoides isp.	1652+bis, 1670, 1900–1910, 1911+bis, 1912+bis, 1913, 1914, 1986+bis, 1987+bis, 1988, 1989, 1990*, INGUJ149P200–210
Spigno S. Giacomo N44°32'29.15", E008°21'00.58"	A roadcut and adjacent slope. A few metres-thick section of mudstones and siltstones with a few intercalations of fine muddy sandstone	<i>Curvolithus</i> isp., <i>Planolites</i> isp.	1729*, 1730, 1731+bis, 1763+bis, 1947, 1948+bis, 1952, 1953, 1962+bis
Lesche N44°30'29.28", E008°25'19.32"	19 m thick section in a natural scarp on a meadow (Fig. 2). Marly mudstones with sparse intercalations of thin siltstones and mudstones.	Thalassinoides isp., Planolites isp., Trichichnus isp., Ophiomorpha isp., Curvolithus isp., cf. Gyrochorte isp., Scolicia isp., Teredolites isp.	1738, 1739+bis, 2044+bis, 2045, 2047, 2061, 2062, INGUJ149P212–221, 223, 224
Fraschetto-Sbernera 2 N44°30'45.59" E008°25'43.63"	Low escarpments and a slope along a dirt road, 8 m of marly mudstone with sparse in- tercalation of sandy siltstones and sand- stones.	Thalassinoides isp.	1557
Giuliani-Bissi N44°31'37.80" E008°23'31.51"	A small exposure of a hard sandstone bed in marly mudstones along a dirt road.		1544
Gallareto-Valla N44°30'45.94" E008°21'06.81"	A small exposure of marly mudstones.		1638

* – Bormida Museum

trace. Consistently, size cannot be the main criterion at the ichnogenus level. The consideration of *Helicorhaphe* as a uniramous meandering graphoglyptid (Buatois et al., 2017) suggests some regular, lateral branches running from the helical turns. However, there is no evidence of such branches in the material available, including the holotype. Therefore, *Helicorhaphe* Książkiewicz, 1970 is included here in *Helicodromites* Berger, 1957.

Augerinoichnus helicalis Minter et al., 2008 from Permian tidal flat deposits in New Mexico, USA, is visible on bedding surfaces as a row of horseshoe-shaped structures and interpreted as a horizontal, helical-spiraled tunnel whose whorls are tilted. However, this interpretation is scarcely applicable to some complex morphological variants of *A. helicalis* (Minter et al., 2008: figs. 3.4, 3.7, 3.8). Alternatively, if this interpretation is true, the general geometry fits that of *Helicodromites*. The tilted whorls



Fig. 2. Main exposures studied A – Lesche; B – Spigno Borroti; measurement stick 1 m long can be considered as a diagnostic feature at the ichnospecies level. However, doubts about the geometry prevent the formal inclusion of *Augerinoichnus* in *Helicodromites*.

Helicodromites helix isp. nov. (Figs. 3–9)

Derivation of name. – From Latin *helix*, from Ancient Greek (helix), meaning something twisted or spiral.

D i a g n o s i s. – Horizontal, non-meandering helical, cylindrical burrow in which the distance between the whorls is mostly smaller than the diameter of the cylinder. The diameter of the helix lumen is approximately equal to that of the cylinder. The number of whorls is usually less than ten.

Holotype and paratypes. – The holotype is specimen 1729 from Spigno S. Giacomo housed in the Bormida Museum, N of Savona, Liguria, Italy (Fig. 4A). Paratype 1 – INGUJ149P14 (Fig. 4B), Lesche. Paratype 2 – INGUJ149P212, Lesche (Fig. 4C). Paratype 3, specimen 1902, Spigno Borroti (Fig. 4D). Paratype 4, 1909, Spigno Borroti (Fig. 4E). Paratype 5, INGUJ149P210, Spigno Borroti (Fig. 4F).

O t h e r m a t e r i a l. – 36 specimens at the Crocefieschi Museum near Genova in Italy (four-digit numbers), 2 specimens at the Bormida Museum (four digit numbers), and 20 specimens at the Nature Education Centre of the Jagiellonian University (CEP) – Museum of Geology in Kraków, Poland (institutional abbreviation and prefix INGUJ149P; Table 1).

Description. – Horizontal or subhorizontal, helical, cylindrical structure, which was observed mainly on the parting surfaces of mudstone or siltstone. Usually only half or less, rarely more than half of the structure, is visible along its general course. The cylinder is 1.7-5.5 mm, mostly 2.5-5 mm, in diameter (mean 3.1 mm; n = 40). The number of observed whorls ranges from 2 to 12 (mean 6, n = 33). The whorls in the main part of the burrow, no more than nine, are regular and tightly spaced. The distance between the whorls is almost always less than a millimetre, very rarely more than 1 mm, but less than 1.5 mm, so less than the diameter of the cylinder. At the ends of the more completely preserved traces, one or a few whorls became less regular, partly straightened, usually narrower and less tightly spaced. The diameter of the regular whorls is 3.8-10.1 mm, mainly 4-8 mm (mean 6 mm, n = 40). The trace fossil is 8-46 mm long (mean 20.9 mm, n = 34). The diameter of the less regular whorls is the same as that of the regular one. The diameter of the cylinder shows a good correlation with the diameter of the regular whorls (correlation coefficient r = 0.67, coefficient of determination $r^2 = 0.45$). The correlation of the diameter of cylinder with its total length or the number of whorls is poor (r = 0.14 and r = 0.18, respectively).

The general course of the trace fossil is mostly straight. However, some specimens are slightly curved or display a sharp turn of up to 55°. The whorls are nearly perpendicular to the axis of the trace fossil, but in some specimens the whorls are inclined as much as 65° to the axis. The morphometric parameters are stable within a given specimen. However, the diameter of the whorls can appear to gradually diminish in one direction in specimens where the parting surface intersects the trace fossil subparallel to the burrow axis, and the trace fossil emerges more from one side than the other. In some incomplete specimens, only casts of the helical structure are visible, and these are counterparts of full-reliefs of the trace fossil.





This trace fossil is probably branched, but the branching point itself has not been detected. If so, the branches run at an acute or right angle.

The terminations of the helix are mostly invisible because they are hidden in the surrounding rock or the specimens are broken. Only in some specimens are fragments of the terminations visible as cylinders of the same diameter and preservation, but showing a course deflected from the last whorl trajectory, running sideways or soon disappearing. Some of the terminating tunnels are branched. A specimen was polished



Fig. 4. Types of Helicodromites helix isp. nov.

