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ICHNOTAXONOMY AND ETHOLOGY OF BORINGS IN SHALLOW-MARINE BENTHIC FORAMINIFERS FROM THE MAASTRICHTIAN AND EOCENE OF NORTHWESTERN AND SOUTHWESTERN TURKEY

JAN KRESTEN NIELSEN[1] & MUHITTIN GÖRMÜŞ[2]

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Abstract. Larger benthic foraminiferal tests from the Maastrichtian and Eocene of western Turkey contain a large variety of borings. Two ichnospecies are defined. *Maeandropolydora osmaneliensis* isp. nov. in tests of *Orbitoides* is distinguished by a tube, winding sinuously in an irregular manner. This boring was formed by a foraging parasite or scavenger, where the tracemaker specifically exploited certain parts of its substrate. *Trypanites helicus* isp. nov. in tests of *Nummulites* is characterized by its tube coiled into a spiral. The boring is interpreted as a dwelling trace. As the boring may be considered to have both idiomorphic and stenomorphic features, it represents an ethological and taxonomic dilemma. To avoid inherent subjectivity within taxonomic classifications, we suggest the exclusion of ethological interpretations from diagnoses. The occurrence of borings may affect the preservational potential of the foraminiferal tests, and thus on the outcome of palaeoenvironmental analyses.

Riassunto. I gusci di grandi foraminiferi bentonici del Maastrichtiano ed Eocene della Turchia contengono una grande varietà di perforazioni. Vengono definite due ichnospecie. *Maeandropolydora osmaneliensis* isp. nov. entro i gusci di *Orbitoides* è distinta da un tubo, che serpeggia in modo irregolare. Questa perforazione è stata prodotta da un parassita o da uno scavatore, che sfruttava certe parti del suo substrato in modo molto specifico. *Trypanites helicus* isp. nov. entro gusci di *Nummulites* é caratterizzato da un tubo avvolto a spirale. La perforazione è interpretata come una traccia di abitazione. Poiché le perforazioni possono essere considerate caratteri sia idiomorfici che stenomorfici, esse rappresentano un dilemma etologico e tassonomico. Onde evitare soggettività nella classificazione noi suggeriamo di escludere interpretazioni etologiche dalla diagnosi. La presenza di perforazioni può diminuire il potenziale di conservazione dei gusci di foraminiferi e quindi le deduzioni che possono derivare dalle analisi paleoambientali.

Introduction

Borings may be potentially of great significance in palaeoenvironmental analyses (Perkins & Halsey 1971; Golubic et al. 1975). Previous studies have shown that bioerosional structures are common in foraminiferal tests and may be interpreted as praedichnia (predational traces), attachment scars and possibly evidence of commensalism, mutualism, parasitism or scavenging (e.g., Livan 1937; Sliter 1971; Matteucci 1978; Baumfalk & Nijholt 1984; Nielsen & Nielsen 2001; Nielsen 2002). Nematodes, for example, may form holes by chemical means into foraminifers to prey on them (Sliter 1971; Bromley 1994).

Borings produced by pascichnial behaviour appear not to have been previously recognized in foraminiferal substrates. Pascichnia include trackways and locomotion traces following a meandering or spiral course, indicating that the tracemakers exploited certain parts of the substrate for food (Bromley 1996). It is thus of great interest that pascichnial borings occur in tests of larger benthic foraminifers from the Maastrichtian of northwestern Turkey (Fig. 1). Also, domichnial borings occur in foraminifers from the Eocene of southwestern Turkey. The borings are formally described in the present paper, and new ichnotaxa are defined. The paper also emphasizes ethology and biological affinities to enhance our knowledge of foraminifers as a nutrient source.

Geological setting

New ichnospecies from shallow-marine clastics and carbonates are exposed at the towns Osmaneli (Bilecik province) and Dinar (Afyon province) (Fig. 1). The Upper Maastrichtian succession at Osmaneli consists of fine to medium grained sandstones (Fig. 2). It includes a me-

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[1] Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark. E-mail: bioerosion@yahoo.dk
[2] SDÜ Mühendislik-Mimarlık Fakültesi, Jeoloji Mühendisliği Bölümü, Çünür-Isparta, Turkey. E-mail: muhittin@mmf.sdu.edu.tr

