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Oriented clusters of the deep-sea trace fossil *Tubulichnium rectum* in the Eocene flysch of the Pindos foreland basin, western Greece

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The trace fossil *Tubulichnium rectum*, probably produced by a soft-bodied wormlike animal, normally consists of a single tube lined with organic-rich pellets, which were stored as a food resource during periods of scarcity (ethological category: sequestrichnia). On a large sandstone bedding surface in the Eocene flysch of western Greece, this trace fossil occurs in fan-shaped clusters oriented almost perpendicular to the direction of sand transport within the host bed. This unusual configuration, documented here for the first time, is attributed to specific palaeoenvironmental conditions in this part of the deep-sea fan depositional system, where the periodic supply of organic matter and the prevailing current direction remained stable over extended periods. The formation of these clusters reflects an adaptive response to changes in flow direction. The near-perpendicular alignment of the tubes to the current may have reduced ventilation, thereby delaying the oxygenation of the stored organic matter within the pellets.

Key words: ichnology, palaeoecology, sequestrichnia, deep-sea environment.

INTRODUCTION

Trace fossils showing preferred orientation likely reflect a rheotactic behaviour of their tracemakers. In aquatic sediments, such traces are typically aligned with the direction of current or the percolation pathways of pore water. Most examples are known from shallow-marine deposits, with records dating back to the Ediacaran (Uchman and Martyshyn, 2020) and continuing throughout the Phanerozoic (e.g., Salter, 1856; Seilacher, 1953, 1959; Hill, 1979; Mason, 1980; Hary et al., 1981; García-Ramos et al., 1984; Pickerill, 1995; Worsley and Mørk, 2001; Bromley et al., 2009; Pandey et al., 2014; Boyer and Mitchell, 2017; Uchman et al., 2016). Oriented recent traces (lebensspuren) are also known from shallow-marine and marginal marine settings, including burrows of decapod crustaceans (Hohenegger and Pervesler, 1985; Pervesler and Hohenegger, 2006), isopod burrows (Koyama, 1983), and surface traces produced by amphipods or isopods (Uchman and Pervesler, 2006). Preferred orientations have also been reported, though more rarely from hard rocky substrates, where bivalve borings may exhibit consistent alignment (Cachão et al., 2011).

Oriented trace fossils from deep-sea deposits are much rarer. Simpson (1970) reported *Cardioichnus* (his "n.f. cf. *Sagittichnus*") from the Eocene Hieroglyphic Beds in the Magura Nappe (Carpathians, Poland), which was oriented parallel to the main flow directions documented by sedimentary structures. From the Aberystwyth Grits (Lower Silurian, Wales), Crimes and Crossley (1980) described *Paleodictyon* and *Squamodictyon* exhibiting elongated mesh structures, which are preferentially oriented parallel to flow on the soles of turbiditic sandstones. Uchman (1995) documented *Ophiomorpha rudis* (as *Ophiomorpha* isp.) from the Miocene turbidites of the Marnoso-arenacea Formation in the Apennines (Italy), also aligned with sediment transport directions. Additionally, Gaillard (1991) described the so-called "FC trace", oriented downslope on the modern muddy slope at depths of 1600–2000 m in the New Caledonia region of the SW Pacific.

In this paper, the trace fossil *Tubulichnium rectum* (Fischer-Ooster, 1858) described from a large bedding surface of a turbiditic sandstone in the Eocene deep-sea deposits of western Greece. Until now, this trace fossil has been known as an inclined, solitary tube lined with pellets, interpreted as a sequestrichnion – i.e. a burrow used for food storage (Uchman and Wetzel, 2017, 2024). However, the specimens described herein

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form fan-shaped, oriented clusters, a configuration not previously documented. This study describes and interprets this newly recognized arrangement, contributing to a deeper understanding of the palaeoecological significance of *T. rectum* in the deep-sea environment.

GEOLOGICAL SETTING

The study area is located in southwestern Greece (Fig. 1) and forms part of the Pindos foreland basin, which is bounded to the east by the Pindos Thrust and to the west by the Ionian Thrust. Minor thrusts, including the Gavrovo Thrust and the Internal and Middle Ionian thrusts, subdivide the basin into elongate, narrow sub-basins that trend roughly parallel to the basin axis in a NNW–SSE direction. The activity of the Pindos Thrust led to the formation of a foredeep basin during the Middle Eocene (IGSRG and IFP, 1966; Avramidis et al., 2002) within the pre-existing domains of the Gavrovo and Ionian zones (Underhill, 1985, 1989; Alexander et al., 1990; Botziolis et al., 2021). Subsequent internal thrusting during the Late Oligocene transformed the foreland in its northern part into a complex foreland basin (Avramidis et al., 2002). Later, during the early Pliocene (in the Zakynthos area; Zelilidis et al., 1998, 2023) or the Middle Miocene (in the Corfu, Paxoi, and Zakynthos areas; Maravelis et al., 2012; Bourli et al., 2022), it evolved into a piggyback basin.

