BIOEROSION BY POLYDORA (POLYCHAETA, SEDENTARIA, VERMES) OFF HELGOLAND, GERMANY[1]

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ABSTRACT

Van der Pers, J. N. C. (1978). Bioerosion by *Polydora* (Polychaeta, Sedentaria, Vermes) off Helgoland, Germany. Geol. Mijnbouw, 57, p. 465-478.

The boring activities of *Polydora* BOSC. 1802, are an important agent in bioerosion. Trace fossils attributed to this worm are very common. From data collected on Recent representatives of *Polydora ciliata* JOHNSTON 1838, it is evident that the boring mechanism of this worm is to be interpreted as a combination of mechanical and chemical processes. *Dodecaceria,* another genus of polychaete worms, is considered to be able to bore chemically in lime-rich substrata.

INTRODUCTION

The present investigation deals with the boring activities of *Polydora* BOSC. 1802, an important agent in bioerosion. The study reported-upon deals mainly with *Polydora ciliata* JOHNSTON 1838.

The boring activity of *Polydora* was described first by SWAMMERDAM (1737), who observed a small worm penetrating the shell of *Littorina.* MCINTOSH (1868) attempted to find an explanation for the boring mechanism. SÖDERSTRÖM (1920) supposed chemical influences to play a role. HEMPEL (1957) contributed some arguments for a purely mechanical mechanism. In the author's opinion a combination of mechanical and chemical processes is most likely, although convincing arguments are still lacking.

Another genus of the polychaeta Sedentaria, dealt with in this paper, is *Dodecaceria.* This worm-type is also able to construct a borehole in calcareous substrates. For the interpretation and taxonomy of trace fossils attributed to *Polydora* and *Dodecaceria* it is imperative to know the Recent boring organisms and the processes which underly their particular behaviour. In this paper, attention is focused on these problems.

THE ANIMALS

The length of *Polydora* specimens may amount to 60 mm (average 15-20 mm). The number of segments in adult specimens is about 100. The body is subdivided into three regions (Fig. 1a): prostomium (the part in front of the mouth), metastomium (the segmented part behind the mouth) and pygidium. The prostomium has two mobile tentacles provided with cilia. These tentacles play an important role in feeding and in constructing the borehole. The segments of the metastomium are trapezoid-shaped and bear dorsal and ventral pairs of appendices; on both sides the noto- as well as neuropodia support the bristles and hooks (Fig. 1b). The shape of the bristles is used for specific determination. The most typical feature of *Polydora* is a pair of bundles consisting of relatively large bristles on both sides of the fifth segment. These bristles are important because of their function in shaping the bore-hole.

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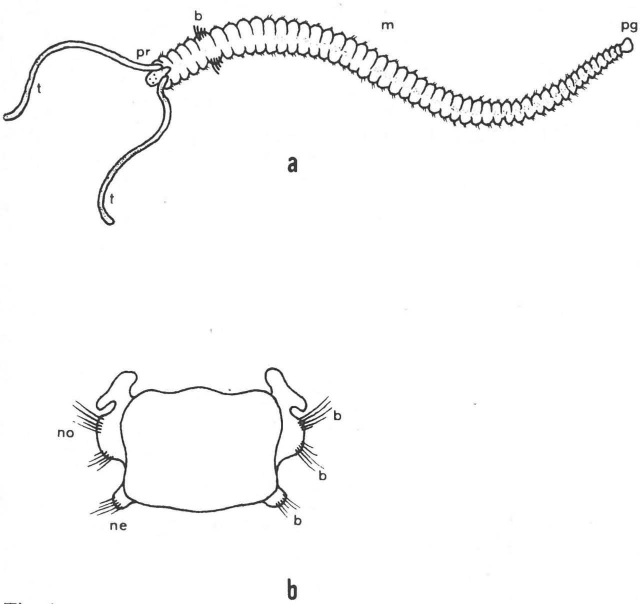


Fig. 1
a: *Polydora* outline. t: tentacles; pr: prostomium; b: modified bristles of the fifth segment; m: metastomium; pg: pygidium.
b: Crosssection of one segment. no: notopodium; ne: neuropodium; b: bristles.

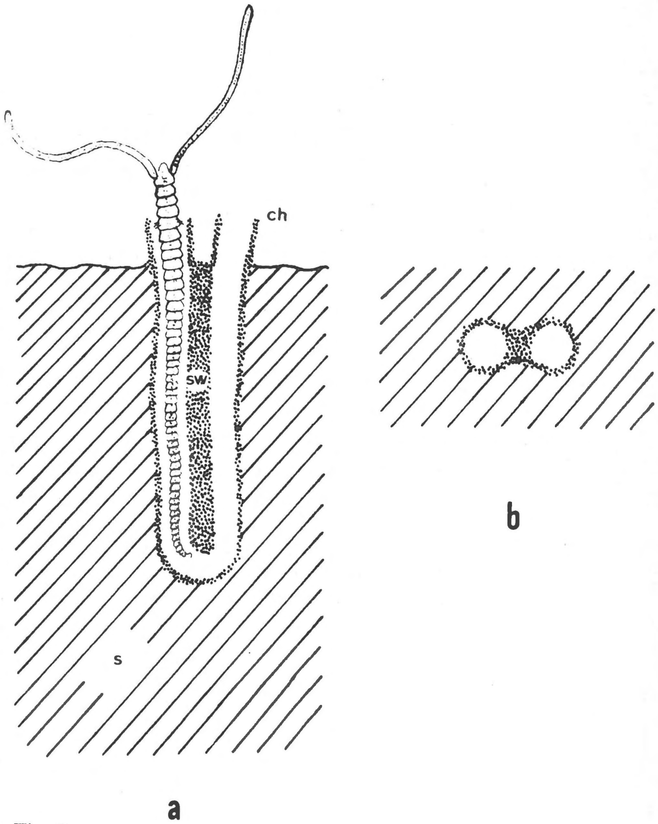


Fig. 2
a: *Polydora* inside its burrow; vertical section. s: substratum; ch: chimney; sw: separation wall.
b: Horizontal section of the burrow.

Polydora lives in a U-shaped cavity with a maximum length of 80 mm and a diameter varying from 1.0 to 1.5 mm (Fig. 2). The two limbs of the burrow protrude from the substratum, thus forming two chimney-like extensions. Inside, the burrows are lined by a wall composed of mucus and fine sand particles. The infilling between the limbs consists of sand and detritus, cemented together by mucus. *Polydora* burrows in unconsolidated sediment and bores in solid material, such as shells of living and dead molluscs. All indurated substrata, penetrated by *Polydora,* typically contain calcium carbonate.

Two specimens of *Dodecaceria concharum* were found boring in Triassic sandstones. Their tunnels are not U-shaped but flatly oval (Fig. 9). The inner wall is lined by a white aragonite layer. *D. concharum* bores a hole of about the same size as *Polydora ciliata* and in the same substratum, but *D. concharum* lacks the special 'bore-bristles'.

