

**BIOEROSION IN THE PLEISTOCENE
OF SOUTHERN ITALY:
ICHOGENERA CAULOSTREPSIS AND MAEANDROPOLYDORA**

RICHARD G. BROMLEY* & ASSUNTA D'ALESSANDRO**

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Riassunto. Sono stati esaminati e ridescritti gli ichnogeneri *Caulostrepis* Clarke e *Maeandropolydora* Voigt, sulla base di nuovo materiale proveniente da depositi cretacei della Svezia meridionale e, soprattutto, da depositi pleistocenici dell'Italia meridionale. Le differenze morfologiche fra i due ichnotaxa sono state interpretate come prodotte da differenti modalità di progressione nel substrato: in *Maeandropolydora* infatti la galleria progredisce dalla estremità di un "ramo" (perforazione assiale), in *Caulostrepis* invece, la galleria avanza dal *vertex* (perforazione laterale). Combinazioni delle due tecniche hanno dato origine a forme intermedie: *Caulostrepis contorta*, in cui prevale la perforazione laterale e *Maeandropolydora decipiens* in cui predomina la perforazione assiale. All'ichnogenere *Caulostrepis* appartengono strutture a U o derivate da complicazioni di questo modello basale (*C. contorta*); la separazione fra le diverse ichnospecie è inoltre basata sulla presenza o assenza del "setto" (*vane*), di "tasche" (*pouches*), di fossette e di "solchi" (*grooves*) in prossimità dell'apertura. Le differenti ichnospecie di *Maeandropolydora* sono caratterizzate dalla presenza o assenza di tasche o dalla tendenza delle gallerie a decorrere appaiate.

Abstract. The ichnogenera *Caulostrepis* Clarke and *Maeandropolydora* Voigt are re-examined and redescribed on the basis of new material from Cretaceous deposits at Ivö (Sweden) and in particular from Pleistocene deposits from southern Italy. The morphological differences between the two ichnogenera are explained as having originated by different modes of substrate penetration. *Maeandropolydora*'s gallery is extended from the end of one limb (axial boring), whereas *Caulostrepis*'s gallery advances at the vertex (lateral boring). Combinations of the two processes give rise to intermediate forms: *Caulostrepis contorta*, in which lateral boring prevails and *Maeandropolydora decipiens*, in which axial boring is predominant. Structures that are U-shaped or produced by elaboration of this basic U-plan (*C. contorta*) are referred to the ichnogenus *Caulostrepis*; the ichnospecies are separated according to presence/absence of vane, pouches, apertural pits and apertural grooves. The different ichnospecies of *Maeandropolydora* are characterized by presence or absence of pouches or by galleries tending to run in pairs.

Introduction.

The coast between Monopoli and Polignano (Fig. 1) exposes rocks belonging to two limestone formations, the *Calcarea di Bari* (Cenomanian—Turonian) on which the transgressive *Calcarenite di Gravina* rests unconformably. The precise age of the latter formation is not known. The geological setting suggests Lower Pleistocene (Iannone & Pieri, 1980), but elements of the fauna may

* Geologisk Centralinstitut, Öster Voldgade 10, DK 1350 København K.

** Istituto di Geologia e Paleontologia dell'Università, via Nicolai 2, 70100 Bari.

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indicate uppermost Pliocene in this region (D'Alessandro & Iannone, in press). In the examined area, the transgressive contact is commonly marked by the presence of a conglomerate containing calcareous, well rounded clasts.

The base of the calcarenite sequence (about 2 m thick) is characterized by the alternation of coarse sediments and medium sands slightly cemented, lacking matrix, with local gravelly lenticular intercalations. Inorganic sedimentary structures are rare, represented by plane-parallel laminae and normal and inverse gradation, whereas bioerosion structures, on the other hand, are the most common features. The trace fossil and body fossil assemblages permit the assessment of the palaeocommunity which is comparable to the recent Mediterranean biocoenosis of the «Photophylic Algae», probably located in the upper part of the infralittoral zone in a relatively protected area (see D'Alessandro & Iannone, in press).

Bioerosion of the limestone substratum and overlying limestone clasts and

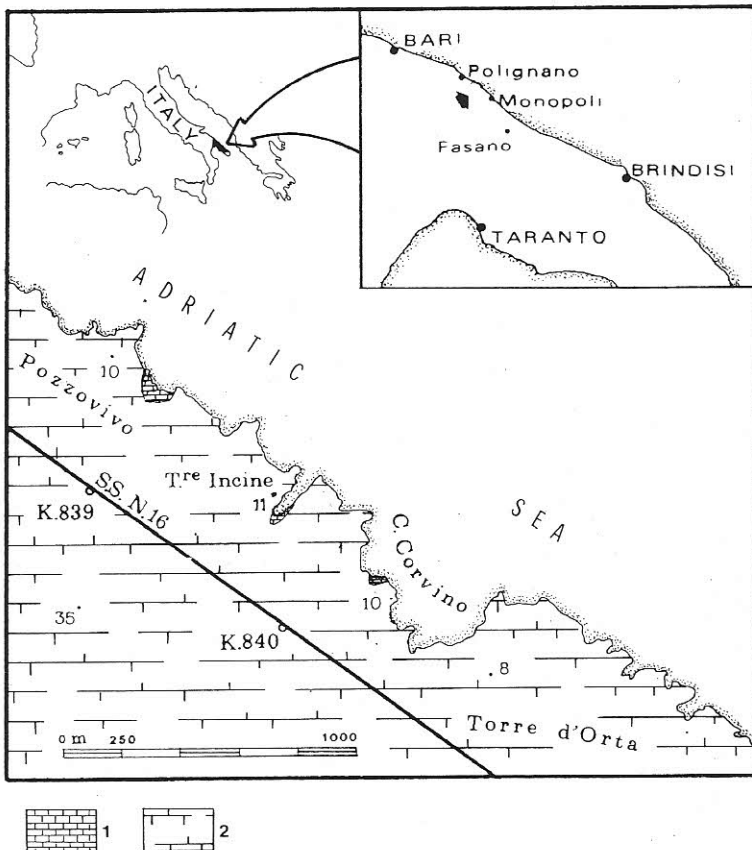


Fig. 1 — Location map of the investigated area. 1) Cretaceous limestone; 2) Pleistocene calcarenite.

shells is dominated by *Entobia* ichnospp. and locally *Gastrochaenolites* ichnospp. Other trace fossils include ichnospecies of *Trypanites*, *Caulostrepsis*, *Maeandropolydora*, *Talpina*, *Radulichnus* and *Gnathichnus*, and the borings of Algae. The bioerosion assemblage is rich in ichnotaxa, most of which require taxonomic re-evaluation. In the present paper, therefore, we shall restrict ourselves to the ichnogenera *Caulostrepsis* Clarke and *Maeandropolydora* Voigt. In order to re-define these forms, it has been necessary to examine material from other locations and ages, in particular the Upper Cretaceous of northern Europe. It is intended to extend our study of the remaining ichnotaxa in later papers.