A – the holotype, specimen 1729, Spigno S. Giacomo, Bormida Museum;
 B – paratype 1, INGUJ149P14, Lesche;
 C – paratype 2, INGUJ149P212, Lesche;
 D – paratype 3, specimen 1902, Spigno Borroti;
 E – paratype 4, 1909, Spigno Borroti;
 F – paratype 5, INGUJ149P210, Spigno Borroti





Fig. 5. Other specimens of Helicodromites helix isp. nov.

A – INGUJ149P218, Lesche; B – INGUJ149P217, Lesche; C – field photograph of specimen 2062, Lesche; D – field photograph of specimen 2061, Lesche; E – specimen 1904, Spigno Borroti; F – side view, INGUJ149P205, Spigno Borroti; G – side view, field photograph; H, I – side and bottom view, respectively, specimen 1914, Spigno Borroti; J – specimen 1910, Spigno Borroti



Fig. 6. Additional specimens of Helicodromites helix isp. nov.

A – specimen 1913, Spigno Borroti; B – specimen 1912, Spigno Borroti; C – specimen 1739, Lesche; D, E – specimen 2045, details 2 and 1, respectively, Lesche

serially to follow the termination; the result corroborates the previous observations. In one case, the tunnel emerges from the whorl.

The surface of the trace is mostly smooth, but some specimens show some perpendicular, irregular, narrow, faint ribs. In several specimens, the surface is covered with brownish waxy material, which adheres to the casts of full-reliefs. The content of the main elements suggests that the material is composed of clay minerals.

Thin sections made along the burrow show that the fill is the same as in the surrounding rock. However, the fill becomes finer and richer in clay minerals close to the margin of the burrow in a zone that is 0.1–0.2 mm wide.

R e m a r k s. – The morphology of the Helicodromites helix fits the diagnosis of Helicodromites, but its morphometric parameters differ distinctly from those of H. mobilis (Fig. 10), especially in the proportions of the diameter of the cylinder to the lumen encircled by whorls, and the proportions between the diameter of the cylinder and the distance between whorls. These parameters are close to 1:1 in H. helix but much smaller in H. mobilis (Fig. 11). The terminations of H. helix and H. mobilis (see comments to the latter) show common features. They are simple or branched prolongations of the less regular whorls. The number of whorls in *H. helix* (no more than ten) is distinctly lower than in some Paleozoic representatives of Helicodromites (see: Other representatives of Helicodromites). The fining of material close to the wall in H. helix (Fig. 7B, C) may be an effect of the adhesion of the finer material to the lining, which may have been covered with mucus.

Helicodromites mobilis Berger, 1957 (Fig. 12A)

*1957 *Helicodromites mobilis* – Berger, p. 539, fig. 1. [Copied in Häntzschel, 1975, p. W67, fig. 41.2.]

1966 Spiralieger Teil des Gangsystems von *Notomastus* – Hertweck and Reineck, fig. 7. [Copied in Reineck et al., 1967, pl. 6, fig. 12.]

1992 Helicodromites isp. - Rindsberg, p. 51, fig. 3E, pl. 6D.

1999 *Helicodromites* – Baldwin and McCave, p. 380, fig. 7A, B. 2003 *Helicodromites mobilis* Berger, 1957 – p. 74, pl. 8, fig. 5, pl. 11, fig. 4.

2005 *Helicodromites mobilis* – Vliet, p. 40, middle fig. in p. 40. 2008 *Helicodromites mobilis* Berger, 1957 – Carmona et al., p. 101, figs. 4.4, 4.5, 7.2.

?2013 *Helicodromites* isp. – Jurkowska and Uchman, p. 620, text-fig. 6G.

non 2014 cf. *Helicodromites mobilis* – Knaust et al., fig. 10G. 2016 *Helicodromites* isp. – Buatois et al., fig. 9.29c.

non 2020 *Helicodromites mobilis* [or *Helicodromites*] – Shillito and Davies, p. 1957, fig. 15e.

D i a g n o s i s. – Horizontal, non-meandering helical, cylindrical burrow in which the distance between the whorls is mostly larger than the diameter of the cylinder. The helix lumen is significantly larger than the diameter of the cylinder. The number of whorls is usually less than ten.

R e m a r k s. – *Helicodromites mobilis* was originally described from the Oligocene (Rupelian) offshore mudstones of Bayern, Germany (Berger, 1957). It occurs also in deep-water



Fig. 7. Thin section and SEM images of Helicodromites helix isp. nov.

A, B – horizontal thin sections through the whorls; C, D – details of B. Note concentration of finest material on margins of the whorls; E – SEM image of the whorl (left and central part of the photograph) plunging into the rock. The whorl is covered with brownish waxy material; F – SEM image of the brownish substance on the whorl surface, which shows a flakey structure



Fig. 8. Dispersed energy spectrum of waxy material on the surface of Helicodromites helix isp. nov.



Fig. 9. Model of Helicodromites helix isp. nov.



Fig. 10. Width of the trace versus thickness of the whorl of Helicodromites helix isp. nov. and other horizontal helical trace fossils



Fig. 12. Some helical or allegedly helical trace fossils

 A – Helicolithus mobilis Berger, INGUJ168P6, Miocene, Mut Basin, Turkey;
 B – Helicodromites tortilis (Książkiewicz, 1970), the holotype, UJ TF 277, Beloveža Beds, Eocene, Lipnica Mała, Carpathians, Poland;
 C – Helicorhaphe meandriformis Plička and Koklusová, 1989, holotype, G23137 in the Moravské zemské museum, Geologicko-paleontologické oddělení in Moravec, Czech Republic, Paleocene flysch in the Carpathians, Czech Republic Campanian deposits of western Germany (Kappel, 2003). Recent occurrences are known from the North Sea at a depth of 31 m (Hertweck and Reineck, 1966), the Gulf of Mexico at a depth of 90–200 m in clayey silt sediment from the outer shelf (Hill, 1985, his trace A), and the western North Atlantic at a depth of 4750 m (Baldwin and McCave, 1999). Rindsberg (1992) described *Helicodromites* in the central basin (his midbay) Holocene facies of an estuary. Carmona et al. (2008) and Buatois and Mángano (2011) recorded *Helicodromites* from the Miocene of the lower shoreface and offshore transition settings of Patagonia. Ferruginization is mediated by microbes and is related to a high content of organic matter, anoxia, and the formation of pyrite, which is oxidized by weathering (Kappel, 2003).

Helicodromites tortilis (Książkiewicz, 1970) (Fig. 12B)

1961 Helicorhaphe (n.f.) - Książkiewicz, 885, pl. 2, fig. 3.

*1970 *Helicorhaphe tortilis* ichnosp. n. – Książkiewicz, p. 286, fig. 1t.