LOCALITIES

The material for this study was collected during the summer of 1973 in the sea around Helgoland, where *Polydora* occurs abundantly. Most of the investigations were carried out at the 'Biologische Anstalt Helgoland'.

The main part of the bottom of the North Sea and the German Bight consists of sand and mud with some scattered gravel banks. Helgoland mainly consists of Early Triassic sandstones (Buntsandstein). Eastward, the sandstones are overlain by Middle Triassic limestones and marls (Muschelkalk) and Cretaceous clays, marls and limestones, including large areas of soft chalk with embedded layers of flint (Fig. 3). More extensive information on Helgoland is provided by PRATJE (1923), WÜRSTER (1962) and HARTUNG (1970).

MATERIAL

Living material

Two species were studied in detail. These were identified as *Polydora ciliata* and *Dodecaceria concharum,* see also HARTMANN (1971).

Substratum

Fragments and boulders with living *Polydora* were collected from the different rocks around Helgoland. Four main types are distinguished:

(1) Soft Early Triassic sandstone with a considerable amount of $CaCO^{3}$.
(2) Soft Middle Triassic marl.
(3) Hard Middle Triassic limestone.
(4) Cretaceous chalk.

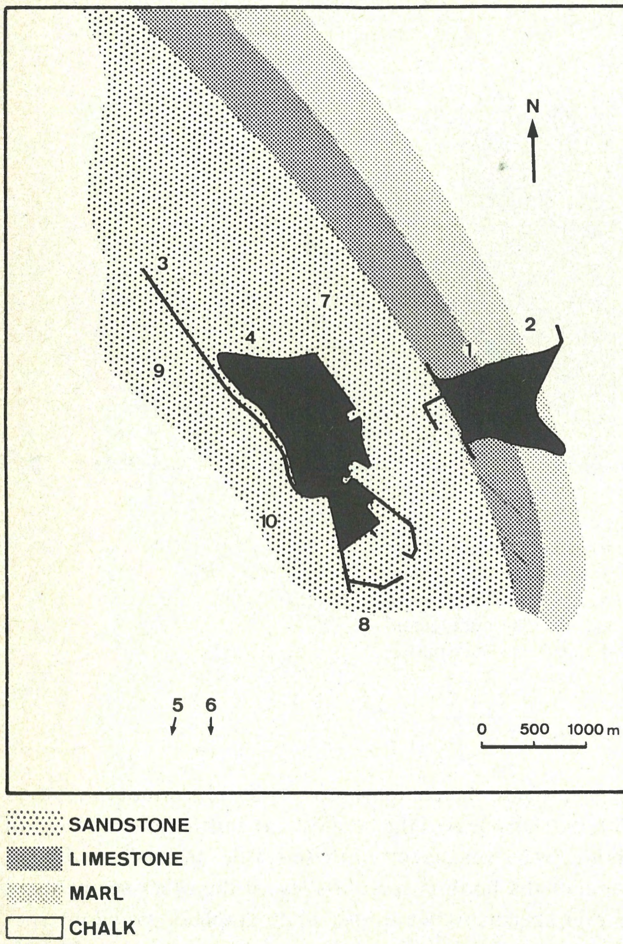


Fig. 3
Map of Helgoland. Left: main island; Right: dune island. The numbers indicate the sampling sites (Table I). Site 5: 'Austerngrund' 54° 10'0 N, 8°2'0 E. Site 6: 'Tiefe Rinne' 54° 8'3 N, 7°52'5 E.

Besides these rocks, two loose fragments of peat and some oyster shells were collected. All these specimens were infested by *Polydora,* the sandstones also by *Dodecaceria.*

METHODS

Sampling

Most of the material was collected by SCUBA-diving. Boulders and fragments were broken off with the help of chisel and hammer. These samples were placed as quickly as possible, mostly within half an hour, in aquaria supplied with running sea water of about 12°C. During low tide, boulder samples were taken from the northern rocky shore of Helgoland. From sites 5 and 6 (Fig. 3), samples were taken by drag-nets (Table I). Even the specimens collected first remained in good condition as long as two months in the aquaria.

Table I
Sampling sites (the numbers refer to Fig. 3), collecting method and substratum.

Site	method	substratum
1	diving	marl, limestone
2	diving	chalk, peat
3	diving	sandstone
4	gathering	sandstone
5	dredging	empty oyster shells
6	dredging	empty oyster shells
7	dredging	sandstone, limestone
8	diving	chalk, sandstone
9	diving	sandstone
10	diving	sandstone

Underwater observations were done on settlements of *Polydora* and its environments during diving. In the laboratory the living material and the substrata were studied with help of a stereomicroscope.

Preparation

Polydora is able to retract itself in its tube. It was observed that when a sample with *Polydora* stands in a disc without refreshing the water for about one day, the animals partly creep out of the tubes, thus allowing extraction of the animals from the substratum. After being put back into running seawater the animals recover quickly, thus remaining available for further examination. Through this procedure it was possible to study both the animal and the corresponding borehole without damaging either of these. Finally the animals were fixated in a solution of 4% formalin in filtered seawater.

Measuring

The size of the animal was measured from prostomium to pygidium, and the number of segments of the metastomium was counted. The average values of these numbers give an impression of the age and growth of the population in various substrata. The length and width of the bore-hole opening at the surface of the substratum was measured using an ocular micrometer.

serial sectioning

In order to check the interrelation between the shape of the borehole and the nature of the substratum it proved necessary to investigate the turn of the borings inside various substrata.

Small blocks were sawn out of three different rock types bored by *Polydora.* Perpendicular to the longitudinal axes of the bore-holes slices of 0.5 mm were cut off successively. The sections were photographed, the outlines of the dissected

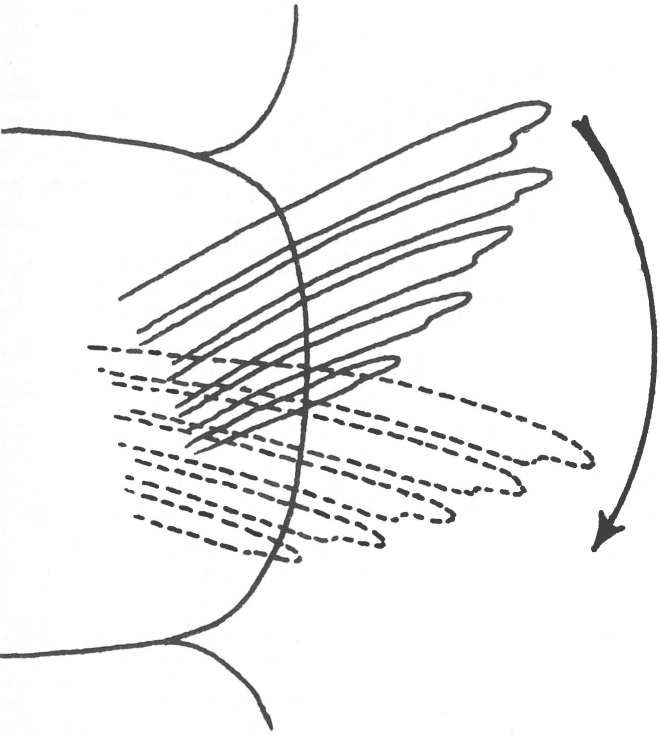


Fig. 4
Movement of the borebristles (schematic).