Methods. In order to examine the details of the morphology of the borings it was necessary to make artificial moulds of these. After emptying the borings of loose sand they were embedded in a synthetic resin made by ITALBEIT (Milan); the resin in question is TIXO 688 to which is added MEK 1043; the limestone substrate was then dissolved away in hydrochloric acid.

Terminology. The two ichnogenera under consideration have rather complex morphology, and there is a need for a terminology to homologise the various parts; the terms here employed are shown in Fig. 2. We have chosen

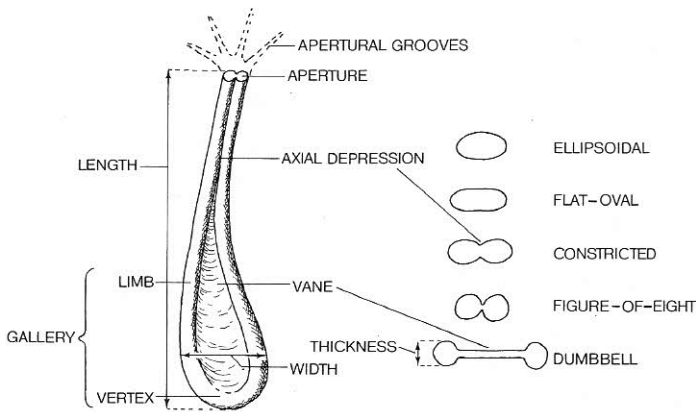


Fig. 2 — Morphological terms as used in this paper.

terms already in use, as far as possible, in other trace fossils having comparable morphology, especially *Diplocraterion* and *Rhizocorallium*; however we avoid the use of «spreite» since the structure between the limbs of *Caulostrepsis* is not equivalent in construction or morphology to the spreite in *Diplocraterion* and *Rhizocorallium*. In *Caulostrepsis* it may be an open slit in the hard sub-

strate, or may be filled with sediment resulting from the boring process (as in the spreite) or collected from outside the substrate. The slit is more closely comparable to the slits occurring in bryozoan borings and called «vanes» by Pohowski (1978, fig. 3D).

Taxonomy

Ichnogenus *Caulostrepsis* Clarke, 1908

1908 *Polydorites* Douvillé, p. 365 (ichnogenus without ichnospecies name).

1971 *Dodecaceria* Voigt (non Örsted), p. 150, pl. 15, fig. 12; pl. 16, fig. 1–9.

1973 *Ramosulcichnus* Hillmer & Schulz, p. 9, text-fig. 1, 6, 9; pl. 1; pl. 2, fig. 1–3, 5–7, 9; pl. 3, fig. 1, 3, 4, 6, 8, 9.

Polydora borings – Authors. We make no attempt to list here the numerous references of this boring-type to the living polychaete genus *Polydora*.

Type-ichnospecies: *Caulostrepsis taeniola* Clarke, 1908

Other ichnospecies: *C. contorta* ichnosp. n.
C. biforans (Gripp, 1967)
C. avipes ichnosp. n.
C. cretacea (Voigt, 1971)
C. ichnosp. 1

Diagnosis. Single-entrance borings or embedment structures having a pouch shape or ear shape produced by a gallery bent in a U. More complex structures can be produced by development of multiple lobes on the same basic U-plan. The limbs may be clearly visible throughout their length and connected by a vane, or they may be fused to produce an oval or flattened pouch lacking a vane. All intermediate states, involving an axial depression, occur. At the distal end the width is at least double the thickness; the cross sectional shape here varies from flat-oval, elliptical or constricted to dumbbell-shaped. At the apertural end the width is normally noticeably less than at the distal end, but the shape of the section may be more or less the same, or subcircular. In some cases symmetrical rows of deep pits may be developed towards the apertural end. The aperture itself may have the same form as the proximal cross section, or it may be modified by the development of superficial branches or apertural grooves, normally 2 to 4 in number, radiating out from it.

Remarks. *Caulostrepsis* differs principally from *Trypanites* in being flattened in cross section. Bromley (1972) included flattened borings within *Trypanites*. However, it is apparent that *Trypanites* should be restricted to borings that have a circular cross section and more or less cylindrical form, e.g. *T. weisei* Mägdefrau, *T. solitarius* (von Hagenow) and *T. fimbriatus* (Stephenson).

Caulostrepsis differs from *Maeandropolydora* in lacking well-developed cylindrical galleries.

Caulostrepsis taeniola Clarke, 1908

Pl. 21, fig. 2; Pl. 25, fig. 2

- 1908 *Polydorites* Douvillé, p. 365.
 1908 *Caulostrepsis taeniola* Clarke, p. 169, pl. 12, fig. 3, 4.
 1921 *Caulostrepsis taeniola* – Clarke, p. 92, text–fig. 84 a, b.
 1928 *Caulostrepsis taeniola* – Richter, p. 224, text–fig. 11, pl. 3, fig. 4.
 1942 Borings of commensal worms Newell, p. 96, pl. 8, fig. 4, 5.
 1944 *Caulostrepsis dunbari* Condra & Elias, p. 549, pl. 10, fig. 1; pl. 11, fig. 8.
 1944 *Polydora* sp. Stenzel & Turner, p. 305, pl. 1, fig. 30 (?), 32, 39, 40.
 1955 *Polydora hoplura* – Schmidt (non Claparède), p. 30, pl. 2, fig. 4.
 1965 *Caulostrepsis taeniola* – Häusel, p. 392, text–fig. 4, 5.
 ?1965 *Polydora* Vialov & Goretskij, p. 41, pl. 3, fig. 2a, b.
 1965 *Caulostrepsis taeniola* – Voigt, p. 206, text–fig. 3a, c.
 1966 *Polydora* borings Boekschoten, p. 358, pl. 3, fig. c.
 1969 *Polydora ciliata* – Radwanski (non Johnston), p. 13, text–fig. 3, pl. 4, fig. 3; pl. 37, fig. 3.
 1969 *Polydora hoplura* – Radwanski, p. 14, text–fig. 4 A, B a–e; pl. 19, fig. 1; pl. 24, fig. 4; pl. 37, fig. 5, 6; pl. 41, fig. 1.

Diagnosis. Gallery cylindrical, bent in a narrow U which is sometimes enlarged in the shape of a tongue. The inward-facing margins of the limbs are always interconnected by a distinct vane. Limbs closer or partially fused towards the apertural extremity. Transverse section dumbbell-shaped, aperture 8-shaped.