From the Middle Eocene to the Early Miocene, the Pindos foredeep was infilled with submarine fan deposits (Fig. 2; Pavlopoulos, 1983; Alexander et al., 1990; Konstantopoulos and Zelilidis, 2012). In the study region, they the basin fill is >2350 m thick (Fig. 3A). The source of these deposits was located at the leading edge of the Pindos Thrust (Piper et al., 1978; Wilpshaar, 1995; Faupl et al., 1998; Avramidis et al., 2002; Konstantopoulos and Zelilidis, 2012). The evolution of the basin and its depositional environments was further influenced by strike-slip faults, which acted synchronously with the main thrust systems (Avramidis and Zelilidis, 2001; Konstantopoulos et al., 2013; Bourli et al., 2022; Botziolis et al., 2023). The accumulation of turbiditic sequences was ultimately driven by westwards-directed deformation within the external Hellenides.

The section studied (Charavgi 2) is located in the Tritea region of southern Achaia, in the Peloponnese. The Cenozoic sedimentary succession in this area is developed over the pre-existing Gavrovo Zone, bounded to the east by the Pindos Thrust and to the west by Gavrovo Thrust, near Skolis Mountain. The section studied represents part of the upper portion of submarine fan deposits and is primarily exposed in a small, abandoned roadside quarry (GPS coordinates: N37.98330°, E21.62302°), situated along the road connecting the villages of Charavgi and Roupakia, south-west of Patras (Fig. 1C). The bedding planes dip towards the W–NW at 40° (295°/40°). The measured section is 14 m thick (Fig. 3B) and comprises fine-grained, quartz-rich sandstones interbedded with greenish-

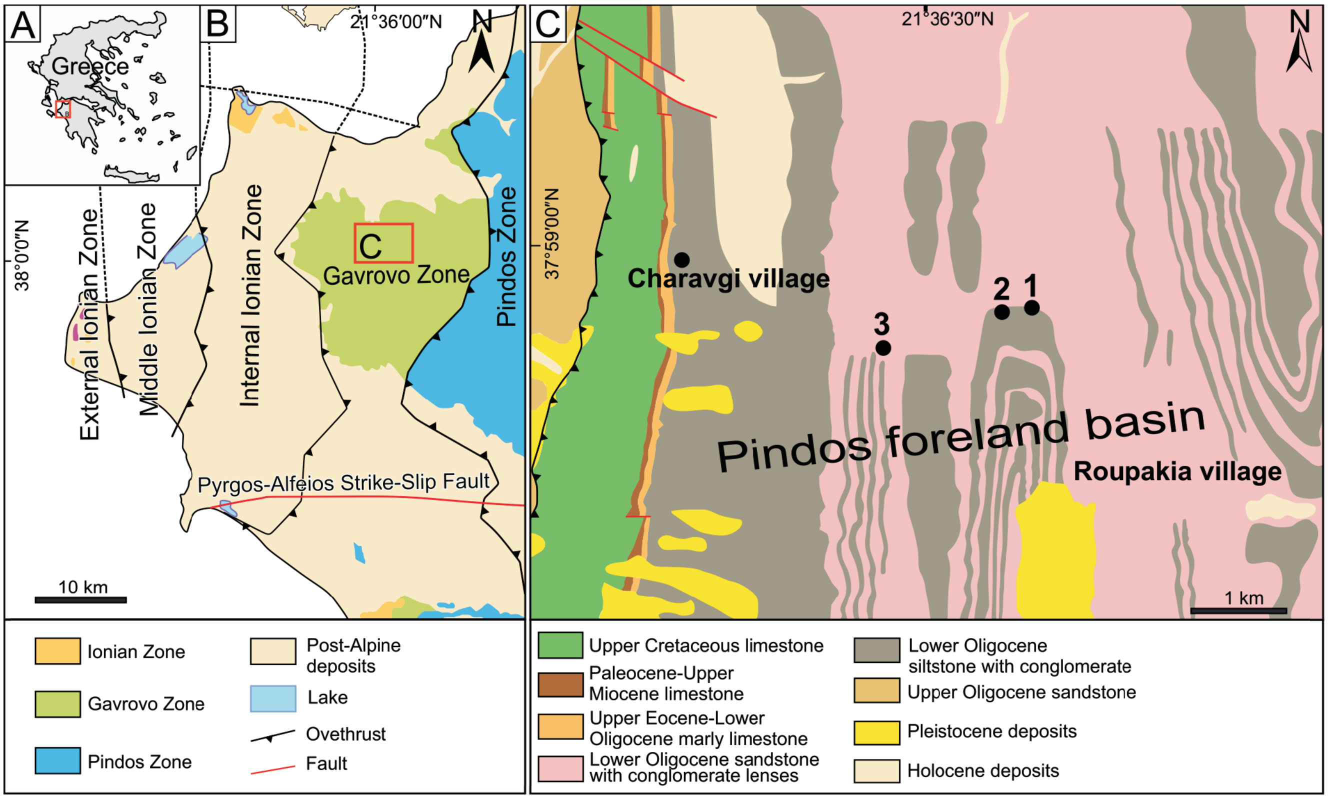

Fig. 1. Location maps

A – location of the study region on a contour map of Greece (Bourli et al., 2022); **B** – general sketch map of the western Peloponnese, with indication of the study area; **B** – study area with indication of the sections studied (1–3) (based on Mpornovas et al., 1981)