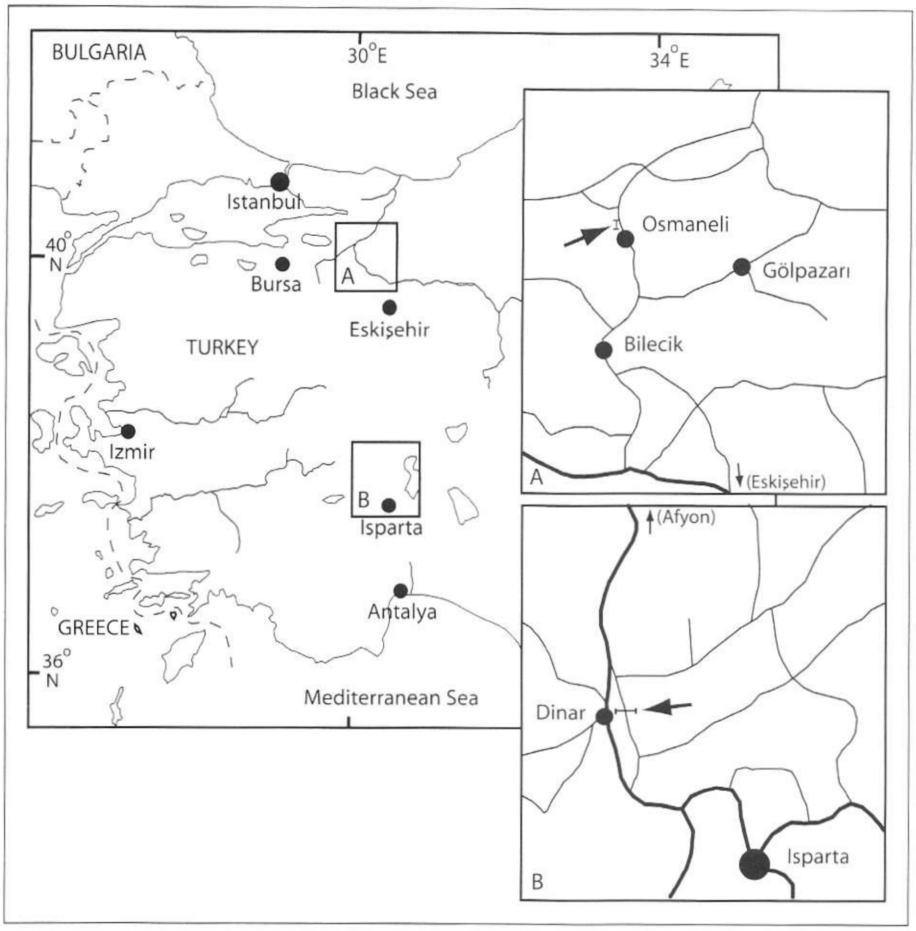


Fig. 1 - Location of the Osmaneli (A) and Dinar (B) type sections (arrows) in western Turkey.

dium bedded, rhythmic succession of barren sandstones and *Orbitoides* bearing sandstones (Fig. 3). The beds are 10 to 60 cm in thickness and green to yellowish coloured. Sandstones from the measured section belong to the upper part of the Taraklı Formation of Gölpazarı Group (Eroskay 1965; Altınlı 1973a, b, 1974; Saner 1978a, b; Görmüş 1996-1997). Bargu (1982) named the formation as Nushetiye Formation. The Gölpazarı Group is underlain by the Campanian-Maastrichtian flysch sediments of Vezirhan Formation. The Palaeogene Selvipınar limestone or the red-coloured clastics of Kızılçay Formation overlie conformably the Maastrichtian sediments (Saner 1978a, b; Yılmaz 1992). Total thickness of the Taraklı formation is between 100 and 300 m (Saner 1978a, b). According to associated faunas (Görmüş 1996-1997), the formation is Maastrichtian in age. The foraminifers examined during the course of the present study were collected from sandy beds of the Taraklı Formation. The macrofauna, which mainly consists of *Exogyra*, *Gryphea*, *Ostrea*, *Pecten* and *Turritella* species, indicates along with the lithology shallow-marine conditions in this part of the Maastrichtian sea.

Eocene sediments at Dinar comprise various carbonates and clastics (Fig. 4). Nummulitic limestones are medium to thick in bedding, i.e., 1 to 20 m in thickness, and are yellowish to grey in colour. It is known as the Garipçe Formation (Görmüş & Yeşilot 1999). Isparta flysch sediments and İncesu conglomerates have lateral and vertical facies changes with the formation (Görmüş & Özkul 1995). Görmüş & Yeşilot (1999) also mention that some researchers accept ophiolites, carbonates