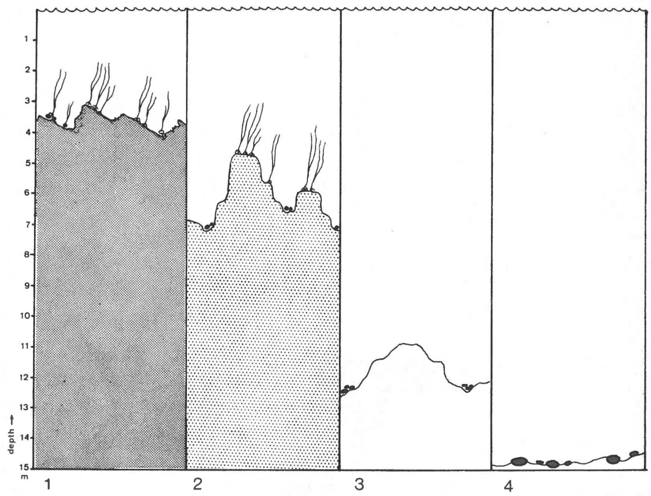


Fig. 5
Schematic bottom profiles.
1: north of the dune island.
2: west and north of the main island.
3: south of the main island.
4: the deeper sandy parts.

boreholes 10x enlarged and transferred onto perspex plates, measuring 10 cm square. Twenty-five of these plates (each corresponding to one saw-plane) were mounted in equidistant sequence. In this way a 3-dimensional view of the tubes inside the rock was obtained.

Scratchability determination

The various substrata differ considerably in mechanical properties, and *Polydora* has to deal with more or less resistance due to these properties. An appropriate measuring method should be analogous to the function of hardness.

Polydora was considered by HEMPEL (1957, 1960) to bore mechanically with the bristles of the fifth segment. The musculate belonging to these bristles is highly developed. It moves the bristles in a scraping fashion as shown in figure 4. A device analogous to this movement was constructed to simulate this movement. A perspex rod with a diameter of 2 mm pressed onto a sawn surface of the substratum. A counting mechanism registrated the number of movements. Before the test the tip of the rod was polished to avoid effects due to irregularities that will scratch the test-surface.

After a definite number of movements the depth of the groove in the substratum was measured with the micrometer. The tests were triplicated and, subsequently, repeated in seawater with 1% acetic acid.

Photography

To investigate the composition of the substratum in relation with the sharpness of the bristles of the fifth sigment, series of photographs were taken of these bristles in fresh specimens. Some of the hook-shaped bristles on the other segments of several specimens were also photographed. *Polydora* speciemens from different substrata were examined and SEM-photographed. Each image was photographed twice to obtain stereoscopic images. In this way the inner surface of some bore-holes could be examined as well.

X-ray analysis

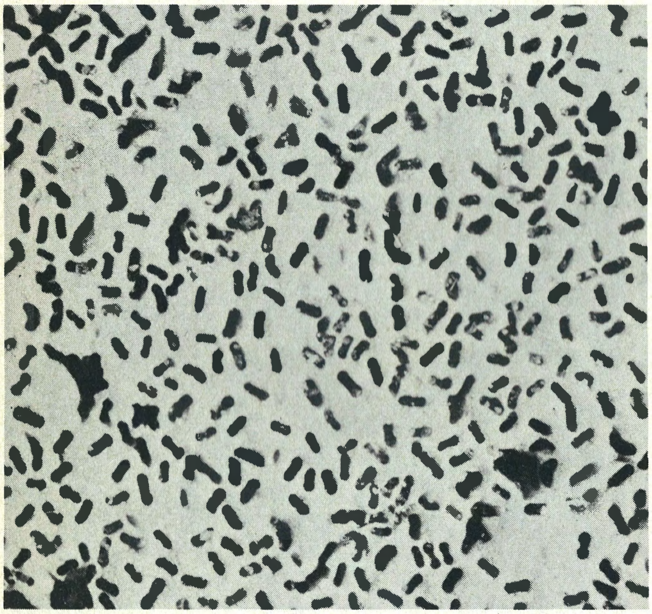
The inner wall of the the tube formed by *Dodecaceria* consists of calcium carbonate in different modifications. To determine the modifications, small amounts of powdered wall material were treated in a Debye-Scherrer camera for one hour with an X-ray beam emitted by a copper anode. The film was compared with standard diagrams.

RESULTS

Underwater observations

While diving, attention was paid to the influence of water movement and bottom features in relation to settlements of *Polydora*. Three main types of environment were distinguished.

North of the dune island, 1-5 m deep – It is densely settled with *Laminaria*. Between the rhizoids of *Laminaria* a suit-



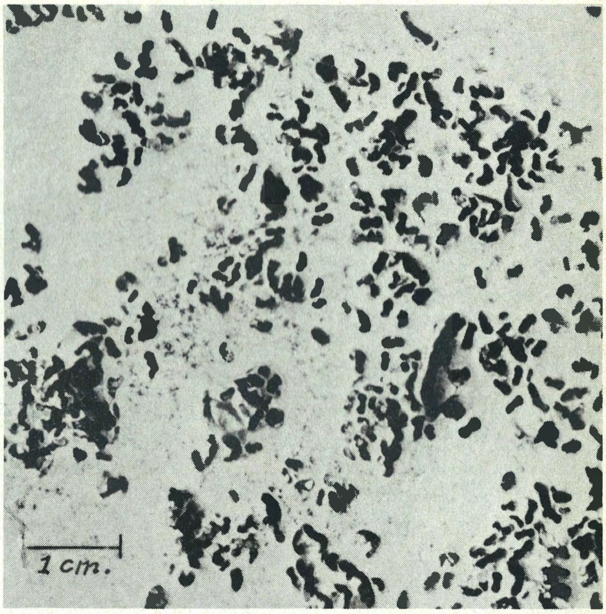


Fig. 6
Two sides of the same stone. One side more infested than the other side and with greater boreholes.

able hiding place is present, but not favoured by *Polydora ciliata.* However, the dense *Laminaria* forests smooth out water movements, thus making it easier for *P. ciliata* to settle at uncovered places.

In cross-section, the area appears saw-like (Fig. 5-11), almost vertical planes (roughly abrased) alternating with gently dipping smooth planes. *Polydora ciliata* was found to be mainly present on the face slopes, boring parallel to the stratification. In contrast, the horizontal surfaces (scoured by sand-loaden currents) are devoid of *P. ciliata,* although many boreholes and boring molluscs (*Barnea, Zirfaea* and *Petricola*) were seen.

Where boulders are found between a depth of 4 and 5 m and unexposed to strong water movements, *P. ciliata* bores on the smooth surfaces of these rock fragments. The upper and lateral parts of the boulders are covered by carpets of *P. ciliata* chimneys, while the lower sides show empty boreholes. It is assumed, that the density of boring of the stones is related to the duration of exposure to *P. ciliata* investation (Fig. 6).