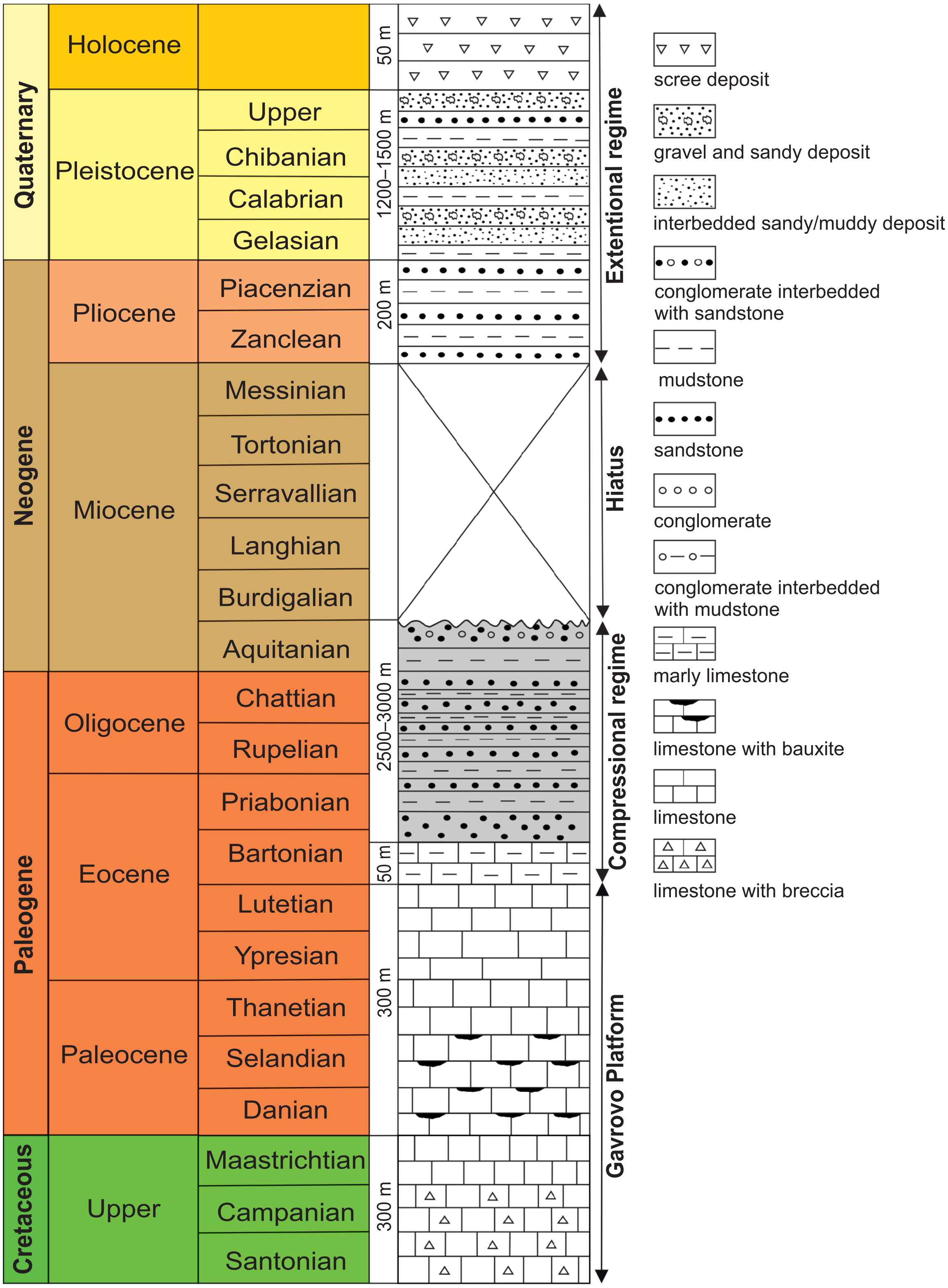

Fig. 2. General stratigraphic column of the Upper Cretaceous-Holocene deposits in the Gavrovo Zone

The deposits studied are shaded in grey; the general phases of geological evolution of the area are indicated (based on Koukouvelas, 2019)