1975 Helicorhaphe tortilis Książkiewicz – Häntzschel, p. W70, fig. 43.4.

1977 Helicorhaphe tortilis Książkiewicz – Książkiewicz, p. 116, pl. 11, fig. 10.

non 1981 Helicorhaphe - Tanaka and Sumi, pl. 6, fig. 1.

non 1989 *Helicorhaphe meandriformis* sp. n. – Plička and Koklusová, p. 113, text-fig. 2, pl. 64, fig. 2.

non 1995 *Helicorhaphe tortilis* Książkiewicz – Crimes and Mc-Call, p. 236, fig. 3a. [*H.* cf. *mobilis* in the present paper.]

1996 *Helicorhaphe crimesi* n. ichnosp. – Kozur et al., p. 136, fig. 38/2.

1988 Helicorhaphe tortilis Książkiewicz – Uchman, p. 173, fig. 78.

?2000 Helicorhaphe isp. - Bąk et al., p. 24, fig. 15b, c.

non? 2003 Helicorhaphe tortilis Książkiewicz – Kappel, p. 76, pl. 8, fig. 3.

2007 Helicorhaphe tortilis Książkiewicz – Uchman, p. 230, pl. 3, fig. 13.

2008 Helicorhaphe isp. - López Cabrera et al., p. 382, fig, 3.10.

D i a g n o s i s. – Very small, horizontal, non-meandering helical, cylindrical burrow, in which the distance between the whorls is mostly smaller than the diameter of the cylinder. The helix lumen is approximately equal to the diameter of the cylinder. The number of whorls is commonly more than ten.

R e m a r k s. – *Helicorhaphe* was first described by Książkiewicz (1961) as a new form but without any species, so as a *nomen nudum*. This was corrected by Książkiewicz (1970) by distinguishing its ichnospecies. However, the morphological features of this trace fossil fall into the diagnosis of *Helicodromites*. Transfer to this ichnogenus does not disallow consideration of *H. tortilis* as a graphoglyptid, because graphoglyptids are an informal group that embraces small, "patterned" trace fossils, usually preserved as hypichnial semireliefs (Seilacher, 1977).

Helicorhaphe crimesi Kozur et al., 1996 from the Permian flysch of Sicily falls into the diagnosis and morphometric parameters of *H. tortilis*. Therefore, it is considered as a junior synonym of *H. tortilis*. Helicorhaphe meandriformis Plička and Koklusová, 1989 belongs neither to Helicodromites Berger nor to Helicorhaphe Książkiewicz (see Other horizontal helical trace fossils). Crimes and McCall (1995) described *Helicodromites* determined as *Helicorhaphe tortilis* Książkiewicz from the lower-middle Miocene of Iran. This is a hypichnial semirelief composed of 16 bars, ~2 mm wide and 10 mm long, suggesting a helical pattern. The distance between bars is more or less equal to the width of the bars. This trace fossil belongs to *Helicodromites*, but is much larger than *H. tortilis*. Therefore, it is rather *H.* cf. *mobilis* because of its size, though the number of whorls is larger and the distance between them is smaller.

H. tortilis is considered to be the burrow of a polychaete (Książkiewicz, 1977).

OTHER REPRESENTATIVES OF HELICODROMITES

Helicodromites aff. mobilis, described by Poschmann (2015) from storm-influenced shallow-marine Devonian deposits in western Germany, belongs to this ichnogenus. It is similar to *H. helix* because the distance between its whorls is generally smaller than the diameter of the cylinder. Nevertheless, it shows a much larger number of whorls, usually a dozen, and commonly more than twenty. Moreover, the diameter of the cylinder and the width of the trace are larger than in *H. helix* and the whorls are commonly tangential to the burrow axis. It deserves a new ichnospecies.

Narbonne (1984) described *Helicodromites* without ichnospecies designation from intertidal and shallow subtidal Upper Silurian carbonates in Arctic Canada. This trace fossil looks like a strongly stretched *H. mobilis* (~8 wide, diameter of tube ~5 mm) but it cannot be ascribed to this ichnospecies, because the coils are distinctly tangentially arranged to the burrow axis; this feature is absent in *H. mobilis*.

Suarez de Centi et al. (1989) described *Helicodromites* from shallow-marine Silurian shelf deposits in northern Spain, whose cylinder is 1–2 mm in diameter and width ~6 mm, with the distance between the whorls close to the diameter of the cylinder. The whorls are distinctly tangentially arranged to the burrow axis. It is much smaller than the other Paleozoic traces considered in this section.

Helicodromites isp. from the Ordovician of Bulgaria is preserved on the bedding surface as bars that are ~4 mm wide and ~4 mm apart. The trace is ~10 mm wide. In one specimen, the bars are perpendicular to the burrow axis, but strongly oblique in the second specimen (Yanev et al., 2000; Aceñolaza and Yanev, 2001). It is similar to *H.* aff. *mobilis* described by Poschmann (2015).

A short, twisted cylindrical structure from shallow-marine clastic deposits of the Silurian (or Ordovician?) Tumblagooda Sandstone in Australia (Shillito and Davies, 2020), determined inconsistently as *Helicodromites mobilis* or *Helicodromites* isp., certainly does not belong to *H. mobilis*, and it is uncertain whether it represents some helical trace fossil.

OTHER HORIZONTAL HELICAL TRACE FOSSILS

Helicoichnus Yang in Yang et al., 1982, typified by *Helicoichnus cylindricum* Yang in Yang et al. (1982: fig. 2, pl. 1, fig. 2) from the Middle Jurassic of Tibet, was declared to be a helical trace fossil. Judging from a line drawing and a photograph in the original paper, it shows perpendicular to oblique annulation rather than helical turns.

Parahelicorhaphe Yang in Yang et al. (1982), typified by *P. bangonghuensis* Yang in Yang et al. (1982), from the Middle Jurassic of Tibet, is also considered here, but its suggested he-

lical morphology is questionable. Doubts are strengthened by its description in Yang et al. (2004), where "parallel annulated striae on the surface" are noted.

Helicorhaphe meandriformis Plička and Koklusová, 1989 from the Paleocene flysch of the Carpathians, Czech Republic (Fig. 12C), represents another ichnogenus, probably *Desmograpton* Fuchs, 1895, because it shows prolongation of the bars in the meandering rows and some bridges between them. They are poorly preserved, though show important evidence of more complex geometry than a simple helical tunnel.

Megagyrolithes ardescensis Gaillard, 1980, is a huge helical structure, 30 cm in diameter and 1.5 m long, from Valanginian hemipelagic deposits of France ascribed to crustaceans. However, Hoareau et al. (2009) suggested that concretions may have formed around helical burrows. Similarly, *Dinocochlea ingens* Woodward, 1922 from the Valanginian of the UK, a huge, horizontal, corkscrew-shaped enigmatic structure, was recently considered to be a concretion nucleated around a burrow resembling *Helicodromites* (Taylor and Sendino, 2011). The authors cited indicated that *Helicodromites* might be a junior synonym of *Dinocochlea* if their interpretation is correct, but the morphology of the original burrow remains only a matter of supposition.