Description. Gallery cylindrical, bent in the form of a long, more or less narrow U (max. preserved length in our samples 22 mm), which may be somewhat sinuous, enlarged in some cases to form a tongue-like shape at the distal end (Pl. 25, fig. 2); the inward-facing margins of the tube are always interconnected by a distinct vane. In transverse section the structures are dumbbell-shaped, with the maximum width from 1.3 to 4.5 mm. Aperture apparently simple 8-shaped, but usually abraded to some degree in the present material. The structure does not always lie within a plane but may curve transversely to the length axis, and more rarely may twist a little along that axis. The surface is smooth. Intersections have not been seen: neighbours tend to avoid each other.

Observations. The trace fossil as distinguished by Vialov & Goretskij (1965) is questionable because of the poor quality of the illustrations; moreover in several cases these authors only illustrated the aperture, rendering ichnospecific attribution impossible (Vialov & Goretskij, pl. 1, fig. 1b; pl. 2, fig. 1a,b; pl. 3, fig. 1). Nevertheless, it is probable that their form belongs to the ichnogenus *Caulostrepsis*. For the same reason we have not placed in synonymy some of the borings illustrated by Radwanski (1969) under the name *Polydora ciliata* (pl. 4, fig. 1–2; pl. 7, fig. 1–2; pl. 31, fig. 1; pl. 36, fig. 1; pl. 37, fig. 4) and *P.*

hoplura (pl. 4, fig. 4; pls. 17, 18, 23, 25; pl. 39, fig. 2). Radwanski's *Polydora hoplura* differs only in its larger size, but this character alone is not sufficient on which to base a different ichnotaxon. The example in pl. 39, fig. 1 of Radwanski's (1969) is dubious since it is possibly a combination of the work of two animals (see his text—fig. 4 B f) or an example of *Maeandropolydora*. Intersections of this type have not been seen in *C. taeniola*. Hölder & Hollmann (1969; fig. 2, 4) also described U-shaped trace fossils, under the name *Polydorites*; however, their brief descriptions and sketches do not permit attribution either to ichnospecies or even with confidence to ichnogenus.

Caulostrepsis dunbari Condra & Elias is tentatively placed in synonymy because the difference is merely one of size, this ichnospecies being wider than *C. taeniola*. It is possible that *C. dunbari* is incomplete, having lost the apertural portion of the boring.

Material. 12 artificial moulds of borings in calcareous pebbles, 3 of borings in valves of *Ostrea edulis* (Linnaeus) from the «Calcarenite di Gravina» Formation, near Monopoli (Bari).

***Caulostrepsis contorta* ichnosp. n.**

Pl. 23; Pl. 25, fig. 4; Fig. 3

1922 Unnamed boring Reis, pl. 7, fig. 3 (*pars*); fig. 4 (*pars*, left).

Derivation of name. *Contortus*, Latin, contorted.

Type series. Holotype, Pl. 23, fig. 2 (MGUH 16056); paratypes, Pl. 23, fig. 3 (MGUH 16071), 1,4 (MGUH 16057); Pl. 25, fig. 4 (MGUH 16058).

Horizon and type locality. «Calcarenite di Gravina» Formation, Polignano, Monopoli (Bari).

Collocation. Geological Museum, University of Copenhagen, Denmark.

Material. 34 artificial moulds in limestone from the type locality.

Diagnosis. Boring curved in a sinuous U-shape or ear-shape to produce complex structures consisting of lobes. Normally, a lobe or a series of them is curved within a plane or twisted along its axis. Vane well developed. Generally the lobes are connected in such a way that each individual element lies in a different plane, sub-parallel or rotated in respect to its neighbour. Aperture apparently simple 8-shaped.

Description. Complex boring system produced by a long, cylindrical gallery of constant diameter, which is bent continually and subdivided into numerous small lobes (U-shaped or like an ear), the inner edges of which are always connected by a vane. Commonly, the interconnected lobes are disposed in the form of a fan or clustered as a bouquet (Fig. 3). More rarely, their disposition is helicoidal (Pl. 23, fig. 2). A more typical characteristic of the system arises

from the different spacial orientation of the various lobes, such that each lobe lies in a different plane from the next. Usually these planes are subparallel or may be rotated to varying degrees. When the structure is formed of a single lobe this may be curved in the plane containing the lobe, or twisted spirally around its longitudinal axis. Aperture is apparently simple 8-shaped.

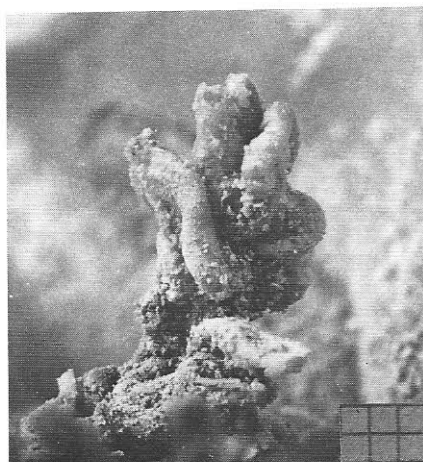


Fig. 3 — *Caulostrepsis contorta* ichnosp. n. MGUH 16061. Lobes are arranged somewhat like a bouquet. Artificial mould of Pleistocene boring in Cretaceous substrate. Example used as model for Fig. 8B. Scale in millimetres.

Observations. The complexity of the structure is not a result of lack of space in the substrate. In fact we find the boring in the limestone surface underlying the conglomerate and in pebbles of very large size relative to the small boring. Neither is it a case of crowding by other borings; normally the *C. contorta* have ample space about them. In contrast to other species of *Caulostrepsis* the structure is often connected with other borings, in particular *Trypanites* ichnosp. (Pl. 23, fig. 3) and to a lesser extent *Entobia* ichnosp.

The new ichnospecies is more complex than the other ichnospecies of *Caulostrepsis*, being composed of more elements. Where the structure is composed of a single element, the edge has a freely sinuous form and normally tends towards a bilobed shape (Pl. 25, fig. 4).

Caulostrepsis contorta differs from *Lapispecus* (Voigt, 1970) in the location of the vane. In *Lapispecus* a vane is normally present as a lateral appendage to a cylindrical gallery, and only very locally joins across sharp U-bends in *Caulostrepsis*-fashion. In the new ichnospecies, the vane connects across

U-lobes; only very rarely is this pattern altered where a short, cylindrical gallery connects two lobes, and here the vane is entirely absent.

In the case of *Maeandropolydora decipiens* Voigt, intermediate forms occur where the lobes of *C. contorta* are narrow, more separated, and interconnected by short *Trypanites*-like galleries.

The example illustrated by Reis (1922) is a little larger than ours. The new boring compares nicely with the illustrations of the borings of the living *Polydora concharum* (Evans, 1969; fig. 4, 6 *pars*, 11, 12 *pars*, 13). Also the borings of *Polydora ciliata* illustrated by Bromley (1970; fig. 4-i *pars*) show characteristics of *C. contorta*.