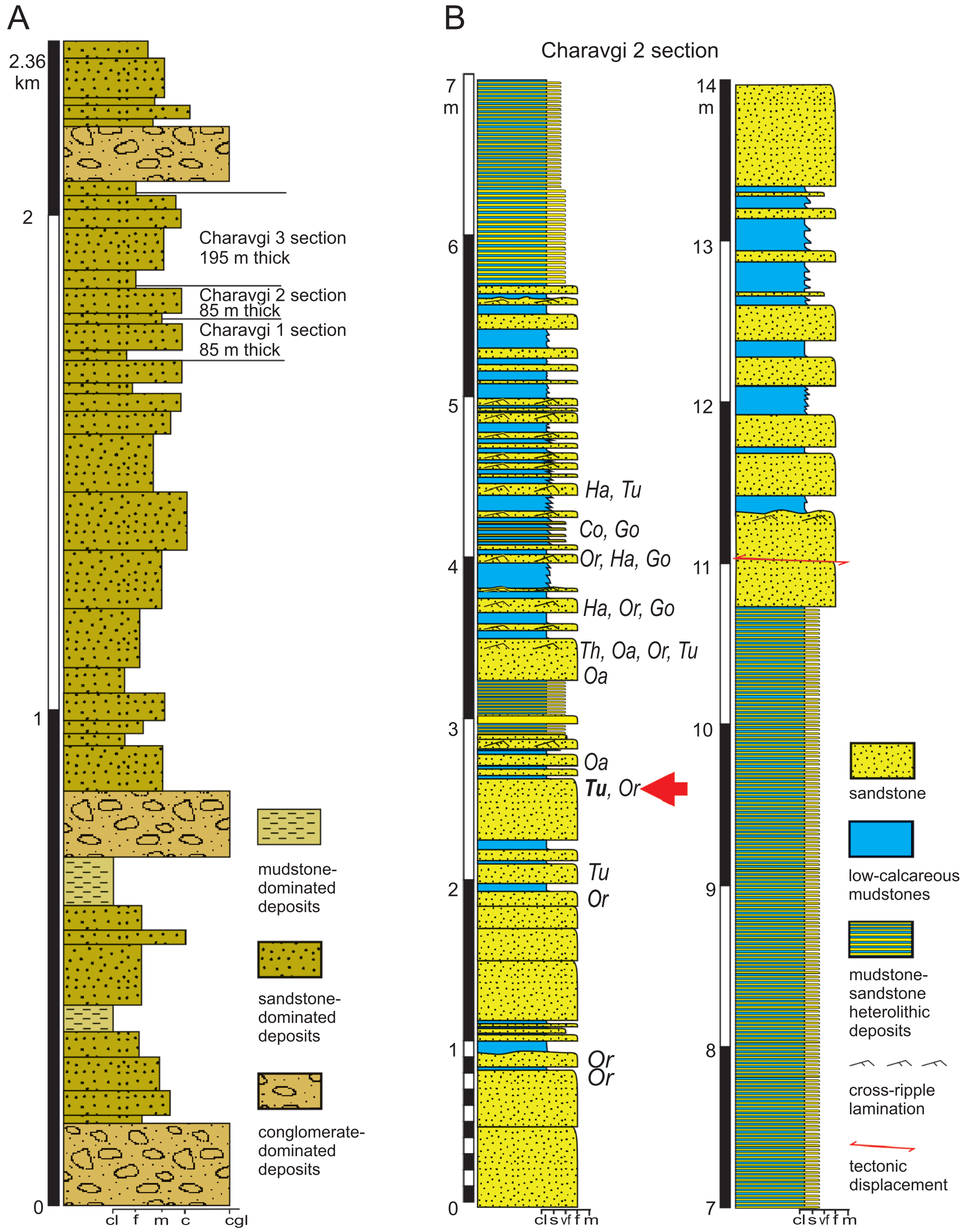

Fig. 3. Stratigraphic column of the Pindos Foreland Basin (A) and the Charavgi 2 section (B)

Red arrow points to the large surface bearing clusters of *Tubulichnium rectum*; *Co – Cosmorhaphe gracilis, Go – Gordia arcuata, Ha – Halopoa imbricata, Oa – Ophiomorpha annulata, Or – Ophiomorpha rudis, Th – Thalassinoides* cf. *suevicus, Tu – Tubulichnium rectum*

grey, poorly calcareous mudstones containing scattered, very fine muscovite flakes and carbonised plant debris.

The lower part of the section (0–5.7 m) is dominated by thick- to medium-bedded sandstones, which grade upwards into a succession of thin-bedded sandstones intercalated with mudstones or sandstone/siltstone-mudstone heterolithic deposits, with an increasing proportion of mudstones towards the top. Two thick sandstone beds in the lower part of the section are well-exposed over wide surfaces measuring ~70 m^2 (with *Tubulichnium*) and 50 m^2, respectively (Fig. 4). The upper surfaces of several beds display linguoid ripples, which also form ripple cross-lamination in the upper parts of the sandstone beds. These ripples indicate sediment transport towards the west (azimuth 240°). Groove and flute casts on the lower sur-

Fig. 4. The Charavgi 2 exposure

A metre-long stick is placed within the white ellipse on the upper bedding plane bearing the clusters of *Tubulichnium rectum*

faces of some beds record also currents towards the southwest. The middle part of the section (5.7–10.8 m) is composed of heterolithic deposits, dominated by thin and very thin sandstone/siltstone beds intercalated with mudstones. The upper part of the section (10.8–14 m) is characterized by thick- and medium-bedded sandstones with intercalations of finer-grained deposits.

TUBULICHNIUM AND ASSOCIATED TRACE FOSSILS

The trace fossils described were observed in the field, primarily on well-exposed bedding surfaces in the lower part of the section. Their positions are indicated in the stratigraphic column (Fig. 3B). The beds in the upper part of the section, consisting mainly of heterolithic deposits, are either heavily weathered or poorly exposed. Consequently, ichnological data from this part of the section are limited or unobtainable.

Tubulichnium rectum (Fischer-Ooster, 1858; Figs. 5 and 6) is present in several beds, but is only readily accessible on the main, extensive upper bedding surface in the quarry. It occurs either as individual tubes or as fan-shaped clusters. The individual tubes are straight to slightly curved and range from subhorizontal to inclined up to 20°. They are 4–18 mm wide, with a characteristic gradual widening in the middle segment and narrowing towards the tips that gives them a car silencer-like (pinching and swelling tube) appearance. The tubes are commonly open at one end, with elevated margins surrounding the aperture. Their interior is thickly lined with elongate, ovoid, muddy pellets (Fig. 5A), which can be ascribed to *Coprulus oblongus* Mayer, 1952 (see Knaust, 2020). These pellets measure up to 1.5 mm in length and up to 1 mm in width, are densely packed, and show variable orientations. The tubes arranged in clusters show the same morphology. Each cluster is composed of up to five tubes, which diverge from a single point at angles ranging from 15° to 30° and penetrate up to 7 cm into the bed. The clusters are fan-shaped, with angles of divergence reaching up to 65°. In some specimens, the lateral tubes diverge slightly outwards, giving the entire structure a palmate outline (Figs. 5C and 6A). On the large bedding surface, the density is ~10–15 tubes per square metre, though locally it may be about half that. The tubes have a consistent orientation, generally trending in a N–NE to S–SW direction (Fig. 7). *Tubulichnium rectum* is interpreted as belonging to the ethological category sequestrichnia, in which the tracemaker (possibly a polychaete worm) lined its burrow with pellets to serve as a food reserve during periods of scarcity (Uchman and Wetzel, 2017, 2024).