DISCUSSION

PRODUCER

Helicodromites mobilis is interpreted as a feeding structure of the ethological category fodinichnia (Carmona et al., 2008; Buatois et al., 2016), produced in the deep tier (Carmona et al., 2008) in oxygenated sediments (Kappel, 2003). The size differences within *Helicodromites mobilis* may be explained by the ontogenetic growth of the producer, as suggested by Carmona et al. (2008) on the basis of the stable relation of the distance between whorls to the diameter of the cylinder.

Hertweck and Reineck (1966) recognized that recent *Helicodromites* (included in *H. mobilis* in this paper) from the North Sea is produced by the capitellid polychaete *Notomastus*. Reineck et al. (1967) observed these spiral traces 12 cm below the sea floor. They are connected to the surface by two steep, locally branched tunnels, which continue from the ends of the spiral; some spirals are connected directly to the shallower U-shaped burrows of *Echiurus echiurus* (Pallas), which, in turn, were connected to the sea floor (Hertweck, 1970). Capitellid polychaetes (43 genera) are widespread burrowers in a wide range of depths, especially in organic-rich sediments; among them, *Notomastus* accounts for 40 species (Hernández-Alcántara et al., 2022).

Hauck et al. (2009), Dashtgart and Gingras (2012) and Poschmann (2015) considered that *Helicodromites* can also be produced by the enteropneust *Saccoglossus kowalevskii*, which produces variably oriented (mostly vertical to oblique) helical burrows in intertidal and subtidal brackish deposits (Gingras et al., 1999, 2008). Nevertheless, fossil *Helicodromites* does not show variable orientation but is horizontal or subhorizontal. Therefore, capitellid polychaetes represented by *Notomastus* are more reliable candidates for the tracemaker of *Helicodromites*. Taking into account the same burrow architecture of *H. mobilis* and *H. helix*, the latter is probably produced by capitellid polychaetes.

Holothurians can produce helical fecal strings (e.g., Heezen and Hollister, 1971). However, the branched terminations in *Helicodromites helix*, especially those that are vertically to obliquely oriented or branched, show that this is a burrow. It is extremely unlikely that long terminations of fecal strings could remain in such a position for a long enough time to be preserved in the fossil state. Short, tightly spaced helical structures can also be visible in coprolites of fishes (Müller, 1971b; Rummy et al., 2021), but they show at least one spindle termination.

Horizontal helical burrows can also be produced in continental deposits. Müller (1967, 1971a) described them from sand dunes on the Black Sea coast (Bulgaria) and on the Baltic Sea coast (Germany), where they were produced shallowly under the surface, probably by arthropods or myriapods. He compared them to *Helicorhaphe*.

FUNCTION

The production of a horizontal helical burrow must have some special function considering that the terminations are *not* helical. Investigations on *Notomastus latericus* Sars from a brackish lagoon in southern Italy show that its sediment reworking is insignificant (Giangrande et al., 2001). The animal works head-down, so its feeding activity is expected in the helical part of the burrow. Commonly, *Helicodromites mobilis* is ferruginized, which suggests a strong geochemical gradient. Kappel (2003) regarded that ferruginization is related to the oxygenation of pyrite and is microbially mediated. Indeed, the main part of the burrows of some species of *Notomastus* are surrounded by anoxic sediment and contain an increased content of microbes (Steward et al., 1996). Therefore, it can be assumed that the helical whorls cause an increase in length and space along a certain level in the sediment, which is appropriate for feeding on microbes. Possibly, the microbes living in the burrow benefit from the chemical gradient between the oxic and anoxic environment. If so, then *Helicodromites* is a chemichnion.

ENVIRONMENT

Fossil *Helicodromites mobilis* is known mostly from fine-grained offshore and deeper deposits and the recent examples from depths of 31 m (Hertweck and Reineck, 1966) to



Fig. 13. Trace fossils co-occurring with Helicodromites helix isp. nov. in the Molare Formation at Lesche

A – Curvolithus isp.; B – Gyrochorte isp.; C – Ophiomorpha isp.; D – Planolites isp.; E – Scolicia prisca; F – Spongeliomorpha isp.; G – Thalassinoides isp.



Fig. 14. Plant fossils from the Molare Formation in Spigno Borroti

A – a piece of wood with cast of insect (?) borings; B – a twig of an undetermined plant fossil

4750 m (Baldwin and McCave, 1999). The depth may be even shallower because *Notomastus latericus*, the producer of *Helicodromites mobilis*, can live in brackish lagoons at a depth of only 0.5 m (Giangrande et al., 2001; see also Rindsberg, 1992). This corroborates the opinion by Buatois and Mángano (2011) that *Helicodromites* (represented mostly by *H. mobilis*)

occurs in sediments deposited at different depths. However, it tends to be more frequent in offshore and deeper fine-grained deposits.

Helicodromites tortilis is known only from deep-sea turbiditic deposits (Książkiewicz, 1977, and papers in its synonymy). It was produced in mud, but is preserved on sandstone beds (Książkiewicz, 1977). The Paleozoic forms described in "Other representatives of Helicodromites" occur in shallow-marine deposits.

Helicodromites helix occurs in the Molare Formation, which was deposited as a fan-delta system (e.g., Gelati et al., 1996; Gelati and Gnaccolini, 2003). The deposits containing H. helix are dominated by mud and silt and can be considered as distal fan-delta facies in an offshore or deeper setting. In such settings, elements of the impoverished Nereites ichnofacies can occur, while more proximal, subaquaeous parts usually contain elements of the impoverished Skolithos, Cruziana, and Zoophycos ichnofacies (Hovikoski et al., 2019). Trace fossils associated with H. helix include Curvolithus (Fig. 13A), Gyrochorte isp. (Fig. 13B), Ophiomorpha isp. (Fig. 13C), Planolites isp. (Fig. 13D), Scolicia prisca (Fig. 13E), Spongeliomorpha isp. (Fig. 13F) and Thalassinoides isp. (Fig. 13G). This trace fossil assemblage resembles rather the impoverished Cruziana ichnofacies. The abundance of plant debris (Fig. 14) shows a strong influence of material supply from the land. The occurrence of Curvolithus is characteristic of fan-delta facies (Curvolithus ichnofacies of Lockley et al., 1987; Hovikoski et al., 2019). Therefore, it seems that the deposits of the sections investigated represent offshore depths.