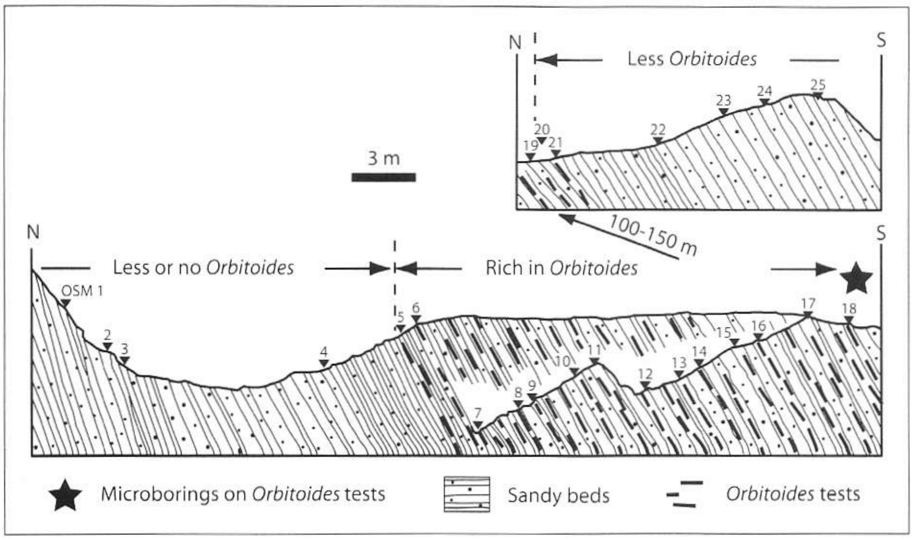


Fig. 2 - Geological cross-section of measured sediments in the Osmaneli area, showing that the amount of microborings increases towards the Cretaceous-Tertiary boundary.

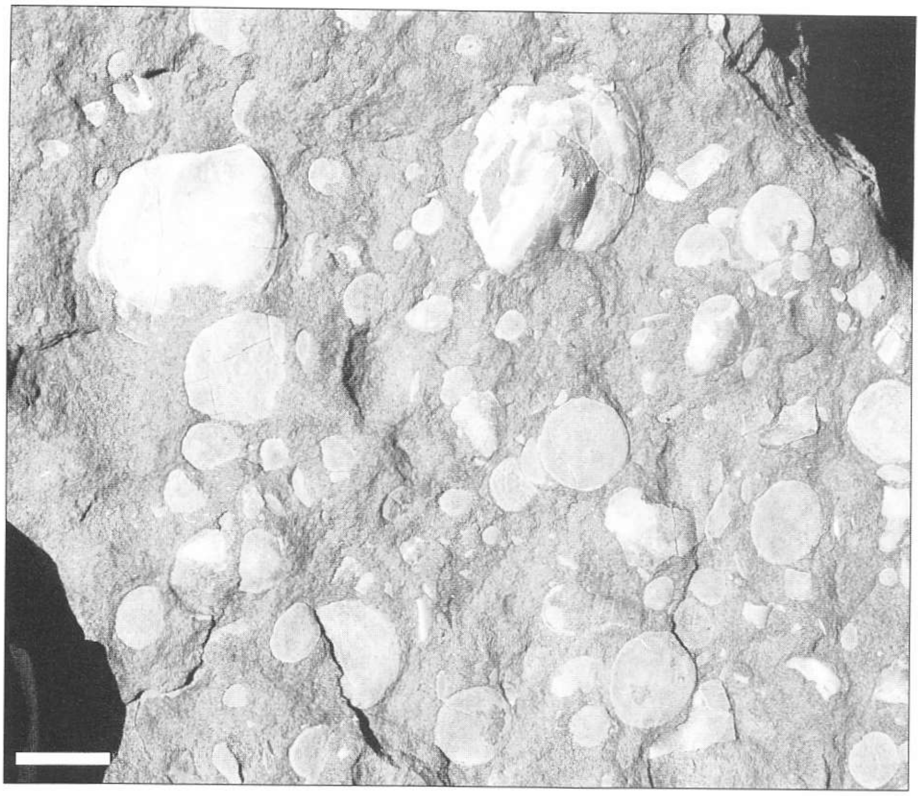


Fig. 3 - Field photograph of *Exogyra* sp. and lenticular *Orbitoides* tests oriented parallel to bedding plane, Osmaneli section. Scale bar 1 cm.

and Eocene sediments as the Lycien nappe system derived from the southern part of the region. The succession of the Garipçe Formation around Dinar Üçler mah. and Suçıkan localities is rich in *Nummulites* and *Assilina* forms. Total thickness of the formation is 60-70 m. The faunal contents indicate a Bartonian age (Görmüş & Yeşilot 1999). The foraminifers investigated in the present study were collected from nummulitic limestones of the Garipçe Formation. Shallow-marine settings are mainly indicated by the foraminifers themselves. *Nummulites* is often dominant in shallow-marine sediments of Middle Eocene (e.g., Matteucci 1978).

Material and methods

Bulk samples were collected from stratigraphical levels rich in foraminiferal tests, mainly Maastrichtian *Orbitoides* spp. and Eocene *Nummulites* spp. The Maastrichtian material consists of 25 samples each with about 40-50 specimens. The percentage of bioeroded specimens (70) in the samples is five. The Eocene material includes 17 samples, each containing about 80 specimens. Bioerosional structures are present in less than two percent (20). The outer surface of the tests was examined to identify possible evidence of bioerosion. Subsequently, the tests were subjected to gradual abrasion using abrasive powder to reveal any borings in the layers of lateral chamberlets and the median, equatorial chamberlet layer. Finally, thin sections were prepared of the remaining slices of tests. The present study also includes the thin sections examined by Görmüş & Sagular (1998).

Type material is housed in the collection of the Geological Department, Süleyman Demirel University, Isparta, with the prefixes DIN and OSM. Additional paratypes are deposited in the Geological Museum, University of Copenhagen, with the prefix MGUH.