***Caulostrepsis biforans* (Gripp, 1967)**

1967 *Polydora biforans* Gripp, p. 9, pl. 1, fig. 3-5.

1968 *Polydora biforans* - Gripp, p. 378, fig. 7, 10, 11.

1969 «*Polydora*» *biforans junior* Gripp, p. 85, pl. 2, fig. 3-7.

1972 *Trypanites biforans* - Bromley, p. 96, fig. 1-j.

1972 *Nygmities solitarius* - Voigt (non von Hagenow), p. 121, pl. 3, fig. 2; pl. 5, fig. 5, 6.

pars 1973 *Ramosulcichnus biforans* - Hillmer & Schulz, p. 10, text-fig. 1 d-e, g-j; pl. 1, fig. 1-3; pl. 2, fig. 5, 9; pl. 3, fig. 1, 3, 4.

Diagnosis. *Caulostrepsis* having no vane, normally lacking an axial depression, flattened-oval cross section distally, approaching circular proximally. Immediately distal of the aperture, a series of paired or double-paired pits. Two or four grooves branch out from the aperture, or these branches may be submerged within the substrate, the true apertures (2 or 4) occurring where the branches break the surface.

Observations. Hillmer and Schulz (1973) included two distinctive forms within their monospecific ichnogenus *Ramosulcichnus*: the pit-bearing form *Polydora biforans* Gripp, and a similar form lacking the characteristic pit structures. We restrict the ichnospecies to Gripp's original form and place this in the ichnogenus *Caulostrepsis*. The form lacking pits we regard as a separate and distinct ichnospecies from *C. biforans*, which we consider new to science and call herein *C. avipes*. The general form of *C. biforans* resembles that of *Caulostrepsis* ichnosp. 1 except for the apertural modifications.

Remarks. This form has not been observed in the Pleistocene material under study, but is included here in order to facilitate a more complete understanding of the ichnogenus *Caulostrepsis*. Gripp's (1967) original material derived from the Maastrichtian in Germany.

***Caulostrepsis avipes* ichnosp. n.**

1922 Unnamed boring Reis, pl. 7, fig. 1–3 *pars*.

pars 1973 *Ramosulcichnus biforans* – Hillmer & Schulz, text–fig. 1a–c, f. 6; pl. 3, fig. 6, 8, 9.

Derivation of name. *Avis, pes*, Latin, bird, foot. Refers to visual impression of the apertural groove structure.

Holotype. Hillmer & Schulz 1973, pl. 3, fig. 8. Artificial mould in rostrum of belemnite, *Belemnella* sp.

Horizon and type locality. Lower Maastrichtian chalk, Krons Moor Quarry, near Lägerdorf, Schleswig–Holstein, N. Germany.

Collocation. Geologisch–Paläontologisches Institut, Hamburg; SGPIH 1682.

Diagnosis. *Caulostrepsis* with or without a vane, dumbbell-shaped to flattened–oval in cross section, characterized by the possession of two to four grooves branched out from the aperture. In some cases the branching occurs beneath the substrate surface so that each diverging branch bears its own aperture.

Observations. *C. avipes* is distinguished from *C. biforans* in lacking the paired pit structures of that ichnospecies. *C. avipes* is otherwise more variable than *C. biforans* in that it appears to possess a vane in some cases.

***Caulostrepsis cretacea* (Voigt, 1971)**

Pl. 21, fig. 1, 3; Pl. 22

1970 *Dodecaceria* (?) sp. Voigt, p. 375, pl. 6, fig. 2–5.

1971 *Dodecaceria cretacea* Voigt, p. 150, pl. 15, fig. 12; pl. 16, fig. 1–9.

1972 *Trypanites cretacea* – Bromley, p. 95, fig. 1–i.

Diagnosis. Galleries bent in a long, narrow U–form with the inward–facing walls of the limbs fused by complete removal; the original position of the median wall is sometimes indicated by a very shallow axial depression along the structure. Vane absent. Transverse section always flattened–elliptical but showing gradual decrease in width toward the aperture. Shape of aperture flattened–oval.

Description. Borings of ribbon–like form, very long, usually >15 mm, flattened, ranging in width from 2 to 4 mm. Transverse section flattened–elliptical, becoming gradually slightly more flattened distally owing to a noticeably greater increase in width than in thickness. Ratio of width/thickness at the distal end ($n = 28$) ranges from 1.9 to 3.2. The structure on the whole may curve in varying degrees along the axis and only in a few cases is there axial torsion. Rare examples show longitudinal depression which, in some, becomes a little more accentuated at the blind end. External surface smooth.

Observations. Our examples have the same characteristic form as *Dodecaceria cretacea* Voigt (Maastrichtian of Maastricht, the Netherlands) and the general shape corresponds in particular with the shape of the holotype (Voigt, 1971, pl. 16, fig. 3) and to Voigt's Santonian examples (1970, pl. 6, fig. 2–5 indicated as *Dodecaceria* (?)). One minor difference is that the Pleistocene structures are a little more flattened. The morphology of this trace fossil closely corresponds to Recent borings of *Dodecaceria* (cf. Evans 1969, *Dodecaceria concharum*, text—fig. 5, 6) but since a trace fossil should not bear the name of a possible trace-maker (Bromley & Fürsich, 1980) we refer the structure to the ichnogenus *Caulostrepsis*.

The difference with *C. taeniola* concerns the transverse section which, in *C. cretacea*, lacks a vane; at most the sides are locally very slightly depressed in a shallow axial groove. Very short examples are commonly produced by taphonomic or bioerosional processes that obliterate all but the most distal part of the boring, which then shows a close resemblance to some acrothoracican borings.

We have not seen interpenetration either with the same ichnospecies or with other borings. In a few cases, very small examples like a pouch begin directly in the wall of *C. cretacea* of large dimensions, thereby producing compound borings. The trace-maker, on approaching a surface of the substrate (particularly where boring within a restricted pebble) makes an angular or curved deviation to avoid penetrating the surface. However, subsequent bioerosional processes commonly break into the superficial parts of such a boring and give the appearance of a structure having two or more apertures.

Material. 28 artificial moulds of borings, many of them incomplete, in calcareous pebbles from the «Calcarenite di Gravina» near Monopoli (Bari).

Caulostrepsis ichnosp. 1

Pl. 21, fig. 5

Description. Borings very narrow club-shaped, produced by a gallery bent in a U having the limbs more or less completely fused, the length axis weakly curved, more rarely straight, 7–10 mm. Distal transverse section flattened-oval, 1.3–1.6 mm wide, the width/thickness ratio from 2 to 2.2; becoming circular in the proximal direction where the diameter is about 0.8 mm. An axial depression is present in the distal half, widened as a genuine vane at the tongue-like vertex. Aperture simple, subcircular or circular.