South of the main island – Here the Cretaceous chalk is densely covered by a carpet of *Polydora ciliata* chimneys (Fig. 5-3). Unsettled spots are seen on Cretaceous flint and granite or quartzite erratics. The water depth varies between 5 and 15 m, thus too deep for algal settlement and with reduced effects of waves and tidal currents compared with the environment described above.

In these areas *Echinus esculentus* browses on these carpets, and large areas devoid of any *Polydora ciliata* result from this predacious activity. *E. esculentus* erodes the uppermost part of the rocky bottom as deep as the *Polydora ciliata* boreholes reach. This behaviour results in a high bioerosion rate since cleaned areas are resettled by *P. ciliata* within short time (KRUMBEIN & VAN DER PERS, 1974).

North of the main island – Mainly red Triassic sandstones are exposed in this area. The bottom consists of irregularly shaped ridges (Fig. 5-2). *Polydora ciliata* was less numerous, although still very common, compared to the previously described environments. Here also *P. ciliata* appeared to prefer settlement in grooves and bursts of the sandstone.

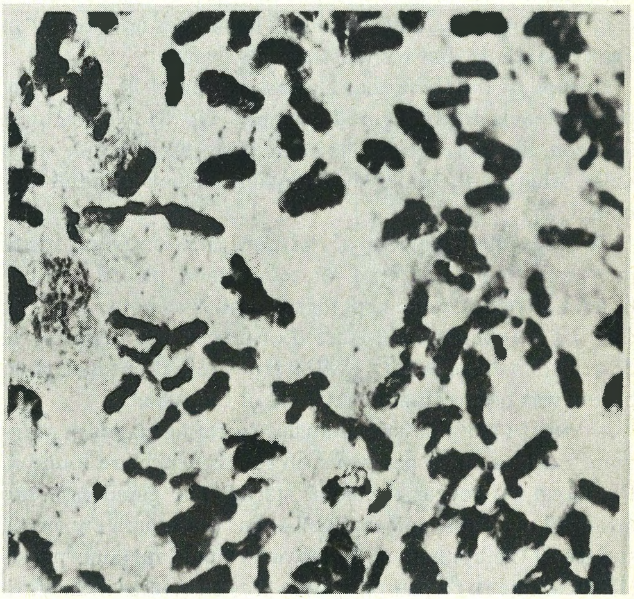


Fig. 7
Closely spaced burrows of varying sizes.

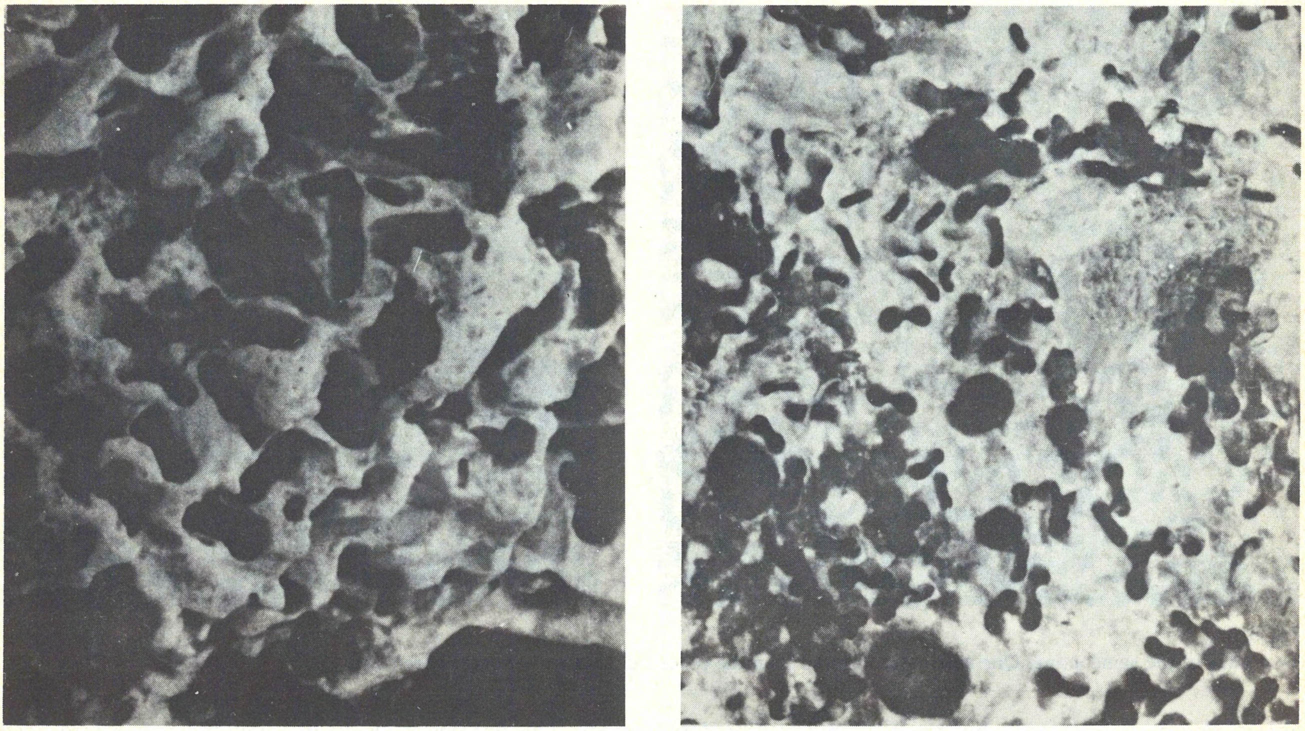


Fig. 8
Two fractures of different age in one stone; fracture a showing large burrows, fracture b small burrows.

Laboratory experiments

After removal of the worms from the hard substratum, the boreholes were examined microscopically. At many places, it was apparent how a new generation of *Polydora ciliata* settled on an already bored surface. Besides larger boreholes of adult animals, a number of much smaller ones was observed (Fig. 7). Obviously, a newly settled larva does not occupy an empty borehole, but will construct its own.

Groups of different year-classes are found in one single piece of rock. In the figured example (Fig. 8) two fractures are seen, the most recent one being perforated by only small holes, whereas the older shows mainly tunnels of adult animals.

To study the behaviour of *Polydora ciliata,* several specimens were removed from Cretaceous chalk, placed on a polished slab of chalk and kept for ten days in an aquarium. The first day a tube was constructed of mucus and particles, as described by DARO & POLK (1973). However, after ten days no boring was observed after removal of the tubes.

HANNERZ (1956) described mucus-secreting glands in *Polydora.* Each segment has two such glands which are found in the larval as well as the adult stages. The gland cells are arranged in a circle and each cell opens out separately on the surface of the epithelium. In larvae prone to metamorphosis (17-20 segments) a pair of opaque grey structures in the fifth segment, centrally to the bristles, represent the glands. These glands disappear after metamorphosis. For this reason, and because boring activity begins at a stage of at least 28 segments, HEMPEL (1960) drew the conclusion that *Polydora ciliata* bores exclusively mechanically by means of the modified bristles of the fifth segment. However, it is not excluded that the product of the glands in all other segments partake in a chemical phase because the mucus is slightly acid (HANNERZ, 1956).