Cosmorhaphe gracilis Książkiewicz, 1977 (Fig. 8A) appears as a hypichnial ridge, ~1.5 mm wide, exhibiting two orders of meanders. The first-order meanders are closely spaced, while the second order may partially interlock. The higher parts of the second-order meanders widen to 6–8 mm, with amplitudes ranging from 10 to 15 mm. *Cosmorhaphe* is a graphoglyptid trace fossil, primarily known from Cretaceous to Neogene flysch deposits (Uchman, 1998).

Gordia arcuata Książkiewicz, 1977 (Fig. 8B) is a hypichnial ridge, 1.0–1.2 mm wide, forming complete or incomplete loops. *Gordia* is considered to be a grazing trace produced by small invertebrates and is known from both low-energy marine (e.g., Gibert et al., 2000) and non-marine deposits (e.g., Buatois and Mángano, 1993; Uchman et al., 2009).

Halopoa imbricata Torell, 1870 (Fig. 8A, C) is observed as straight to slightly curved, mostly simple, and occasionally branched ridges, ~10 mm wide, marked by longitudinal, discontinuous, uneven striae and wrinkles. This trace fossil is common in the Eocene turbiditic deposits of the Pindos foreland basin in the Peloponnese. It was produced by deposit feeders (probably priapulids) in the sandy portions of beds, with the striae and wrinkles resulting from tension during the intrusion of the tracemaker into the sediment (Uchman, 1998).

Helminthoidichnites isp. (Fig. 8C) is a hypichnial, semicylindrical, smooth, winding ridge, rarely forming loops, 0.8–1.0 mm wide. *Helminthoidichnites* is interpreted as a locomotion and possibly feeding trace; it occurs in both marine and non-marine environments (e.g., Fillion and Pickerill, 1990; Uchman, 1995, 1998; Wetzel et al., 2007). It may show transitional forms to *Gordia* (Hofmann and Patel, 1989).

Thalassinoides cf. *suevicus* (Rieth, 1932; Figs. 6A, B and 8D) is mainly found on the second large bedding surface of the adja-