Observations. The most important characteristic of this boring is the morphological change from one end to the other, representing an intermediate form between *Trypanites* (proximally) and *Caulostrepsis*. It differs from *Trypa-*

nites fimbriatus (Stephenson) (Cenomanian, Texas) in the suboval form of the transverse section of the distal part. Possibly this form is comparable with some examples of *C. cretacea* illustrated by Voigt (1971, p. 16, fig. 1) in which the proximal end appears to have a circular transverse section.

Material. 3 artificial moulds of borings in limestone pebbles from the «Calcarene di Gravina» Formation near Monopoli (Bari).

Ichnogenus *Maeandropolydora* Voigt, 1965.

Voigt (1965) erected this ichnogenus apparently to comprise borings combining characteristics of *Trypanites* and *Caulostrepsis*. The ichnogenus contained two ichnospecies, the one (*Maeandropolydora decipiens*) a complete boring sunken within the substrate, the other (*M. sulcans*) occurring as discontinuous grooves in the substrate surface. Some of Voigt's material derived from Ivö Klack (Campanian) in Sweden. Examination of much new material from this locality indicates that although the two ichnospecies are distinct, nevertheless Voigt's criterion for separating them is not valid. The groove stratinomy of *M. sulcans* may be explained in terms of the taphonomic history of the substrates rather than the genetic development of the borings. Where the trace fossil grooves occur on the inner surface of mollusc shells, it is preserved at the aragonite/calcite interface of pectinacean bivalves in which the aragonite layer has been dissolved during diagenesis. Furthermore, where the grooves occur on the outer surface of shells, this is normally demonstrated to be the cementation surface of an oyster, the substrate to which it was attached having been lost during diagenesis. In both cases, therefore, only half the boring is preserved. More material is now available than was seen by Voigt (1965), also in a greater variety of substrate materials including limestone. We are therefore in a position to be able to give a more detailed ichnogenetic diagnosis, which we do on the basis of material both from Voigt's localities and from the Pleistocene deposits of southern Italy. We conclude that the inherent morphologies of Voigt's two ichnospecies are different, and therefore emend their diagnoses on the basis of new criteria.

Type-ichnospecies: *Maeandropolydora decipiens* Voigt, 1965

Other ichnospecies: *M. sulcans* Voigt, 1965

M. elegans ichnosp. n.

Diagnosis. Long cylindrical galleries having two or more apertures, running through the substrate sinuously or in irregular contortions. Galleries may run parallel in contact with each other in pairs, with or without fusion. Loose or tight loops may occur; the limbs of these may be connected by a vane or form a pouch.

Maeandropolydora decipiens Voigt, 1965

Pl. 24, fig. 1, 3; Pl. 25, fig. 3; Fig. 4

1965 *Maeandropolydora decipiens* Voigt, p. 204, pl. 27, fig. 1, 2.1965 *Maeandropolydora sulcans* Voigt, pl. 27, fig. 4.1968 *Caulostrepsis taeniola* – Müller, pp. 35–37, fig. 15–17 (group IX).

Fig. 4 – *Maeandropolydora decipiens* Voigt. Artificial mould of Pleistocene boring in limestone pebble, showing pouches (arrows). Scale in millimetres. MGUH 16062.

Diagnosis. Galleries cylindrical, irregularly disposed, bent in loops, the inner sides of the limbs of some of these connected by a vane. The most characteristic feature is the presence of pouches. Two or more apertures.

Description. Cylindrical gallery (diameter commonly 0.7–1.0 mm) disposed irregularly, possibly having dichotomous branching; at various distances the gallery is bent into lobes of varying lengths; the lobes may be enlarged as pouches, or the inner walls may be connected by a vane. Tight loops where the limbs nevertheless are not interconnected (as is characteristic of *M. sulcans*) also occur. Apertures are circular and may number two or more.

Material. Five examples (possibly more) as artificial moulds from Pleistocene «Calcarene di Gravina» Formation near Monopoli (Bari); numerous specimens in oysters from uppermost Lower Campanian at Ivö Klack, southern Sweden.

Maeandropolydora sulcans Voigt, 1965

Pl. 21, fig. 4, 6; Pl. 24, fig. 2; Fig. 5

1901 *Dodekaceria* (?) sp. Rovereto, p. 228, pl. 28, fig. 1, 4 c.1965 *Maeandropolydora sulcans* Voigt, p. 204, pl. 26, fig. 5, 6; pl. 27, fig. 3, 5 (?) (non fig. 4).

Diagnosis. Cylindrical gallery having at least two apertures, irregularly contorted, commonly bent in loops, never showing fusion where walls are in mutual contact; vane absent.

Description. Long, cylindrical gallery of constant diameter (0.6 – 1.5 mm) irregularly twisted into complicated convolutions, commonly looping round and coming into contact with itself; loops are variable in size, always lacking vane or pouch development. In cementation surfaces of oysters the boring tends to follow the substrate/oyster interface. In limestone, belemnite rostra and other substrates, the system twists freely in three dimensions. Two or more circular apertures.



Fig. 5 — *Maeandropolydora sulcans* Voigt in valve of *Ostrea edulis* (Pleistocene). Scale in millimetres. MGUH 16063.

Material. Three artificial moulds in pebbles and one in shell of *Ostrea edulis* from the «Calcarenite di Gravina» Formation near Monopoli (Bari); one in belemnite rostrum and numerous in oysters from uppermost Lower Campanian of Ivö Klack, southern Sweden.

***Maeandropolydora elegans* ichnosp. n.**

Pl. 25, fig. 1; Fig. 6

Derivation of name. *Elegans*, Latin, elegant

Type series. Holotype, Pl. 25, fig. 1 (MGUH 16059); paratype, Fig. 6 (MGUH 16060).

Horizon and type locality. «Calcarenite di Gravina» Formation near Monopoli (Bari).

Collocation. Geological Museum, University of Copenhagen, Denmark.

Material. Artificial moulds: one good example and one fragment in oyster, and two poor examples in limestone from the type locality.

Diagnosis. System composed of cylindrical galleries of constant diameter, irregularly sinuous, tending to run in paired fashion, the limbs touching but normally not fused. Numerous apertures.

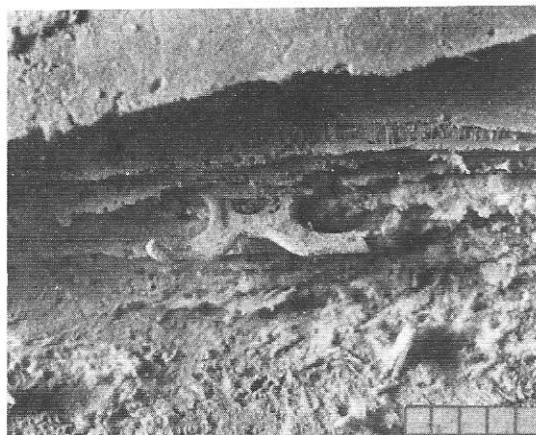


Fig. 6 – *Maeandropolydora elegans* ichnosp. n. Paratype. Artificial mould in valve of *Ostrea edulis*. Scale in millimetres. MGUH 16060.