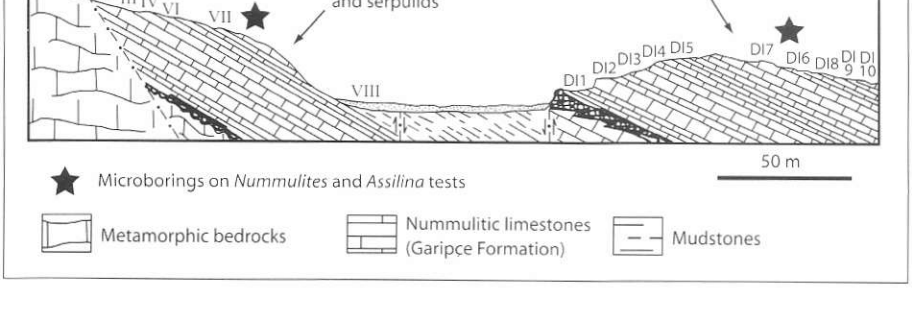
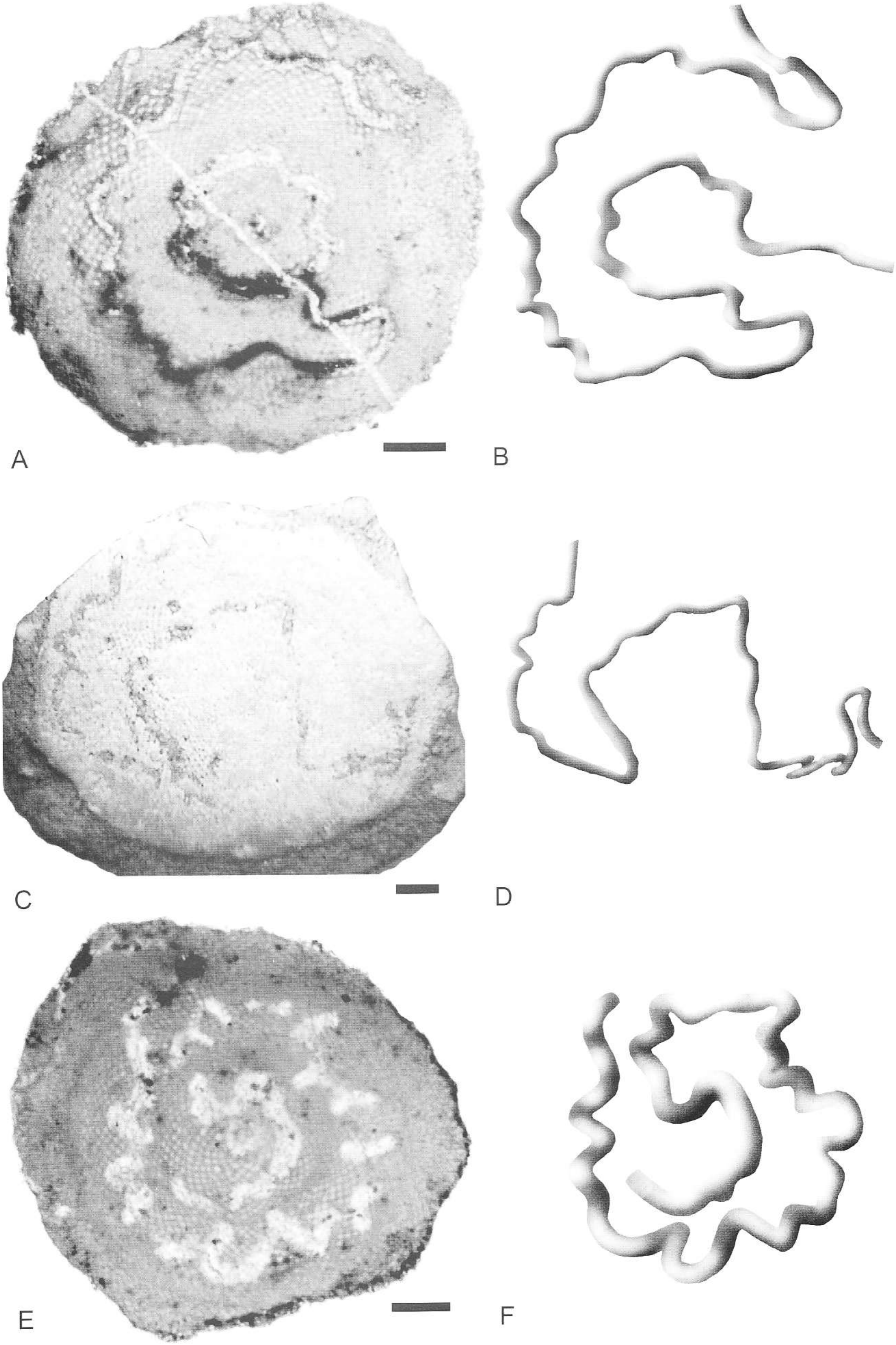


Fig. 4 - Geological cross-section of measured sediments in the Suçıkan area (Dinar, Afyon) showing levels with microborings.