As mentioned above *D. concharum* bores in the same substratum as *P. ciliata,* but lacks special 'bore-bristles' (Fig. 9). Obviously, such bristles are not undispensible for boring polychaetes.

Animal size

The number of segments of worms obtained from different substrata were counted (Fig. 10). It was found that there is no difference in the number of segments as related to the various substrata.

Bore-hole dimensions

From each of the four main substrata the length and width of 100 bore-hole openings were measured (Fig. 11 a-d). A large variation in the size of the boreholes is seen, but there is no apparent relation between substratum and bore-hole size, the ratio between length and width being rather uniform (Fig. 12). This ratio lies between 2.3 and 2.8, with an average of 2.5. Additional measurements of burrows in a small piece

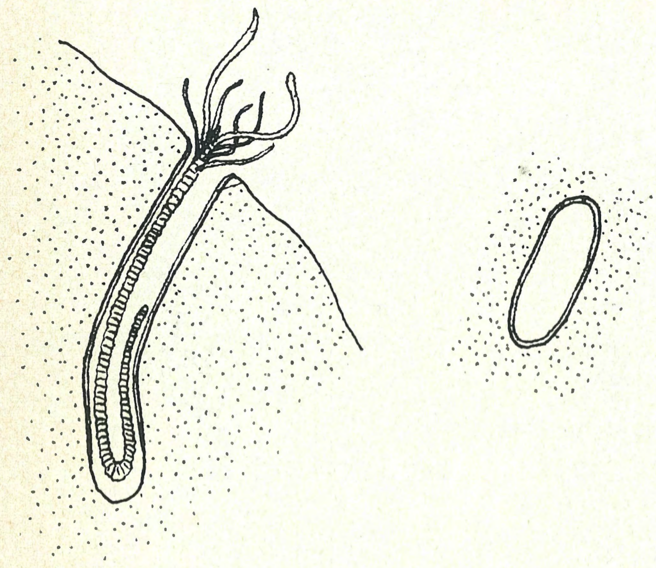


Fig. 9
Dodecaceria concharum inside its tunnel.
Left: longitudinal section; right: cross section of the tunnel.

Table II
Results of substratum hardness measurements.

substratum	*number of movements*	*depth of the groove* seawater	seawater with 1% acetic acid
sandstone	1000	1.62 mm	1.58 mm
		1.35	1.54
		1.46	1.67
marl	500	1.85	1.79
		1.73	1.87
		1.92	1.95
limestone	25000	0.05	0.11
		0.04	0.15
		0.04	0.17
chalk	25000	0.11	3.95
		0.08	4.03
		0.12	3.58
Nova Scotia limestone	25000	0.00	0.27
		0.00	0.29
	250000	0.00	0.25
		0.00	0.05 (with 0,1% acetic acid)

of peat show the same ratio (Fig. 11e). There exist only minor differences of this ratio between the various substrata and the average value of 2.5 appears to be characteristic for the investigated populations of *Polydora ciliata.*

Bore-hole shape

Many different forms of *Polydora* bore-holes were described from both shells of a great variety of living and dead molluscs and solid substrata.

The largest variety in shape was found in recent and fossil mollusc shells for various species of *Polydora,* as described by BLAKE & EVANS (1973). Many of these boreholes differ more or less from the basic form of the elongated U-shaped tube (Fig. 2). There exist unbranched as well as repeatedly branched forms, and mud blisters are also formed.

During the present study only unbranched boreholes were observed. The basic U-shaped borings are present in all rocky substrata. In most cases the borehole is slightly curved (Fig. 13). From the reconstruction of the turn of the borehole by serial sectioning of a piece of Triassic limestone it appeared that there is a tendency to diverge at the lower end of the borehole (Fig. 14). Obviously the animals avoid a crossing of

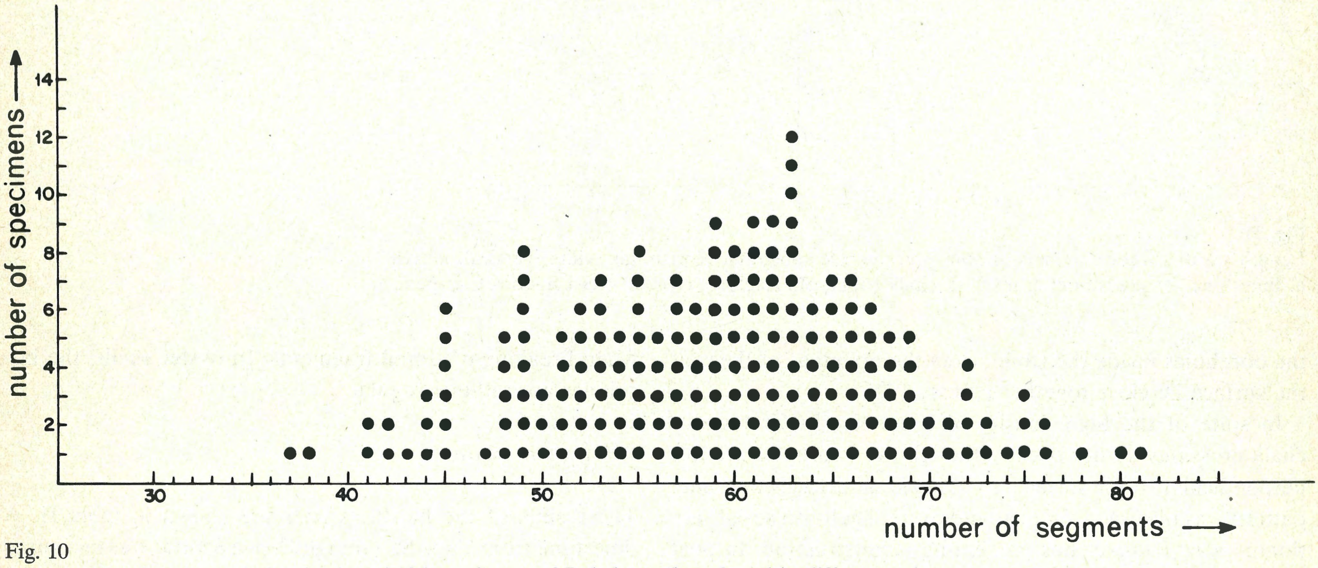


Fig. 10
Diagram showing the variation in size of 185 specimens of *Polydora ciliata* found in different substrata.