Description. System composed of thin cylindrical galleries having constant diameter (0.4 – 0.8 mm) which normally run as parallel, paired limbs over relatively long distances. The course is irregularly sinuous in all directions. The pair of limbs may show axial torsion. At various distances the members of the pair may part at an acute or obtuse angle, and each limb receive a new partner to produce a new pair of limbs (Pl. 25, fig. 1). In some cases the gallery loops acutely back on itself producing the pair of limbs; in such cases the two limbs are normally unfused, or possess a deep axial depression; at the vertex a minute vane may be present. The gallery appears to have few, possibly only two, main apertures; however, short side branches arise at irregular intervals along the main gallery and give rise to numerous accessory apertures.

Conclusions.

The borings grouped in the ichnogenera *Caulostrepsis* and *Maeandropolydora* in this study show two radically different modes of substrate penetration, which may be termed «axial boring» leading to loops and «lateral boring» leading to vanes and pouches. Different combinations of the two processes are the basis of distinction of the two ichnogenera.

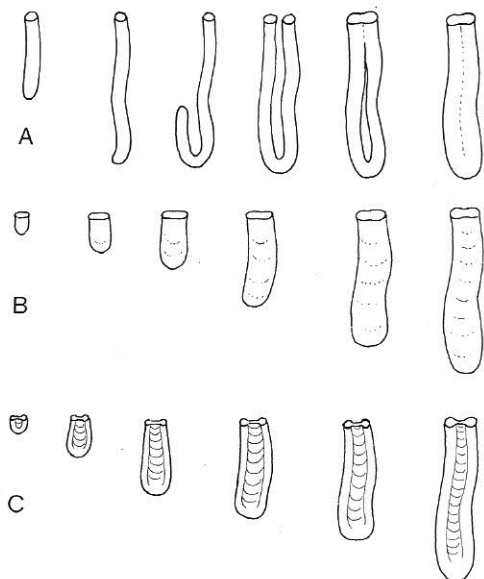


Fig. 7 — Three ontogenetic series leading to the production of different pouch structures. A) The organism bores in a «head-on» manner, turning to produce a hair-pin loop, the second limb running close to and parallel with the first. The intervening partition may break down between the limbs to produce a continuous pocket-like chamber, but an axial depression usually remains along the former position of the partition. B) Lateral boring by an organism bent in a U, producing an open pocket structure. Transverse ornament may reflect growth stages. C) Lateral boring similar to B, but the limbs and vertex of the U-gallery are enlarged with the growth of the organism. Correspondingly, the vane, produced by the advancing vertex, is a slit showing a progressive increase in thickness distally until, at the present position of the vertex, it has the same thickness as the U-gallery.

1) Axial boring. The gallery is extended along the direction of its axis. Loops are produced by bending the direction of boring (Fig. 7 A), until the gallery is curved back on itself and isolates an island of substrate within the loop.

2) Lateral boring. The gallery is extended somewhat as in soft-substrate ichnogenera *Diplocraterion* and *Rhizocorallium* to produce a pouch. With growth of the organism, the gallery diameter enlarges, so that its earlier position is represented between the limbs as a relatively narrow slit (Fig. 7 C). More rapid lateral boring, or lack of tangible growth, results not in a narrow slit but in a pouch having the full thickness of the gallery (Fig. 7 B).

Combination of these boring techniques produces a morphological series where one end member is a single pouch or group of them: ichnospecies of *Caulostrepsis*; at the opposite end are *Maeandropolydora elegans* and *M. sulcans*, which lack pouches. *Maeandropolydora decipiens* represents an intermediate form having elements of both boring techniques together (Fig. 8).

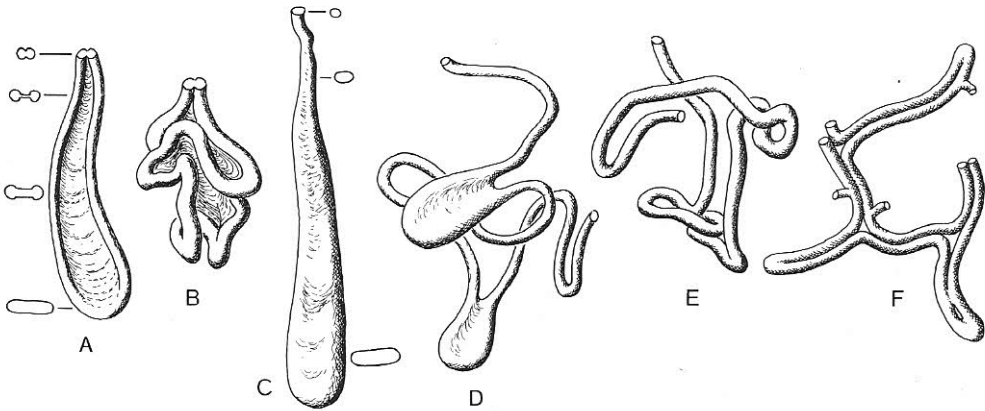


Fig. 8 – The morphological series shown by the ichnospecies present in the Pleistocene material. A) *Caulostrepsis taeniola*; B) *C. contorta*, based on Fig. 3; C) *C. cretacea*; D) *Maeandropolydora decipiens*; E) *M. sulcans*, based on Pl. 21, fig. 4; F) *M. elegans*, based on holotype (Pl. 25, fig. 1). Forms A) to D) have true pouches, the limbs in A) and B) being connected by a narrow vane, those in C) and D) being broadly continuous as a wide pouch. Forms E) and F) lack true pouches, although the partition in narrow hair-pin loops may break down secondarily to produce a pouch-like structure. Characteristic cross sections are shown in A) and C).

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PLATE 21

Fig. 1 — *Caulostrepsis cretacea* (Voigt). Also seen are *Gastrochaenolites* ichnosp. (left, upper) and *Caulostrepsis contorta* ichnosp. n. (arrow) on *Entobia* ichnosp. (right). MGUH 16064.

Fig. 2 — *Caulostrepsis taeniola* Clarke. MGUH 16065.

Fig. 3 — *Caulostrepsis cretacea* (Voigt). The apertural end is down. MGUH 16066.

Fig. 4 — *Maeandropolydora sulcans* Voigt, and *Entobia* ichnosp. MGUH 16067.

Fig. 5 — *Caulostrepsis* ichnosp. 1, MGUH 16068.