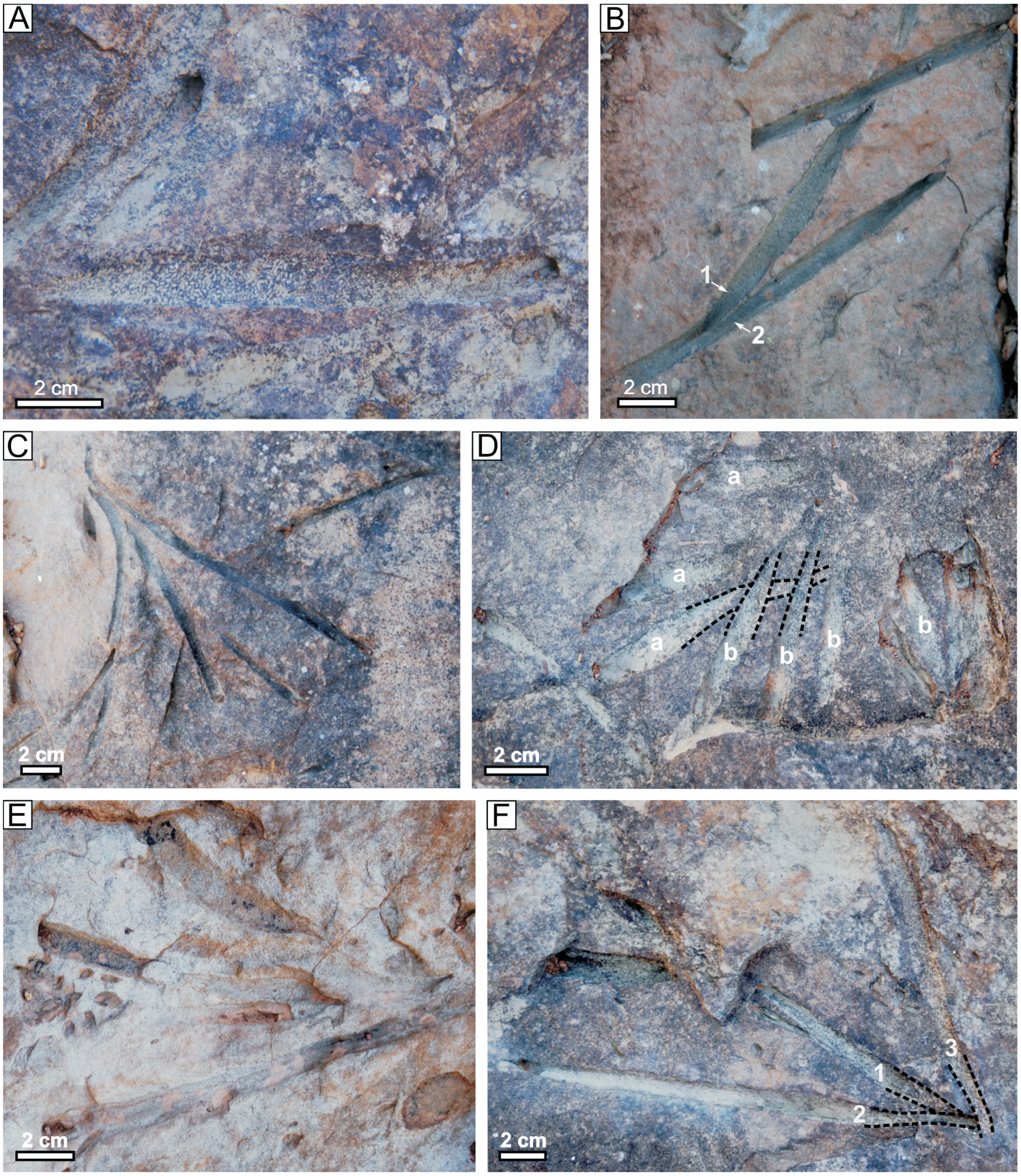

Fig. 5. *Tubulichnium rectum* on the large, upper bedding surface

A – tube lined with pellets; **B** – a single tube alongside a cluster composed of two successive tubes (tube 2 overlaps tube 1); **C** – cluster composed of several tubes; **D** – two clusters of tubes (cluster a is overlapped by cluster b); **E** – another cluster composed of several tubes; **F** – cluster composed of three successive tubes (tube 2 overlaps tube 1 and is overlapped by tube 3)

cent bed. It is an epichnial, straight to winding, cylindrical, branched, sand-filled burrow, 10–25 mm wide. The branches are Y-shaped, and the branching points are enlarged. These features resemble *T. suevicus* (Rieth, 1932), although the distance between branching points appears greater than in the typical examples of this ichnospecies. *Thalassinoides* is a feeding and dwelling burrow, primarily produced by decapod crustaceans, typically in shallow marine settings (e.g., Schlirf, 2000), although it may also occur in deep-sea deposits (e.g., Uchman, 1998).

DISCUSSION

Studies of the Pindos foreland basin (e.g., Avramidis et al., 2002; Botziolis et al., 2022, 2023), along with sedimentary features, basin fill characteristics, and trace fossils from the section studied, point to a deep-sea fan depositional system. In particular, graphoglyptid trace fossils such as *Cosmorhaphe,* which are also found in nearby exposures of the same succession

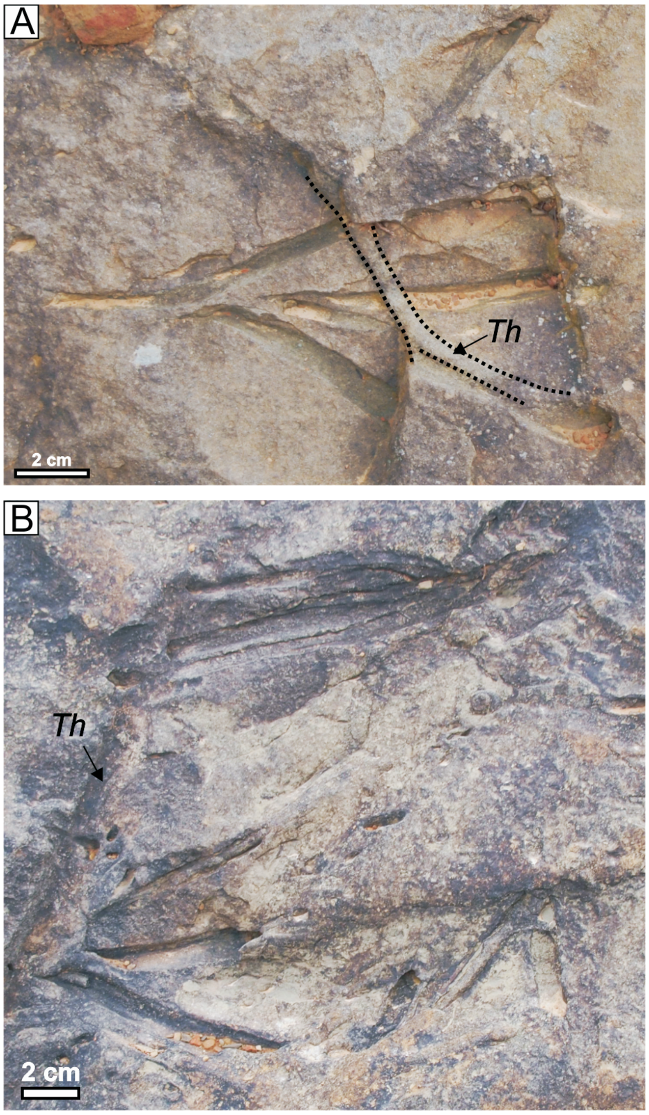

Fig. 6. *Tubulichnium rectum* and *Thalassinoides* cf. *suevicus* (*Th*) on the large, upper bedding surface

(e.g., *Paleodictyon, Helminthorhaphe, Spirorhaphe* in the Charavgi 3 section; for the location, see Figs. 1 and 3) are characteristic of the Nereites ichnofacies (Uchman and Wetzel, 2012), further supporting interpretation of a deep-sea environment. In the section Charavgi 1, *Ophiomorpha rudis, Tubulichnium rectum,* and *Halopoa imbricata* have been identified. The lower part of the Charavgi 2 section, where the large bedding surface with *Tubulichnium incertum* is located, displays a thinning- and fining-upwards trend within a broader thickening- and coarsening-upwards interval of the sedimentary succession of the Pindos foreland basin in the study area (Fig. 3A). This arrangement of beds in the part of the Charavgi 2 section discussed suggests a local channel-fill deposit developed on a depositional lobe within a deep-sea fan system.