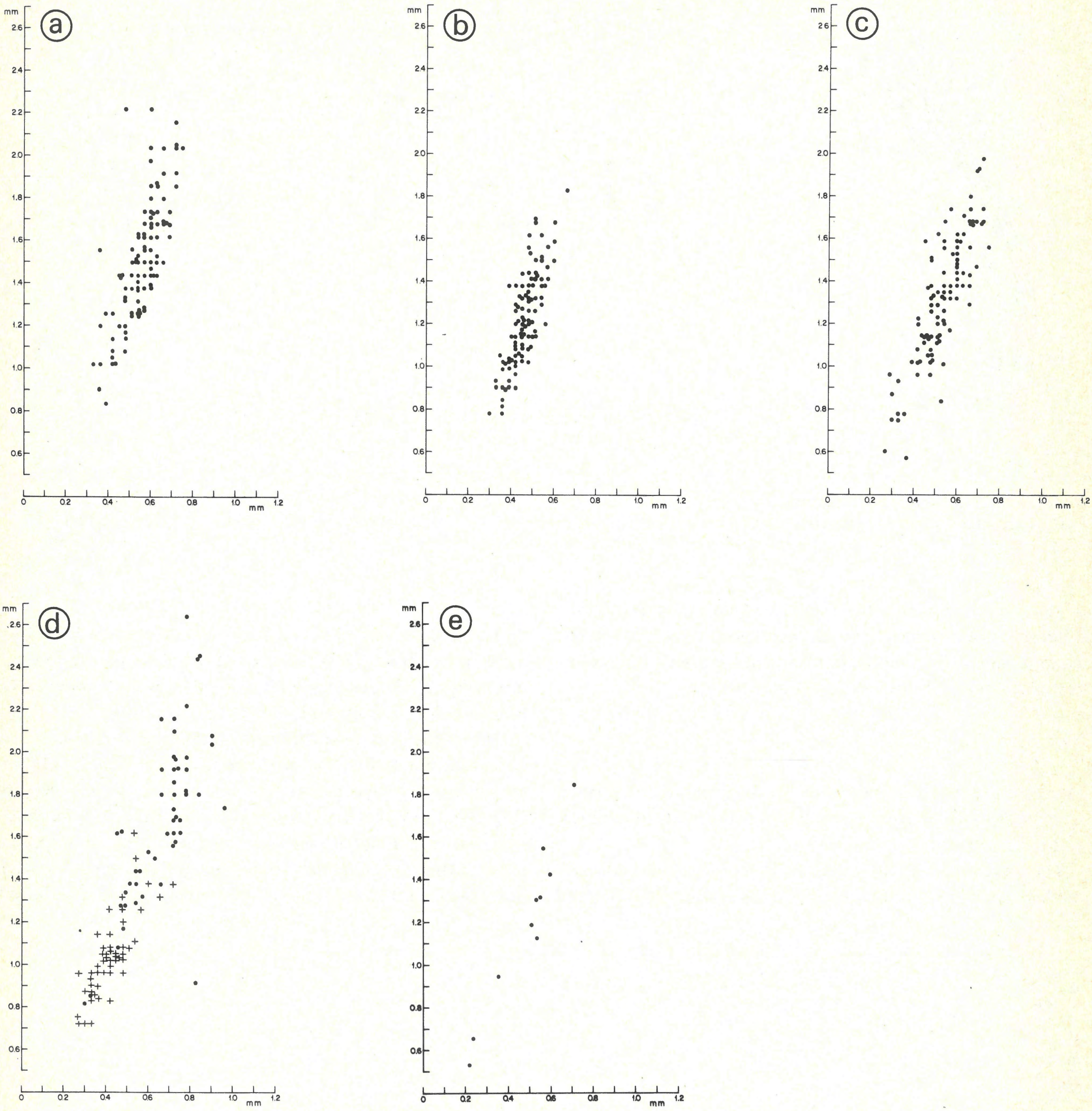


Fig. 11
Length/width scatter diagrams of bore-holes in five substrata. Horizontal: width; vertical: length.
a: limestone; b: sandstone; c: marl; d: chalk (dots: old fracture; crosses: fresh fracture); e: peat.

the boreholes inside the stone when the openings of these at the surface lie close together (PRELL, 1926).

In spite of the high density of boreholes in Cretaceous chalk crossings do not occur although the boreholes are not perpendicular to the surface. In Triassic sandstones the same pattern was observed. In peat and oyster shells no serial sectioning was possible thus preventing reconstruction. In peat the borings are similar to those in stone as was observed when breaking off small fragments. In oyster shells, the boreholes are rather irregular.

Substratum hardness

The results of the hardness tests are shown in table II. A limestone from Cape St. George (Nova Scotia) was measured as well. The influence of acetic acid on the erosion velocity,

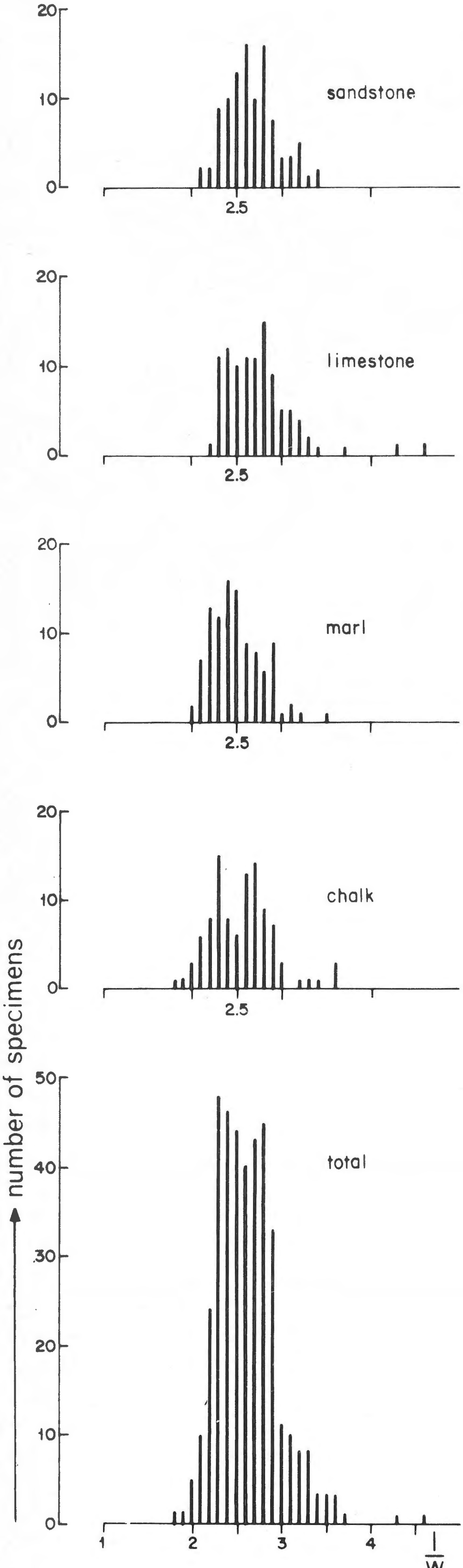


Fig 12
Length/width distribution of 100 boreholes in sandstone, limestone, marl and chalk and of the total number of the 400 specimens.