Fig. 6 — *Maeandropolydora sulcans* Voigt. MGUH 16069.

All the samples are artificial moulds in limestone clasts from «Calcarenite di Gravina» Formation near Monopoli, south of Bari. Scales in millimetres.

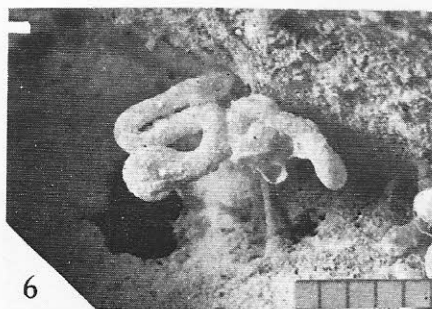
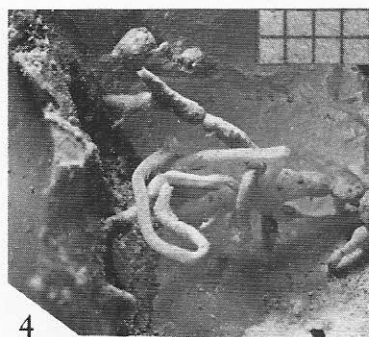
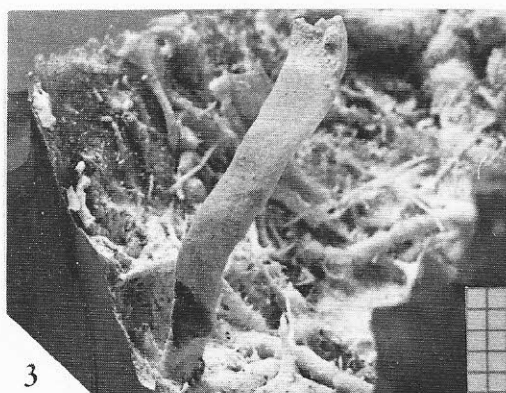
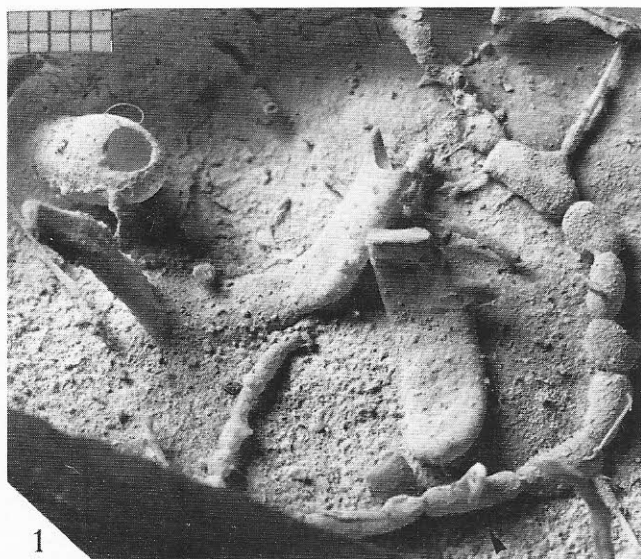


PLATE 22

Fig. 1 — *Caulostrepis cretacea* (Voigt) (arrow) and *Entobia* ichnosp. Scale in millimetres.
MGUH 16070.

Artificial mould of borings in limestone clasts from «Calcarenite di Gravina» Formation near Monopoli, south of Bari.

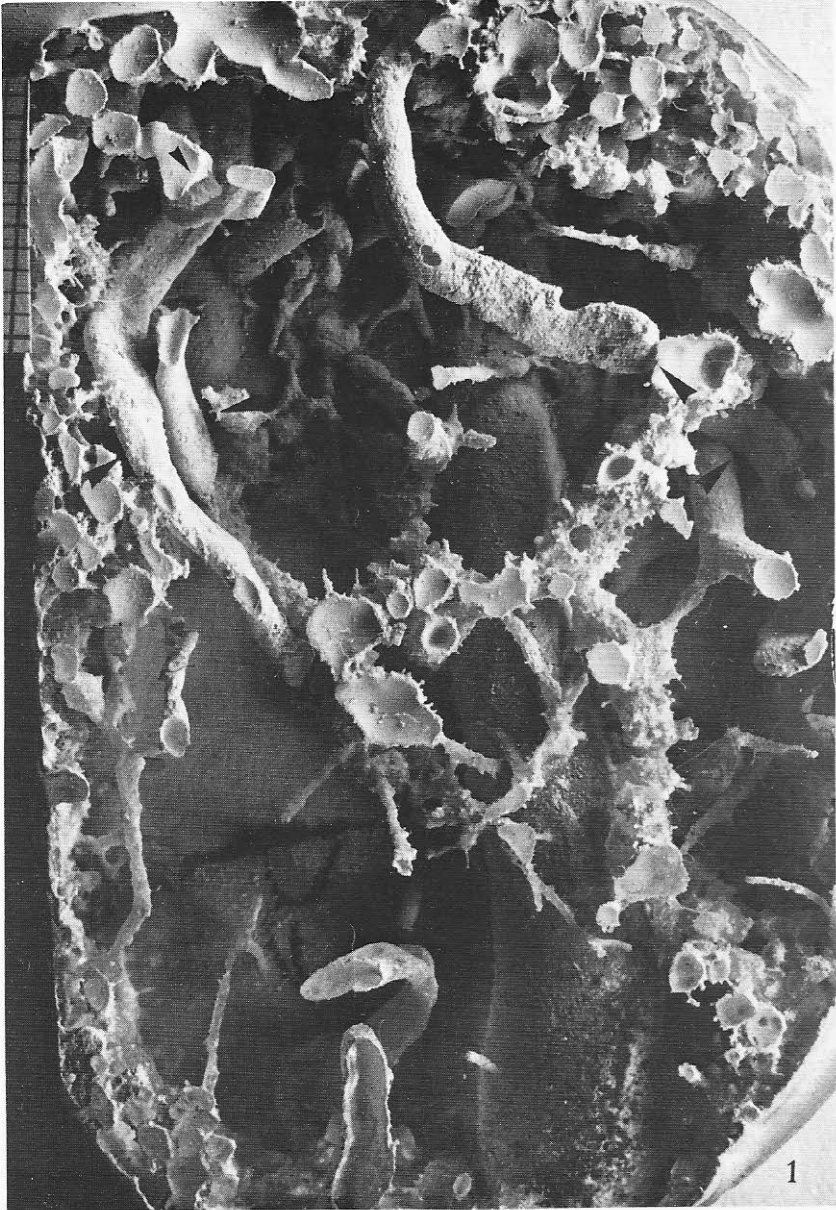


PLATE 23

Fig. 1, 4 – *Caulostrepis contorta* ichnosp. n. Paratype. Same boring viewed from above (fig. 1) and laterally (fig. 4). MGUH 16057.