CONCLUSIONS

The marine trace fossil *Helicodromites* Berger, 1957 includes *H. mobilis* Berger, 1957, *H. tortilis* (Książkiewicz, 1970), *H. helix* isp. nov., and some unnamed Paleozoic ichnospecies forms. All are horizontal, non-meandering helical deep-tier burrows connected to the seafloor by simple or branched shafts. They differ in the number of whorls and the proportions between the diameter of the burrow and the helical whorls, and they occupy a confined range of sizes. *H. mobilis* occurs at different depths, mostly in fine-grained deposits. *H. tortilis* is known only from deep-sea turbiditic deposits and *H. helix* only from offshore fan-delta deposits.

Acknowledgements. A.U. was supported by the Fondazione Luigi, Cesare e Liliana Bertora, and a grant from the Faculty of Geography and Geology under the Strategic Programme Excellence Initiative at Jagiellonian University. A.K. Rindsberg (Livingstone, Alabama) and P. Leonowicz (Warsaw) provided constructive reviews, which helped very much to improve the manuscript.

REFERENCES

- Aceñolaza, F.G., Yanev, S.I., 2001. El Ordovícico del sector occidental de Stara Planina (Montes Balcanes), Bulgaria: icnofósiles e implicaciones paleobiogeográficas. Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', n.s., 3: 55–72.
- Artoni, A., Di Biase, D., Fava, L., Iaccarino, S., Mavilla, M., Mutti, E., Papani, L., Sgavetti, M., Turco, E., 1999. Nuovi dati per l'interpretazione stratigrafico-deposizionale dell'Oligocene

superiore e Miocene inferiore nel Bacino Terziario Piemontese. Riunione del gruppo informale di sedimentologia del CNR: 1–10.

Azpeitia Moros, F., 1933. Datos para el estudio paleontlógico del Flysch de la Costa Cantábrica y de algunos otros puntos de España. Boletín del Instituto Geologico y Minero de España, 53: 1–65.

- Bąk, K., Uchman, A., Bąk, M., 2000. Agglutinated foraminifera, radiolaria and trace fossils from Upper Cretaceous deep-water variegated shales at Trawne Stream, Grajcarek Unit, Pieniny Klippen Belt, Carpathians, Poland. Bulletin of the Polish Academy of Sciences, Earth Sciences, 48: 1–32.
- Baldwin, C.T., McCave, I.N., 1999. Bioturbation in an active deep-sea area: implications for models of trace fossil tiering. Palaios, 14: 375–388; https://doi.org/10.2307/3515463
- Barbieri, C., Carrapa, B., Di Giulio, A., Wijbrans, J., Murrell, G.R., 2003. Provenance of Oligocene synorogenic sediments of the Ligurian Alps (NW Italy): inferences on belt age and cooling history. International Journal of Earth Sciences, 92: 758–778; https://doi.org/10.1007/s00531-003-0351-x
- Berger, W., 1957. Eine spiralförmige Lebensspur aus dem Rupel der bayerischen Beckenmolasse. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, (1957): 538–540.
- Bertling, M., Braddy, S., Bromley, R.G., Demathieu, G.D., Genise, J.F., Mikuláš, R., Nielsen, J.-K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M., Uchman, A., 2006. Names for trace fossils: a uniform approach. Lethaia, 39: 265–286; https://doi.org/10.1080/00241160600787890
- Bertling, M., Buatois, L.A., Knaust, D., Laing, B., Mángano, M.G., Meyer, N., Mikuláš, R., Minter, N.J., Neumann, C., Rindsberg, A.K., Uchman, A., Wisshak, M., 2022. Names for trace fossils 2.0: theory and practice in ichnotaxonomy. Lethaia, 55; https://doi.org/10.18261/let.55.3.3
- Bitner, M.A., Uchman, A., Rattazzi, B., 2020. Brachiopods from the Palaeogene clastic deposits of north-western Italy. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 298: 165–176; https://doi.org/10.1127/njgpa/2020/0942
- Buatois, L.A., Mángano, M.G., 2011. Ichnology: organism-substrate interactions in space and time. Cambridge, University Press.
- Buatois, L.A., Carmona, N.B., Curran, H.A., Netto, R.G., Mángano, M.G., Wetzel, A., 2016. The Mesozoic marine revolution. Topics in Geobiology, 40: 19–134; https://doi.org/10.1007/978-94-017-9597-5_9
- Buatois, L.A., Wisshak, M., Wilson, M.A., Mángano, M.G., 2017. Categories of architectural designs in trace fossils: a measure of ichnodisparity. Earth-Science Reviews, 164: 102–181; https://doi.org/10.1016/j.earscirev.2016.08.009
- Capponi, G., Crispini, L., Federico, L., Piazza, M., Fabbri, B., 2009. Late Alpine tectonics in the Ligurian Alps: constraints from the Tertiary Piedmont Basin conglomerates. Geological Journal, 44: 211–224; https://doi.org/10.1002/gj.1140
- Carmona, N.B., Buatois, L.A., Mángano, M.G., Bromley, R.G., 2008. Ichnology of the Lower Miocene Chenque Formation, Patagonia, Argentina: animal-substrate interactions and the modern evolutionary fauna. Ameghiniana, 45: 93–122.
- Crimes, T.P., McCall, G.J.H., 1995. A diverse ichnofauna from Eocene-Miocene rocks of the Makran Range (S.E. Iran). Ichnos, 3: 231–258; https://doi.org/10.1080/10420949509386394
- Dallagiovanna, G., Gaggero L., Seno S., Felletti, F., Mosca, P., Decarlis, A., Pellegrini, L., Poggi, F., Bottero, D., in press. Note Illustrativie della Carta d'Italia alla scala 1:50,000, Foglio 228 Cairo Montenotte. Roma (Servizio Geologico d'Italia).
- Dashtgart, S.E., Gingras, M.K., 2012. Marine invertebrate neoichnology. Developments in Sedimentology, 64: 273–295; https://doi.org/10.1016/B978-0-444-53813-0.00010-1
- d'Atri, A., Piana, F., Tallone, S., Bodrato, G., Roz Gastaldi, M., 1997. Oligo–Miocene tectonics of the Alto Monferrato stratigraphic succession (Tertiary Piedmont Basin) and of the northwestern part of the Voltri Group (Acqui Terme-Cassinelle, Al.). Atti Ticinesi di Scienze della Terra, 5: 85–100.
- Di Giulio, A., Marini, M., Felletti, F., Patecci, M., Rossi, M., Amadori, C., 2019. Control exerted by collisional tectonics on basin topography and depositional styles: the Tertiary Piedmont Basin in the Alps-Apennines Junction (NW Italy). In: Sedimentology of Face Societal Challenges on Risk, Resources and Record of the Past (eds. M. Vigliotti, M. Tropeano, V.