A
B
C
D
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F

Systematic ichnology

The defined ichnotaxa are distinguished by three main ichnotaxobases, i.e. the outline of the margin, the curvature of the borings in three-dimensions and possible occurrence of ornamentation. These ichnotaxobases have been recognized in numerous studies (e.g., Bromley 1981; Kelly & Bromley 1984; Nielsen & Nielsen 2001). The ichnotaxa are compared to previously described trace fossils that are placed in synonymy lists.

Maeandropolydora Voigt, 1965

Maeandropolydora osmaneliensis isp. nov.

(Figs 5, 6)

1998 Undulating shaped tunnels - Görmüş & Sagular, p. 61, pl. 1, fig. 1-3, pl. 2, fig. 3-4.

Derivation of name. "*osmaneliensis*", refers to the town Osmaneli (Bilecik) in the Marmara Region, NW Turkey.

Type locality and age. Section about 1.5 km northwest of Osmaneli, Marmara Region: the Tarakli Formation of the Gölpazarı Group, Maastrichtian.

Holotype. OSM18.30, thin section 16 (Fig. 5A, B), a specimen in the test of a benthic foraminifer, *Orbitoides* sp. (sample OSM18.30).

Paratypes. OSM18.101 (Fig. 5C, D), sample OSM18; OSM19.30, thin section 19 (Fig. 5E, F), sample OSM19.30; MGUH 26838 (Fig. 6A), sample OSM19-stone; MGUH 26839 (Fig. 6B), sample OSM19-stone. All paratypes are situated in tests of *Orbitoides* spp.

Occurrence. Maastrichtian of northwestern Turkey.

Diagnosis. Tubular boring having a simple cylindrical and unbranched form, situated within skeletal substrate. The tube is sinuous and largely positioned in the same plane of the substrate. Both ends of the tube are connected to the substrate surface.

Description. The tube may reach more than 29 mm in length. The tube ranges in diameter from 0.2 to 0.5 mm (N = 20) and has an average diameter of about 0.3 mm. Individual tubes have a uniform diameter, and the margin is smooth. The tube winds irregularly in three dimensions and in a single bend may turn up to 330 degrees. The tube mainly occurs in the median plane of *Orbitoides* and is inclined to pass through close to the centre of the substrate, i.e., the embryonic chamber of *Orbitoides*. Both ends of the tube are oriented obliquely or perpendicularly to the substrate surface. The ends are only seen to be connected to the edge of *Orbitoides* tests, within the median plane. The tube may contain clasts, micrite and calcitic cement. The substrate is up to 10 mm in size.

Remarks. The boring bears some resemblance to previously defined ichnotaxa. Cyanobacteria and fungi have been implicated in the bioerosion of calcareous substrates. The cylindrical microborings of cyanobacteria and fungi, however, are significantly less winding and smaller than our boring. The former are usually microns or tenth of microns in diameter (Gatrall & Golubic 1970; Schmidt 1990; Glaub & Bundschuh 1997; Vogel et al. 1999; Vogel et al. 2000).

The morphology also differs from known larger-scale borings. For example, *Pseudopolydorites radwanskii* Głazek et al., 1971 is distinguished by its U-shape and closely spaced straight limbs. The latter may be slightly curved near the openings. Our boring also differs from *Talpina* ispp., consisting of a regular pattern of side branches and opening at regular intervals (Voigt 1975; Bromley 1994).

The boring resembles specimens of *Maeandropolydora sulcans* Voigt, 1965, which is considered as an intermediate stage within the developmental sequence from *Trypanites solitarius* (Hagenow, 1840) to *M. decipiens* Voigt, 1965 (Bromley & D'Alessandro 1983, 1987). *Maeandropolydora sulcans* is the only ichnospecies of *Maeandropolydora* lacking pouches or a vane. This ichnospecies is characterized by tubular borings grading from winding U-shaped borings and branched U-shaped borings to complex networks. *M. sulcans* tends to have gentle curves (see e.g., Bromley & D'Alessandro 1987; Taddei Ruggiero & Annunziata 2002). Our borings, however, are significantly more winding, smaller in size and do not show ramification. Thus, we consider the borings to represent a new ichnotaxon. They are tentatively placed in *Maeandropolydora* on the basis of their close similarity in morphology to *M. sulcans*.

Trypanites Mägdefrau, 1932

Trypanites helicus isp. nov.

(Fig. 7)

Derivation of name. "*helicus*" (Latin *helica*), whorl, refers to its spiral shape of the trace fossil.

Type locality and age. Section in the Şeytan Tepesi (Devil's Hill) situated at the northeastern periphery of the town Dinar, Afyon province, SW Turkey: the Garipçe Formation, Eocene.

Holotype. DIN Dinar7, thin section 28 (Fig. 7), sample DI 7, a specimen in the test of a benthic foraminifer, *Nummulites* sp.