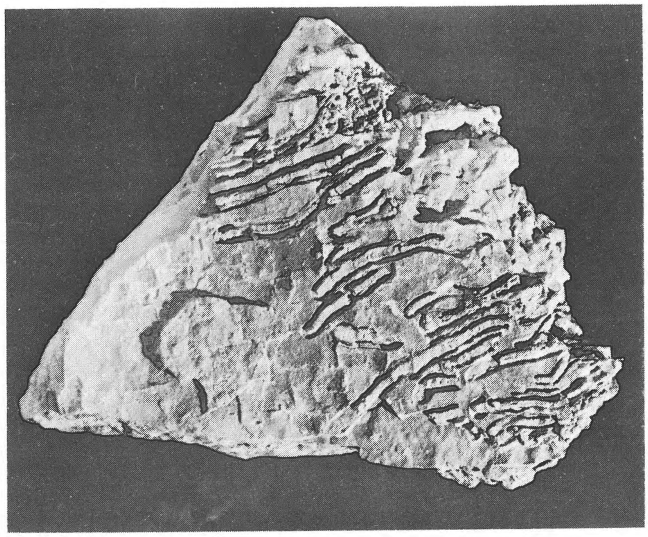


Fig. 13
Burrows of *Polydora ciliata* in marl.

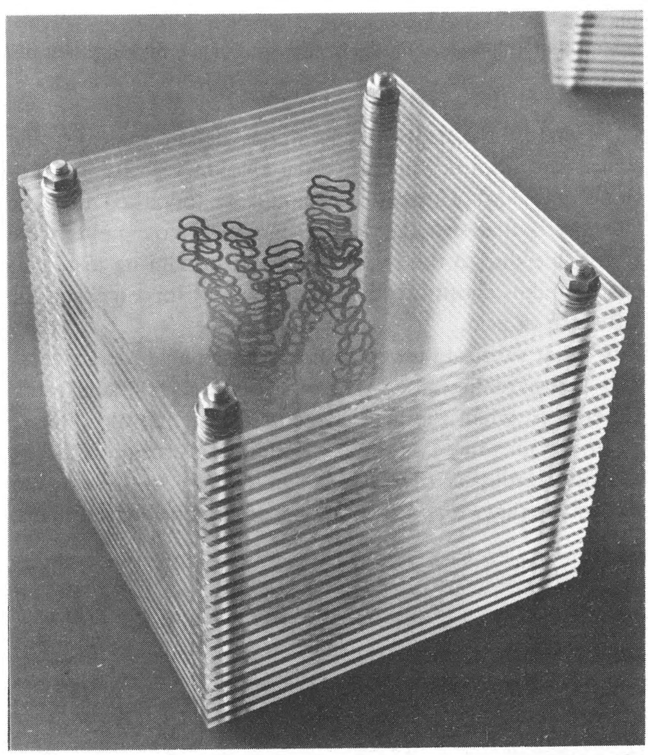


Fig. 14
Reconstruction of the turn of *Polydora ciliata* in chalk. The cube consists of 25 perspex plates, measuring 10 cm square, which is 10 times the actual size.

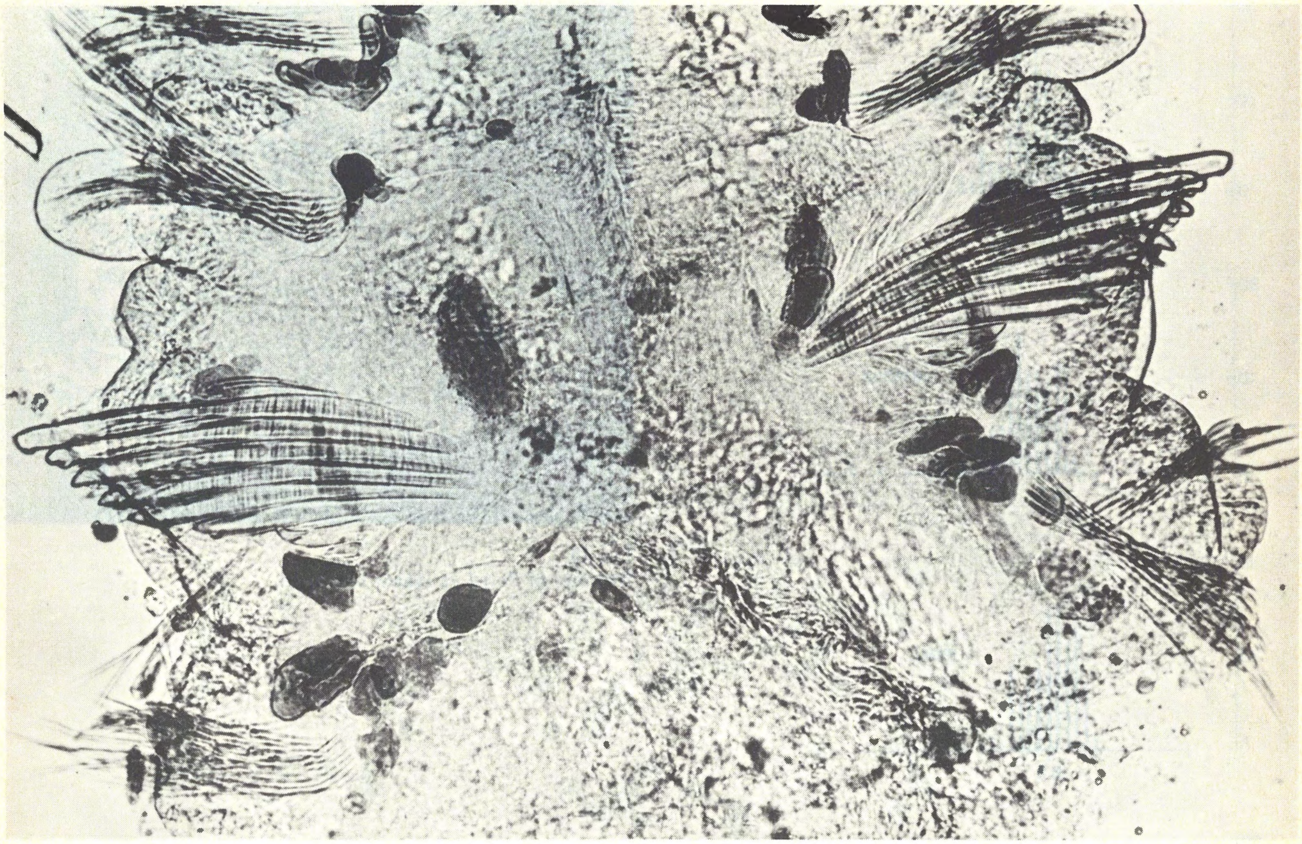


Fig. 15
Microphotograph showing the borebristles of the fifth segment of *Polydora ciliata* (400 X).

expressed by the depth of the groove marks, indicates that acetic acid does not influence the erosion velocity in sandstone and marl. However, it should be remarked that the material is that soft that more than 1000 movements were impossible due to the rapid desintegration during test. This process takes about two minutes, too short for a measurable influence of acid.

In other substrata the influence of acetic acid is considerable. The hard limestone of Nova Scotia shows clearly this effect even when the acid concentration is tenfold diluted. After 10^6 movements (about 40 hours) no erosion could be measured unless acid is present. On the basis of these results we assume that *Polydora* applies an acid in boring its tunnels.