The most intriguing aspect is the occurrence of *Tubulichnium rectum* in clusters and their orientation. This is unusual, as the orientation is almost perpendicular to the inferred direction of sediment transport. *T. rectum* is interpreted as a sequestrichnion, produced by a tracemaker that stored its own faecal pellets along the burrow walls during periods of organic matter abundance on the sea floor, subsequently using them as a food resource during times of scarcity. Feeding was likely mediated by microbial activity (Uchman and Wetzel, 2017, 2024).

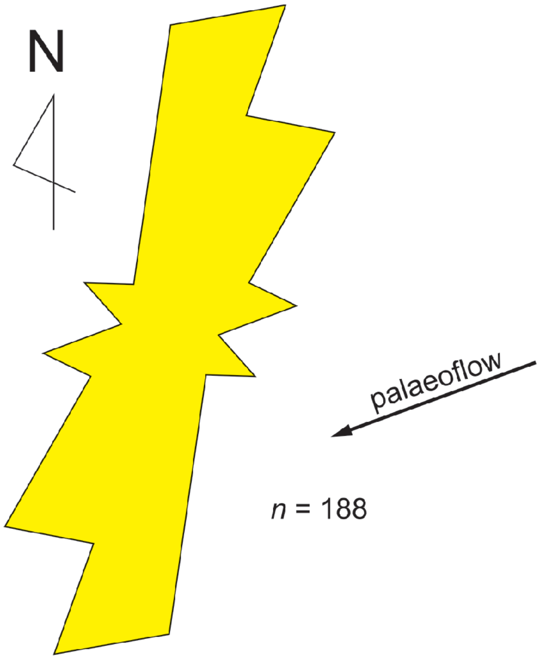

Fig. 7. Rose diagram showing the orientation of *Tubulichnium rectum* galleries on the large, upper bedding surface, with an indication of the direction of transport based on linguoid ripples

Until now, *Tubulichnium rectum* has mostly been reported as solitary burrows, primarily from Upper Cretaceous to Paleogene turbiditic deposits (Uchman and Wetzel, 2017). The occurrence in the form of clusters, as described in this paper, is exceptional. It is possible that such occurrences are not really rare, but that previous observations, commonly restricted to small bedding surfaces, have simply failed to capture these clusters. Alternatively, the clusters may represent three-dimensional structures that manifest on exposed bedding planes only as a single visible burrow, thereby obscuring their true complexity.

In some clusters, the tubes overlap, with older tubes being partially truncated by younger ones (Fig. 5B, F). This suggests that the tubes were produced successively, and more likely by a single tracemaker rather than different individuals. If so, the clusters would have developed over a relatively extended period. The trace makers appear to have dominated the sea floor habitat, at least within the deeper tier as shown by the burrows penetrating up to 7 cm into the beds, and the observed absence of other trace fossils. In rare cases, the clusters are cross-cut by sand-filled *Thalassinoides* (Fig. 6A), likely originating from a younger colonisation surface at the top of one of the overlying sandstone beds. This pattern suggests that an older tube was abandoned, and a new one produced from approximately the same proximal position, diverging distally in a slightly different direction. Some clusters overlap such that tubes of one cluster crosscut those of another (Fig. 6D), indicating that the cut cluster had already been abandoned. If so, colonization by the tracemaker occurred in multiple phases.

This prolonged colonisation of the sea floor suggests that the supply of organic matter for sequestration was not incidental but recurrent and predictable. It is plausible that each tube in a