Paratypes. DIN Dinar I.11, thin section 25, sample DI 11; MGUH 26840, sample DI 2. All paratypes are situated in tests of *Nummulites* sp.

Occurrence. Bartonian (Eocene) of southwestern Turkey.

Diagnosis. *Trypanites* having a simple tubular form, coiled in a spiral shape and largely positioned within the same plane of the substrate.

Description. A distinctive feature is the regularly coiled outline, i.e. the axis of the boring is shaped as a planispiral. The number of whorls is between 1.5 and 2. The boring is about 0.2 mm in diameter and 13 mm in length. The filling consists of calcitic spar cement. Lining and ornament have not been observed.

Fig. 5 - *Maeandropolydora osmaneliensis* igen. et isp. nov., drawings show three-dimensional reconstructions of borings. A-B, OSM18.30, thin section 16, holotype. C-D, OSM18.101, paratype. E-F, OSM19.30, thin section 19, paratype. Scale bars 0.5 mm.

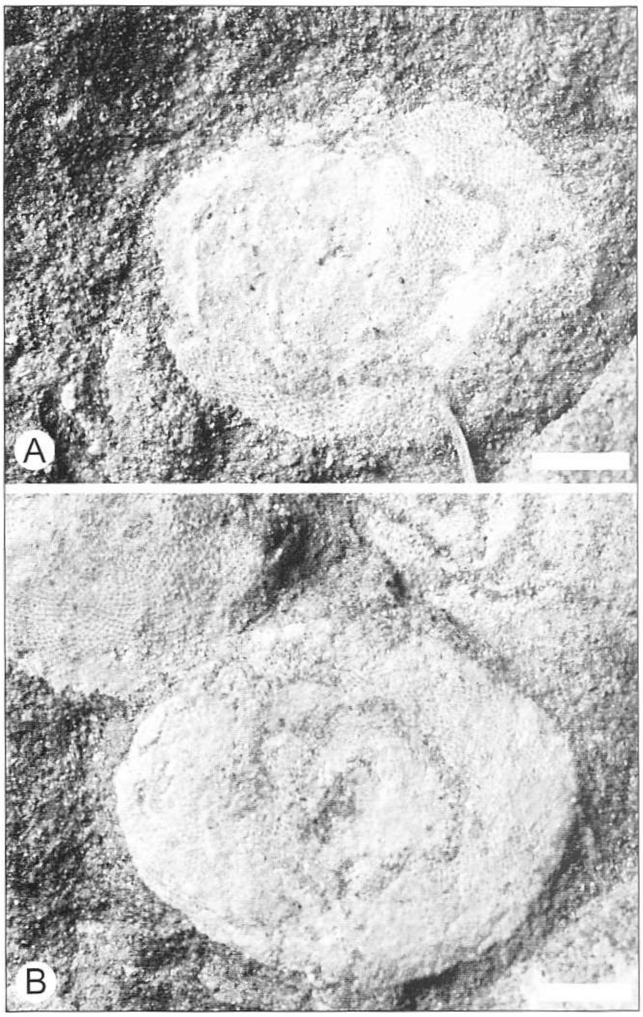

Fig. 6 - *Maeandropolydora osmaneliensis* igen. et isp. nov. A, MGUH 26838, sample OSM19-stone, paratype. B, MGUH 26839, sample OSM19-stone, paratype. Scale bars 2 mm.

Remarks. Bromley and D'Alessandro (1987, p. 403) emended the diagnosis of *Trypanites* as containing "single-entrance, cylindrical or sub-cylindrical, unbranched borings in lithic substrates, having circular cross-section throughout length. The axes of the borings may be straight, curved or irregular". Following this diagnosis, the boring is ascribed here to *Trypanites* Mägdefrau, 1932. The boring resembles *T. solitarius* (Hagenow, 1840) and *T. weisei* Mägdefrau, 1932. The taxonomic status of these two ichnotaxa is unsure for the reason that intermediate specimens exist. Both ichnotaxa are characterized by a uniform diameter throughout their length. They have been distinguished by their attitudes in relation to the surface of the substrate. Another feature used is the course of the boring. However, these features appear to be unsuitable ichnotaxobases. *Trypanites weisei* and *T. solitarius* were based on idiomorphic and stenomorphic borings, respectively (Bromley & D'Alessandro 1987). *Trypanites fosteryeomani*, which was defined exclusively on size by Cole & Palmer (1999), was based on idiomorphic borings similar to *T. weisei*. None of these ichnotaxa has shown to have a spiral shape. Intermediate specimens have not been recorded (e.g., Bromley & D'Alessandro 1987; Cole & Palmer 1999). In the present study, however, the boring clearly has a regular spiral shape within *Nummulites*. Although the tracemaker had the ability of bioeroding, no other configurations of *Trypanites* are seen in *Nummulites* or other substrates.