Pascucci, D. Ruberti and L. Sabato): 257–288. 34th IAS International Meeting of Sedimentology, Rome, 10–13 September 2019, Field Trips – Guide Book. Università di Roma, Rome.

- Franceschetti, B., 1967. Studi geologici sulla regione ad ovest di Ovada (Provincia di Alessandria). Memorie della Società Geologica Italiana, 6: 379–420.
- Fravega P., Piazza, M., Stockar R., Vannucci, G., 1994. Oligocene coral and algal reef and related facies of Valzemola (Savona, NW Italy). Rivista Italiana di Paleontologia e Stratigrafia, 100: 423–456; https://doi.org/10.13130/2039-4942/8610
- Fuchs, T. 1895. Studien über Fucoiden und Hieroglyphen. Denkschriften der k.k. Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Classe, 62: 369–448.
- Gaillard, C., 1980. *Megagyrolithes ardescensis* n. gen., n. sp., trace fossile nouvelle du Valanginien d'Ardeche (France). Geobios, 13: 465–472; https://doi.org/10.1016/S0016-6995(80)80083-0
- Gelati, R., 1968. Stratigrafia dell'Oligo-Miocene delle Langhe tra le valli dei fiumi Tanaro e Bormida di Spigno. Rivista Italiana di Paleontologia e Stratigrafia, 74: 865–967.
- Gelati, R., 1971. Bacino Terziario Piemontese. In: Note Illustrative della Carta Geologica d'Italia alla scala 1:100 000, Foglio 81 Ceva (V. Francani, R. Gelati, B. Martinis, G. Orombelli, G. Pasquarè, P.M. Rossi and G. Sfondrini): 47–70. Servizio Geologico d'Italia, Roma.
- Gelati, R., Gnaccolini, M., 2003. Genesis and evolution of the Langhe Basin, with emphasis on the latest Oligocene–earliest Miocene and Serravallian. Atti Ticinensi di Scienze della Terra, 44: 3–18.
- Gelati, R., Gnaccolini, M., Falletti, P., Catrullo, D., 1993. Stratigrafia sequenziale della successione Oligo–Miocenica delle Langhe, Bacino Terziario Ligure-Piemontese. Rivista Italiana di Paleontologia e Stratigrafia, 98: 425–452.
- Gelati, R., Gnaccolini, M., Maioli, A., 1996. The stratigraphic record of Oligocene-early Miocene events at the south-western end of the Piedmont Tertiary Basin. Rivista Italiana di Paleontologia e Stratigrafia, 102: 65–76; https://doi.org/10.13130/2039-4942/5211
- Gelati, R., Gnaccolini, M., Petrizzo, M.R. 1998. Synsedimentary tectonics and sedimentation in the Tertiary Piedmont Basin, northwestern Italy. Rivista Italiana di Paleontologia e Stratigrafia, 104: 193–214; https://doi.org/10.13130/2039-4942/5331
- Gelati, R., Gnaccolini, M., Polino, R., Mosca, P., Piana, F., Morelli, M., Fioraso, G., In press. Note illustrative della Carta Geologica d'Italia alla scala 1:50,000, Foglio 211, Dego. V. of 124. Servizio Geologico d'Italia, Roma.
- Ghibaudo, G., Massari, F., Chiambretti, I., d'Atri, A., 2014. Oligo-Miocene tectono-sedimentary evolution of the Tertiary Piedmont Basin southern margin, Roccaverano area-Langhe Sub-basin (NW Italy). Journal of Mediterranean Earth Sciences, 6: 1–51.
- Giangrande, A., Licciano, M., Fanelli, G., 2001. Bioturbation behaviour in two Mediterranean polychaetes. Journal of the Marine Biological Association of the United Kingdom, 81: 341–342; https://doi.org/10.1017/S0025315401003836
- Gingras, M.K., Pemberton, S.G., Saunders, T., Clifton, H.E., 1999. The ichnology of modern and Pleistocene brackish-water deposits at Willapa Bay, Washington: variability in estuarine settings. Palaios, 14: 352–374; https://doi.org/10.2307/3515462
- Gingras, M.K., Dashtgard, S.E., MacEachern, J.A., Pemberton, S.G., 2008. Biology of shallow marine ichnology: a modern perspective. Aquatic Biology, 2: 255–268; https://doi.org/10.3354/ab00055
- Gnaccolini, M., 1974. Osservazioni sedimentologiche sui conglomerati oligocenici del settore meridionale del Bacino Terziario. Ligure-Piemontese. Rivista Italiana di Paleontologia e Stratigrafia, 80: 85–100.
- Gnaccolini, M., 1978. Depositi Oligocenici di "fan-delta" nella regione Compresa tra Bosio e la Cresta di Cravara (Bacino terzrarro ligure-piemontese). Rivista Italiana di Paleontologia e Stratigrafia., 84: 673–699.

- Gnaccolini, M., Gelati, R., Falletti, P., 1998. Sequence stratigraphy of the "Langhe" Oligo-Miocene succession, Tertiary Piedmont Basin, Northern Italy. SEPM Special Publications, 60: 235–246; https://doi.org/10.2110/pec.98.02.0233
- Häntzschel, W., 1975. Trace fossils and problematica. In: Treatise on Invertebrate Paleontology, part W, Miscellanea, Supplement I (ed. C. Teichert): W1–W269. Boulder, Colo., Lawrence, Kans. (Geological Society of America and University of Kansas).
- Hauck, T.E., Dashtgard, S.E., Pemberton, G., Gingras, M.K., 2009. Brackish-water ichnological trends in a microtidal barrier Island-embayment system, Kouchibouguac National Park, New Brunswick, Canada. Palaios, 24: 478–496; https://doi.org/10.2110/palo.2008.p08-056r
- Heezen, B.C., Hollister, C.D., 1971. The Face of the Deep. New York: Oxford University Press.
- Hernández-Alcántara, P.E., García-Garza, M., Solís-Weiss, V. 2022. Notomastus bermejoi, a new species of Capitellidae (Annelida, Polychaeta) from the Gulf of California, with morphological remarks on species with hooks in thoracic chaetigers. ZooKeys, 1102: 43–58;