Fig. 2 – *Caulostrepis contorta* ichnosp. n. Holotype. MGUH 16056.

Fig. 3 – *Caulostrepis contorta* ichnosp. n. modifying an earlier *Trypanites*. MGUH 16071.

All the samples are artificial moulds in limestone clasts from «Calcarene di Gravina» Formation near Monopoli, south of Bari. Scales in millimetres.

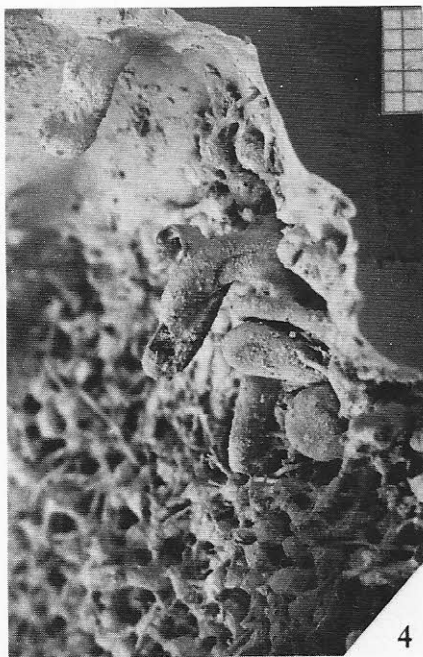
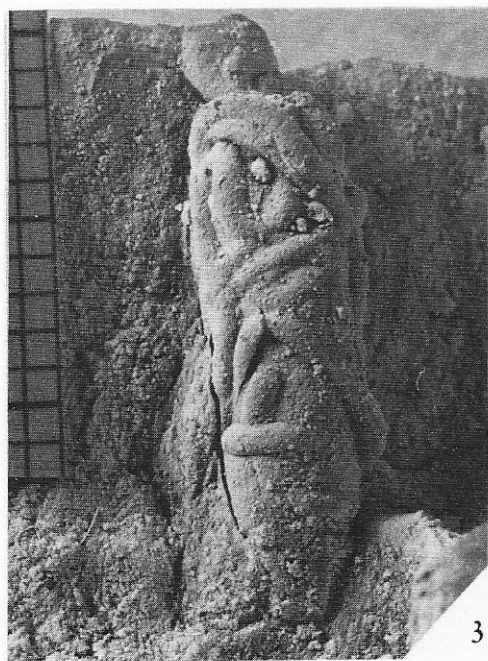
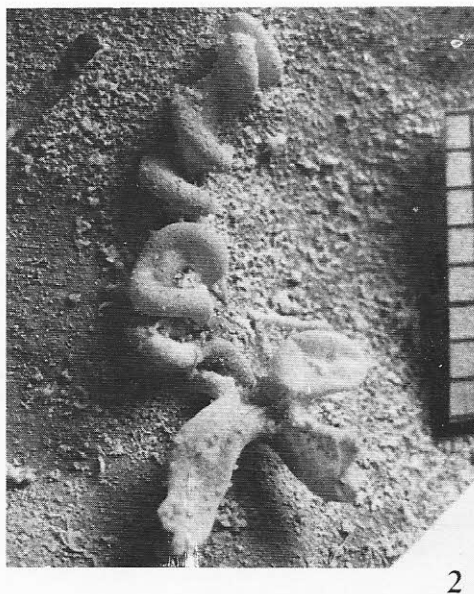
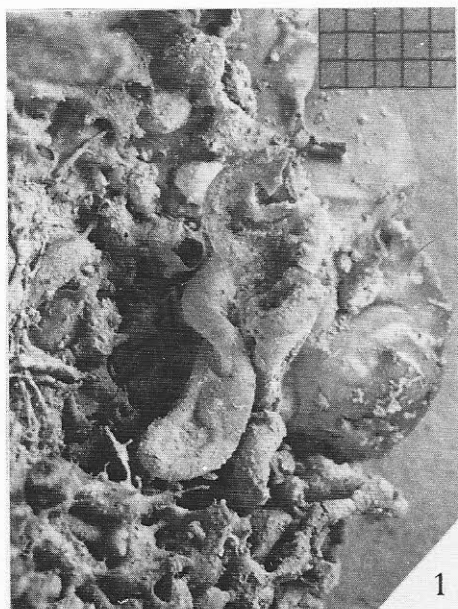


PLATE 24

Fig. 1, 3 – *Maeandropolydora decipiens* Voigt. Outer surface of oysters from uppermost Lower Campanian. Ivö Klach, Sweden. MGUH 16072 & 3.

Fig. 2 – *Maeandropolydora sulcans* Voigt. In a belemnite rostrum from Lower Campanian. Ivö Klach. MGUH 16074.

Scales in millimetres.

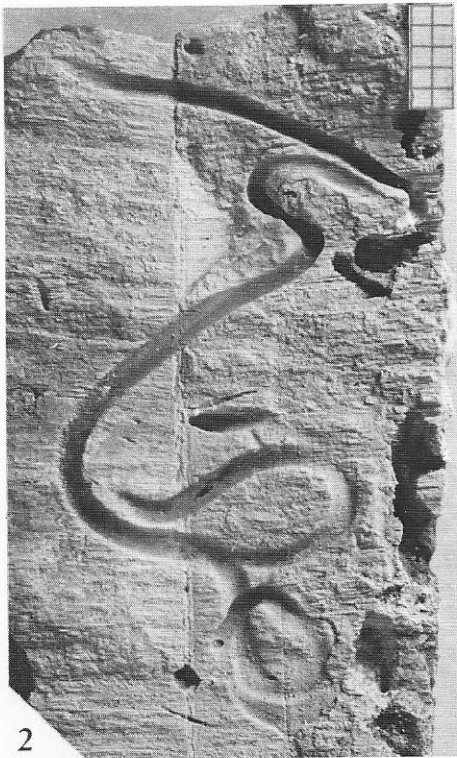


PLATE 25

Fig. 1 – *Maeandropolydora elegans* ichnosp. n. Holotype. MGUH 16059. It is accompanied by *Caulostrepsis contorta* (arrow). Artificial mould from boring in valve of *Ostrea edulis*.

Fig. 2 – *Caulostrepsis taeniola* Clarke. Artificial mould in pebble. MGUH 16075.

Fig. 3 – *Maeandropolydora decipiens* Voigt. A vane connecting the limbs is clearly visible (arrow). Artificial mould in pebble. MGUH 16076.

Fig. 4 – *Caulostrepsis contorta* ichnosp. n. Single element with a bilobed shape. Paratype MGUH 16058.

Scales in millimetres. All the artificial moulds are made in clasts or shells from Pleistocene «Calcarene di Gravina» Formation near Monopoli, south of Bari.