The *Nummulites* tests range up to 5 cm in diameter and may be encrusted by bryozoans and serpulids; however, *T. helicus* isp. nov. only occurs in tests smaller than 2 cm. This indicates that large substrates were available to colonization, but they did not become bioeroded by *Trypanites* tracemakers. The specimens of *T. helicus* isp. nov. represent a certain recurrent way of behaviour and therefore they are formally named herein.

Discussion and conclusion

Ethology. The behavioural pattern responsible for the production of the borings took place before and/or after the death of the foraminifers. The tracemakers may have bioeroded and exploitated the living substrate, i.e., the living foraminifers. Alternatively, the foraminifers were already dead before the bioerosional activity, leaving their tests with decaying organic matter to be fed upon by scavengers or to be used as domiciles for other organisms.

The tracemaker of *Maeandropolydora osmaneliensis* isp. nov. appears to have entered *Orbitoides*, when the latter was fully grown or dead. The borings cross-cut the test structure of *Orbitoides* and did not induce local test regeneration. The entrance was through an aperture at the periphery of *Orbitoides*. The winding course of the boring indicates that the foraminifers were a nutrient source for the tracemakers. The equilateral layer of *Orbitoides* was exploited specifically for its mineral and nutrient content. Additionally, the equilateral layer possibly was easier to bioerode than the layers of lateral chamberlets. The tracemaker typically avoided damaging the embryonic chambers of *Orbitoides*, which possibly would have been lethal for the foraminifer. This may be related either to a parasitic way of living, or to the poorer accessibility of these chambers. Görmüş & Sagular (1998) suggested that the borings reflect parasitism. This would imply that the tracemaker (parasite) for all or some part of its life derived food from the living *Orbitoides* (host), which was harmed to some extent by this association. If so, the boring may be classified as a praedichnion, presupposing that the tracemaker caught and killed *Orbitoides* for food. There is no evidence, however, to support predational behaviour. Alternatively, the tracemaker may have been a vagile scavenger forming foraging traces. Although the forward locomotion of the tracemaker is not directly evi-

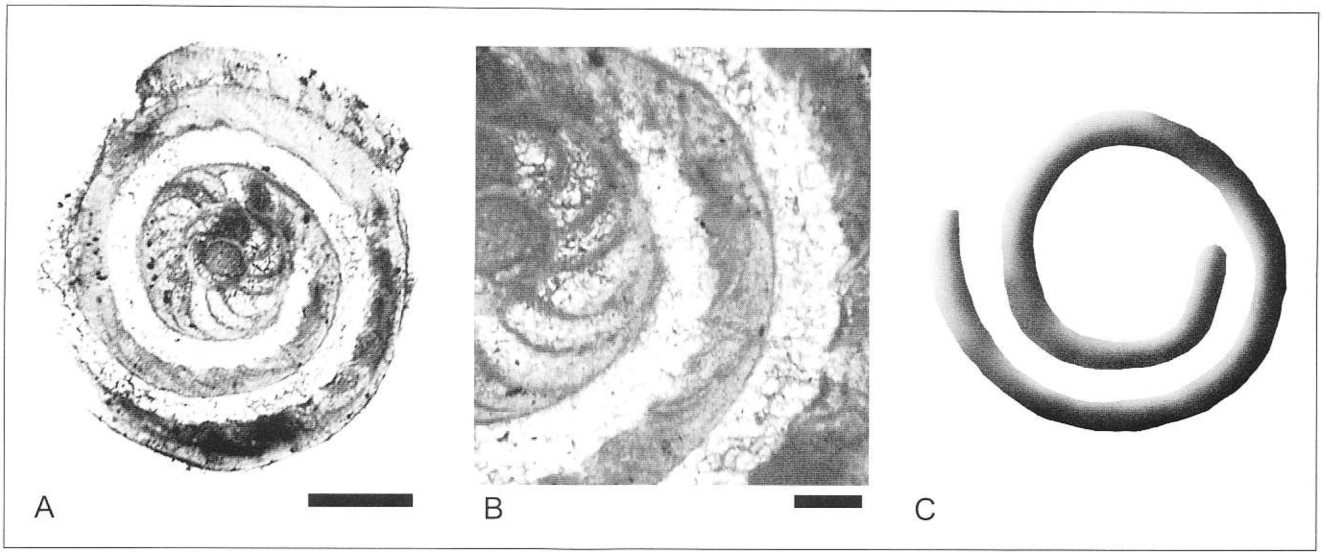

Fig. 7 - *Trypanites helicus* isp. nov. A, DIN Dinar7, thin section 28, holotype. Scale bar 1 mm. B, Close-up showing that the filling consists of calcitic cement. Scale bar 0.3 mm. C, Three-dimensional reconstruction of the holotype.

dent, the tracemaker (or at least a body part) must have moved through the *Orbitoides* tests to bioerode. Similarly, the stellate gnawing traces, *Gnathichnus pentax*, of grazing regular echinoids are considered as pascichnia (Bromley 1994); signs of locomotion of the tracemakers are not morphologically evident, but known from the life habits of Recent echinoids (see Bromley 1975). Thus, we interpret *M. osmaneliensis* isp. nov. as a pascichnion produced by parasites or scavengers.