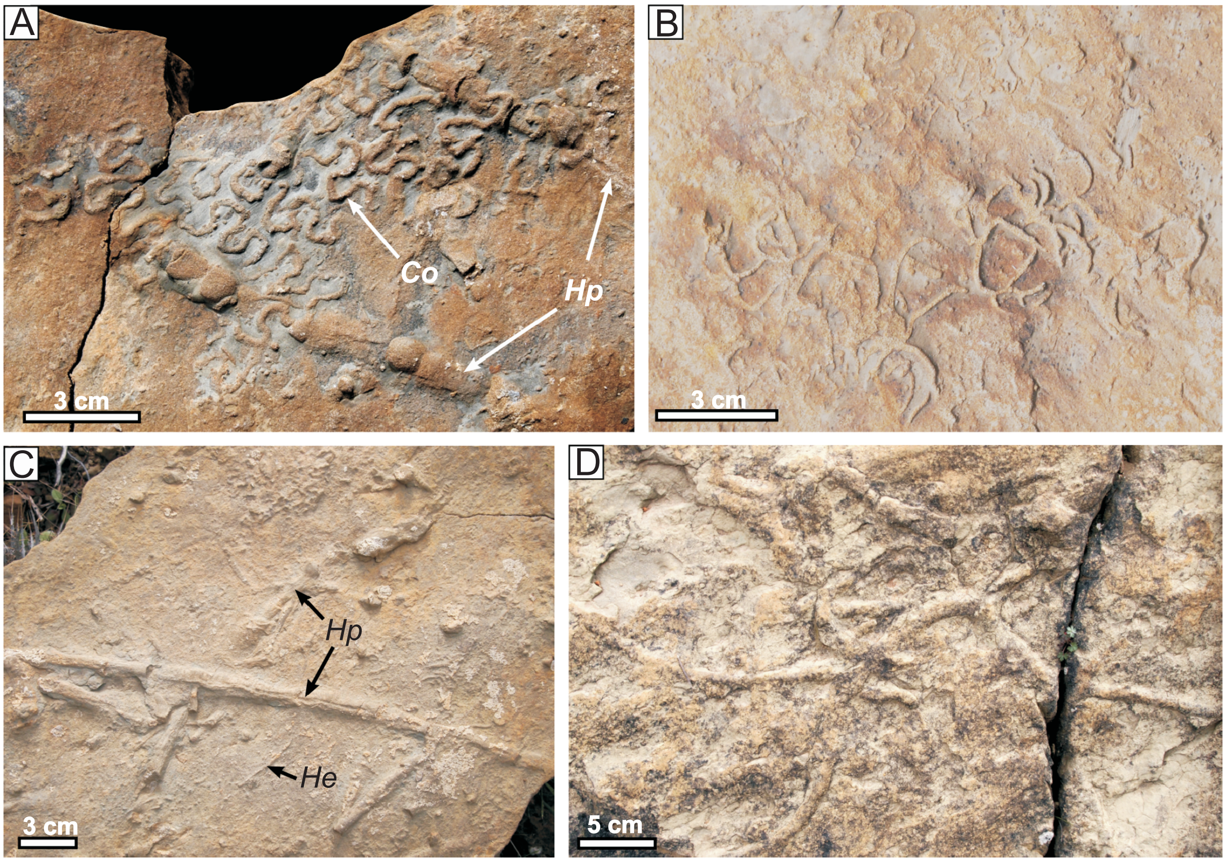

Fig. 8. Associated trace fossils

A – *Cosmorhaphe gracilis* (*Co*) and *Halopoa imbricata* (*Ha*); **B** – *Gordia arcuata*; **C** – *Halopoa imbricata* (*Ha*) and *Helminthoidichnites* isp. (*He*); **D** – *Thalassinoides* cf. *suevicus*

cluster represents a response to one such episode of organic matter availability. However, this raises the question: Why were new tubes created, rather than reusing the existing one? A possible explanation is that the clustered arrangement was a behavioural adaptation to fluctuating current directions. Alternatively, though less likely, extended periods between food supply events may have compelled the tracemaker to construct multiple storages – that is, tubes lined with pellets for future feeding. The current responsible for depositing the sand was not necessarily the same as the one influencing burrow orientation, as the apertures of the tubes were probably situated on the surface of the overlying mud, and the burrows may have been in use long after the sand was deposited. Unfortunately, the mudstone is heavily weathered, hindering reliable analysis of its sedimentary and bioturbation structures. If the burrows were aligned with a current roughly perpendicular to the sand-transporting current, the clusters would be expected to diverge consistently in one direction. However, examples of clusters diverging in opposite directions (Fig. 6B) suggest that the burrows were more likely oriented relative to currents roughly parallel to the depositional current. This raises another question: Why, then, are the clusters generally oriented perpendicular to the inferred current direction?

Animals typically align their burrows with prevailing currents to enhance ventilation, particularly passive ventilation in burrows with two apertures (e.g., Vogel, 1978; Pervesler and Hohenegger, 2006). Ventilation may occur not only through the burrow apertures but also through sediment pore spaces (Meysman et al., 2005). In the case of *Tubulichnium* the opposite strategy may have been beneficial. Degradation of organic matter within the faecal pellets would proceed more slowly under low-oxygen conditions, thereby preserving the nutritional value of the pellets for a longer period. If this interpretation is correct, the orientation of the clusters may reflect a behavioural adaptation aimed at reducing ventilation and thus enhancing food conservation. Nevertheless, the cluster orientations may record behavioural adjustment by the tracemaker to ambient current directions, and the orientation of individual tubes may reflect an optimization in response to current deviations.

A working hypothesis to explain the occurrence of (1) clustered and consistently oriented *Tubulichnium versus* (2) isolated and randomly oriented forms could be as follows: the former suggests long-term, predictable episodes of organic matter supply, separated by extended intervals, in an environment influenced by a stable, oxygen-rich bottom current. The latter may indicate more frequent but less predictable episodes of organic matter availability, occurring in the absence of stable bottom currents or in settings where the currents were oxygen-depleted and/or variable in direction.

CONCLUSIONS

The trace fossil *Tubulichnium rectum*, occurring in fan-shaped clusters oriented almost perpendicular to the direction of sediment transport, is interpreted as an adaptation by its tracemaker to facilitate the prolonged sequestration of food to be used during periods of scarcity. Such behaviour could have minimised the oxidation of organic matter stored within the pelleted linings of the tubes. This distinctive occurrence of *T. rectum* suggests long intervals between episodes of organic matter supply and a stable, oxygenated bottom current of predictable direction.

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