https://doi.org/10.3897/zookeys.1102.83198

- Hertweck, G., 1970. The animal community of a muddy environment and the development of biofacies as effected by the life cycle of the characteristic species. Geological Journal, Special Issue, 3: 235–242.
- Hertweck, G., Reineck, H.-E., 1966. Untuersuchungsmethoden von Gangbauten und anderen Wühlgefügen mariner Bodentiere. Natur und Museum, 96: 429–438.
- Hill, G.W., 1985. Ichnofacies of a modern size-graded shelf, Northwestern Gulf of Mexico. SEPM Special Publications, 35: 195–210; https://doi.org/10.2110/pec.85.35.0195
- Hoareau, G., Odonne, F., Debroas, E.-J., Maillard, A., Monnin,
 C., Callot, P., 2009. Dolomitic concretions in the Eocene Sobrarbe delta (Spanish Pyrenees): fluid circulation above a submarine slide scar infilling. Marine and Petroleum Geology,
 26: 724–737; https://doi.org/10.1016/j.marpetgeo.2008.03.012
- Hovikoski, J., Uchman, A., Alsen, P., Ineson, I., 2019. Ichnological and sedimentological characteristics of submarine fan-delta deposits in a half-graben, Lower Cretaceous Palnatokes Bjerg Formation, NE Greenland. Ichnos, 26: 28–57; https://doi.org/10.1080/10420940.2017.1396981
- Jurkowska, A., Uchman, A., 2013. The trace fossil Lepidenteron lewesiensis (Mantell, 1822) from the Upper Cretaceous of southern Poland. Acta Geologica Polonica, 63: 611–623; https://doi.org/10.2478/agp-2013-0026
- Kappel, J., 2003. Ichnofossilien im Campanium des SE-Münsterlands. Münsterische Forschungen zur Geologie und Paläontologie, 96: 1–163.
- Knaust, D., Warchoł, M., Kane, I.A., 2014. Ichnodiversity and ichnoabundance: revealing depositional trends in a confined turbidite system. Sedimentology, 61: 2218–2267; https://doi.org/10.1111/sed.12134
- Kozur, H.W., Krainer, K., Mostler, H., 1996. Ichnology and sedimentology of the Early Permian deep-water deposits from the Lercara-Roccapalumba area (Western Sicily, Italy). Facies, 34: 123–150.
- Książkiewicz, M., 1961. On some problematic organic traces from the flysch of the Polish Carpathians (part II) (in Polish with English summary). Kwartalnik Geologiczny, 5 (4): 882–890.
- Książkiewicz, M., 1970. Observations on the ichnofauna of the Polish Carpathians. Geological Journal, Special Issue, 3: 283–322.
- Książkiewicz, M., 1977. Trace fossils in the Flysch of the Polish Carpathians. Palaeontologia Polonica, **36**: 1–208.
- Lanés, S., Manceñido, M., Damborenea, S., 2007. Lapispira: a double helical burrow from Jurassic marine nearshore environments. SEPM Special Publications, 88: 59–77; https://doi.org/10.2110/pec.07.88.0059
- Lange, W. 1932. Über spirale Wohngänge, Lapispira bispiralis gen. nov. spec. nov., ein Leitfossil aus der Schlotheimien-stufe des Lias Nord-deutschlands. Zeitschrift der Deutschen Geologischen Gesellschaft, 84: 537–543.

- Lockley, M., Rindsberg, A., Zeiler, R., 1987. The paleoenvironmental significance of the nearshore *Curvolithus* ichnofacies. Palaios, 2: 255–262; https://doi.org/10.2307/3514675
- López Cabrera, M.I., Olivero, E.B., Carmona, N.B., Ponce, J.J., 2008. Cenozoic trace fossils of the *Cruziana, Zoophycos* and *Nereites* ichnofacies from the Fuegian Andes, Argentina. Ameghiniana, 45: 377–392.
- Lorenz, C., 1979. L'Oligo-Miocène ligure: un exemple de transgression. Bulletin de la Société Géologique de France, 21: 375–378; https://doi.org/10.2113/gssgfbull.S7-XXI.4.375
- Lorenz, C., 1984. Evolution stratigraphique et structural des Alpes Ligures depuis l'Eocène Supérieur. Memorie della Società Geologica Italiana, 28: 211–228.
- Maino, M., Decarlis, A., Felletti, F., Seno, S., 2013. Tectono-sedimentary evolution of the Tertiary Piedmont Basin (NW Italy) within the Oligo–Miocene central Mediterranean geodynamics. Tectonics, 32: 593–619; https://doi.org/10.1002/tect.20047
- Minter, N.J., Lucas, S.G., Lerner, A.J., Braddy, S.J., 2008. Augerinochinus helicalis, a new helical trace fossil from the nonmarine Permian of New Mexico. Journal of Paleontology, 82: 1201–1206; https://doi.org/10.1666/07-129.1
- Monaco, P., Trecci, T., Uchman, A., 2012. Taphonomy and ichnofabric of the trace fossil Avetoichnus luisae in Paleogene deep-sea fine-grained turbidites: examples from Italy, Poland and Spain. Bolletino della Società Geologica Italiana, 51: 23–38; https://doi.org/10.4435/BSPI.2012.04
- Müller, A.H., 1967. Besondere Lebensspuren und Sedimentmarken auf Rezenten Flugsanddünen. Natur und Museum, 97: 354–366.
- Müller, A.H., 1971a. Über Ichnia von typ Helicorhaphe und Helicodromites aus Gegenwart und geologischer Vergangenheit. Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin, Geologie und Mineralogie, 13: 72–79.
- Müller, A.H., 1971b. Einiges über spirale und schraubenförmige Strukturen bei fossilen Tieren unter besonderer Berücksichtigung taxonomischer und phylogenetischer Zusammenhänge. Teil 4. Monatsberichte der deutschen Akademie der Wissenschaften zu Berlin, Geologie und Mineralogie, 13: 613–624.
- Mutti, E., Davoli, G., Tinterri, R., Zavala, C., 1996. The importance of ancient fluvio-deltaic systems dominated by catastrophic flooding in tectonically active basins. Memorie di Scienze Geologiche di Padova, 48: 233–291.
- Mutti, E., Di Biase, D., Fava, L., Mavilla, N., Sgavetti, M., Tinterri, R., 2002. The Tertiary Piedmont Basin. In: Revisiting Turbidites of the Marnoso-Arenacea Formation and their Basin-Margin Equivalents: Problems with Classic Models: Florence (Italy), Turbidites Workshop, Excursion Guidebook. Part II (eds. E. Mutti, F. Ricci Lucchi et al.): 1–25, Dipartimento di Scienze della Terra (Universita` di Parma) and Eni-Divisione Agip, Parma.
- Mutti, E., Papani, L., Biase, D., di, Davoli, G., Mora, S., Segadelli, S., Tinterii, R., 1995. Il Bacino Terziario Epimesoalpino e la sue implicazioni sui rapporti tra Alpi ed Appennino. Memorie di Scienze Geologische, 47: 217–244.
- Narbonne, G.M., 1984. Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada. Journal of Paleontology, 58: 398–415
- Plička, M., Koklusová, A., 1989. Helicorhaphe meandriformis sp. n. a new fossil trace from Carpathian flysch of Czechoslovakia. Západné Karpaty, séria Paleontológia, 13: 113–117.
- Poschmann, M., 2015. The corkscrew-shaped trace fossil *Helico-dromites* Berger, 1957, from Rhenish Lower Devonian shallow-marine facies (Upper Emsian; SW Germany). Paläontologische Zeitschrift, 89: 635–643; https://doi.org/10.1007/s12542-014-0232-6
- Quaranta, F., Piazza, M., Vannucci, G., 2009. Climatic and tectonic control on the distribution of the Oligocene reefs of the Tertiary Piedmont Basin (NW Italy). Italian Journal of Geosciences, 128: 587–591; https://doi.org/10.3301/IJG.2009.128.2.587
- Reineck, H.-E., Gutmann, W.F., Hertweck, G., 1967. Das Schlickgebiet siidlich Helgoland als Beispiel rezenter Schelfablagerungen. Senckenbergiana Lethaea, 48: 219–275.