Trypanites helicus isp. nov. is distinguished by its regular, coiled course within the substrate, cross-cutting the skeletal structure of the *Nummulites* tests. The tracemaker entered the test by utilizing its structural weaknesses, i.e., bioeroding through the tubular openings (stolons) in chamber walls. The tracemaker only entered the test at its margin. Generally, *Trypanites* ispp. are interpreted as domichnia (Bromley 1994). The tracemaker of *T. helicus* isp. nov. may have used the tests as domiciles, being specialized in using *Nummulites* tests following structural weaknesses. If not, the boring would be expected to have a more variable course. Alternatively, the tracemaker could have been carnivorous in various ways, e.g., parasitic or scavenging by exploiting specific parts of the test. Predaceous behaviour is less likely as the embryo and numerous adjacent chambers are intact. *Trypanites helicus* isp. nov., however, is interpreted as a domichnion, being the simplest interpretation.

Trypanites helicus isp. nov. represents an ethological and taxonomic dilemma: did the tracemaker bioerode through the structural weaknesses of the test because of (1) substrate construction, or (2) exploiting the substrate efficiently by forming a spiral boring? *Trypanites helicus* isp. nov. cannot explicitly be interpreted as an idiomorphic or stenomorphic boring. No consensus exists on how to solve the dilemma. All trace fossils have been formed by interaction between tracemakers and substrates. The behaviour of the tracemakers was partly controlled by substrate properties such as grain size, texture and consistency (e.g., Bromley 1994, 1996). Tracemakers may have been constricted by the outline of the substrate and formed stenomorphic traces. These traces are characterized by having an irregular course that is not recurrent. Stenomorphic traces usually have intermediate specimens grading toward idiomorphic specimens (e.g., Bromley & D'Alessandro 1987). If *Trypanites helicus* isp. nov. is considered to be stenomorphically, it is unusual by lacking an irregular course and intermediate specimens. As the dilemma remains unsolved, inherent subjectivity may obscure the application of ichnotaxonomic classifications. Ichnotaxa should exclusively be distinguished by morphology (Bromley & Fürsich 1980; Pickerill & Donovan 1998; Nielsen & Nielsen 2002). We therefore suggest excluding ethological interpretations from diagnoses for stenomorphic as well as idiomorphic trace fossils.

Biological affinity. The foraminiferal tests were infested by euendolithic organisms. Evidence of the taxonomic position of the tracemakers has not been found. The borings have only a superficial resemblance to those made by cyanobacteria and fungi, differing in size and curvature (see above). Green algae (Chlorophyta) and red algae (Rhodophyta) appear not to form cylindrical borings and are unlikely to be the tracemakers (see Golubic et al. 1975; Kobluk & Risk 1977). Instead, *Maeandropolydora osmaneliensis* isp. nov. may have been produced by a worm-like organism having a cylindrical shape. Its affinity, however, remains unknown.

Trypanites helicus isp. nov. may have been caused by worms, which generally are considered to be tracemakers of *Trypanites* (e.g., Cole & Palmer 1999). Polychaetes, *Lithotrya*, sipunculans and at larger scales even crustaceans and echinoids are possible tracemakers of this ichnogenus (Bromley 1994). Living nematodes ranging in length from 250 to 500 μm may occur tightly coiled in the tests of benthic foraminifers (Sliter 1971). It is thus possible that nematodes are tracemakers of *T. helicus* isp. nov.

Palaeoenvironmental implications. Correct interpretations of foraminiferal assemblages require more than a knowledge of the living habitat of the organisms. Decaying and empty tests are subjected to currents that may sort and redistribute the tests. Understanding the hydrodynamic settling behaviour of unbioeroded and bioeroded tests of different foraminiferal species may lead to insights about the processes governing: (1) test distribution in shallow-marine environments, and (2) preservational potential. Firstly, the hydrodynamic properties of tests are affected by test shape, size, density and occurrences of chambers and cavities (Martin & Liddell 1991). Thus, the behaviour of tests as sedimentary particles can be partly related to borings. Secondly, the taphonomical effects of bioerosion possibly altered the preservation potential of the foraminiferal tests (Peebles & Lewis 1988; Martin & Liddell 1991). Certain parts of the tests were removed by tracemakers, e.g., the median, equatorial layer of *Orbitoides*, and the tests probably became less resistant to breakage and abrasion. The empty borings may as well have enhanced the flow of dissolving and precipitating fluids through the tests. This may have resulted in precitation of the calcitic cement in most of the studied borings (see Golubic et al. 1975; Nielsen 2002; Fig. 7B). Differential infestation of shallow-marine benthic foraminifers by bioeroding organisms is known from Recent environments, and is at least partly related to the microstructural construction of tests (Peebles & Lewis 1988). It is therefore likely that some foraminifer species are more susceptible to interacting taphonomical processes than others.

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