- Rindsberg, A.K., 1992. Holocene ichnology of eastern Mississippi Sound, Alabama. Geological Survey of Alabama, Circular, 167: 1–75.
- Rossi, M., Craig, J., 2016. New perspective on sequence stratigraphy of syn-orogenic basins: insights from the Tertiary Piedmont Basin (Italy) and implications for play concepts and reservoir heterogeneity. Geological Society Special Publications, 436: 93–133; https://doi.org/10.1144/SP436.10
- Rossi, M., Mosca, P., Polino, R., Rogledi, S., Biffi, U., 2009. New outcrop and subsurface data in the Tertiary Piedmont Basin (NW-Italy): Unconformity-bounded stratigraphic units and their relationships with basin-modification phases. Rivista Italiana di Paleontologia e Stratigrafia, 115: 305–335; https://doi.org/10.13130/2039-4942/6386
- Rummy, P., Halaclar, K., He, C., 2021. The first record of exceptionally-preserved spiral coprolites from the Tsagan-Tsab formation (Lower Cretaceous), Tatal, western Mongolia. Scientific Report, 11: 7891; https://doi.org/10.1038/s41598-021-87090-5
- Saporta, G., 1884. Les organismes problematiques des anciennes mers. Masson, Paris.
- Seilacher, A., 1977. Pattern analysis of *Paleodictyon* and related trace fossils. Geological Journal, Special Issue, 9: 289–334.
- Seilacher, A., 1989. Spirocosmorhaphe, a new graphoglyptid trace fossil. Journal of Paleontology, 63: 116–117; https://doi.org/10.1017/S0022336000041032
- Shillito, A.P., Davies, N.S., 2020. The Tumblagooda Sandstone revisited: exceptionally abundant trace fossils and geological outcrop provide a window onto Palaeozoic littoral habitats before invertebrate terrestrialization. Geological Magazine, 157: 1939–1970; https://doi.org/10.1017/S0016756820000199
- Steward, C.C., Nold, S.C., Rimngelberg, D.B., White, D.C., Lovelll, C.R., 1996. Microbial biomass and community structures in the burrows of bromophenol producing and non-producing marine worms and surrounding sediments. Marine Ecology Progress Series, 133: 149–165.
- Suarez de Centi, C., Garcia-Ramos, J.C., Valenzuela, M., 1989. Icnofósiles del Silúrico de la Zona Cantábrica (NO de España). Boletín Geológico y Minero, 100: 339–394.
- Tanaka, K., Sumi, Y., 1981. Cretaceous paleocurrents in the Central Zone of Hokkaido, Japan. Bulletin of the Geological Survey of Japan, 32: 65–114.
- Taylor, P.D., Sendino, C., 2011. A new hypothesis for the origin of the supposed giant snail *Dinocochlea* from the Wealden of Sussex, England. Proceedings of the Geologists' Association, 122: 492–500; https://doi.org/10.1016/j.pgeola.2011.03.007

- Turco, E., Duranti, D., laccarino, S., Villa, G., 1994. Relationships between foraminiferal biofacies and lithofacies in the Oligocene Molare Formation and Rigoroso Marl: preliminary results from the Piota River section (Tertiary Piedmont Basin, NW Italy). Giornale di Geologia, 56: 101–117; https://doi.org/10.1080/17445647.2015.1100561
- Uchman, A., 1998. Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. Annales Societatis Geologorum Poloniae, 68: 105–218.
- Uchman, A., 2007. Trace fossils of the Pagliaro Formation (Paleocene) in the North Apennines, Italy. Beringeria, 37: 217–237.
- Uchman, A., 2010. Taxonomy of helical trace fossils. In: IV International Workshop on Ichnotaxonomy, Moscow – St. Petersburg, June 21–26, 2010, Abstracts (ed. A.V. Dronov): 42–43. PIN RAN [Paleontological Institute of Russian Academy of Sciences], Moscow.
- Uchman, A., Hanken, N.-M., 2013. The new trace fossil *Gyrolithes lorcaensis* isp. n. from the Miocene of SE Spain and a critical review of the *Gyrolithes* ichnospecies. Stratigraphy and Geological Correlation, 21: 72–84; https://doi.org/10.1134/S0869593813030088
- Uchman, A., Rattazzi, B., 2011. The new complex helical trace fossil Avetoichnus luisae igen. n. et isp. n. from the Cainozoic deep-sea sediments of the Alpine realm: a non-graphoglyptid mid-tier agrichnion. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 260: 319–330; https://doi.org/10.1127/0077-7749/2011/0140
- Vannucci, G., Piazza, M., Pastorino, P., Fravega, P., 1997. Le facies a coralli coloniali e rodoficee calcaree di alcune sezioni basali della Formazione di Molare (Oligocene del Bacino Terziario del Piemonte, Italie nord-occidentale. Atti della Società Toscana Scienze Naturali, Memorie, Seria A, 104: 13–40.
- Vliet, H.J., van, 2005. Een drietal opmerkelijke fossielen in 'Zwinstenen'. Afzettingen, 26: 39–41.
- Woodward, B.B., 1922. On *Dinocochlea ingens*, n. gen. et sp., a gigantic gastropod from the Wealden Beds near Hastings. Geological Magazine, 59: 242–248; https://doi.org/10.1017/S0016756800109665
- Yanev, S.N., Acenñlaza, F.G., Tenchov, Y.G., 2000. New data for the trace fossils in the Ordovician in western Bulgaria. Comptes rendus de l'Académie bulgare des Sciences, 53: 65–68.
- Yang, S., Song, Z., Liang, D., 1982. Middle Jurassic to Early Cretaceous flysch trace fossils from Ngari Region, Tibet. Acta Geologica Sinica, 4: 301–313.
- Yang, S., Zhang, J., Yang, M., 2004. Trace fossils of China. Beijing.