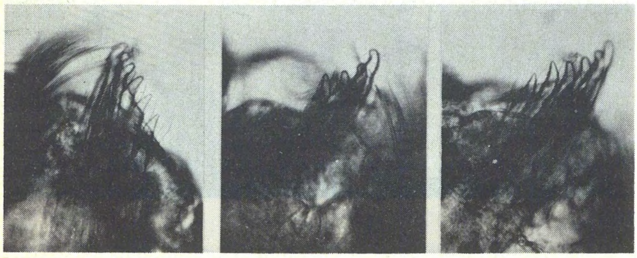


Fig. 16
Microphotographs of *Polydora ciliata* borebristles from oyster shells.

Wear of bristles

HEMPEL (1957) compared the bristles of the fifth segment (Fig. 15) of specimens of *Polydora ciliata* that bored in a shell with those that construct a tube in loose sediment. She observed that the tips of the bristles of the former were rounded, whereas those of the latter were sharply pointed. Consequently, it was concluded that *P. ciliata* bores in a mechanical way only.

On the present investigation the bristles of *P. ciliata* boring in oyster shells, sandstone, marl, limestone and chalk were carefully observed. Although these substrates differ markedly in hardness, no correlation between the wear of the bore-bristles and the hardness of the bored substratum could be found. Figure 16 shows three borebristles of *P. ciliata* from oyster shells; figure 17 a-d those from Cretaceous chalk, Triassic marl, Triassic limestone and Triassic sandstone, respectively. Some bristles have rounded tips, mostly only the first (and longest) bristle, but with no correlation between roundness -or wear- and the hardness of the bored material.

On the other hand, there appears to exist a negative correlation between bristle erosion and calcium carbonate content of the bored substratum. Sandstone containing about 20% $CaCO^3$ carries *Polydora* bristles with a relatively high

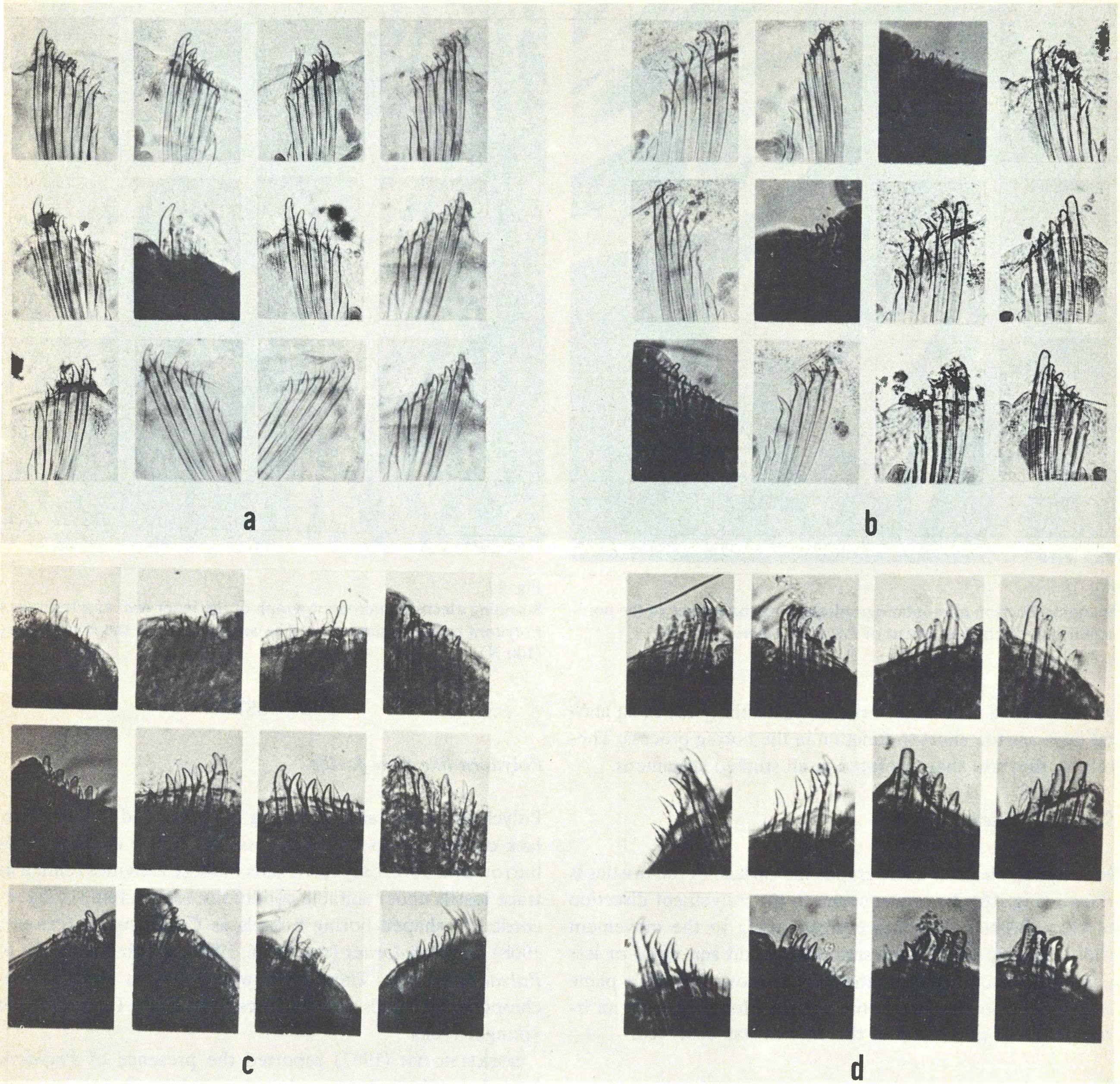


Fig. 17
Microphotographs of *Polydora ciliata* borebristles from: a: chalk; b: marl; c: limestone; and d: sandstone.

degree of wear, whereas chalk with more than 95% of $CaCO_3$ does scarcely erode the bristles, as demonstrated by the microphotographs. This relationship is only understandable when it is assumed that in the boring process an acid desintegrates the chalky substance in the stone. The measurements cited on the hardness of the substratum, with and without acid dissolved in the sea water (see above), point to the same explanation. It is assumed that by the action of the acid the limecement can be dissolved, thus loosening the particles, which, subsequently, can be removed by the aid of the bristles, similarly as *Polydora ciliata* does in soft-sediment substrata. In case of lime-cemented sandstones with low amounts of $CaCO_3$, many sand particles are to be removed, thus causing a high degree of wear on the bristles. In case of chalks with a very high $CaCO_3$ content and only a few siliceous particles to be removed, the opposite is true.

From the microphotographs it is evident that not all bristles of specimens that bored in sandstones are equally worn. In some cases, a juvenile *Polydora* may have used an empty borehole and thus the bristles will have remained sharp. However, it was observed that most larvae bored in or close to the wall of old boreholes.

Unequal wear can be explained also by assuming replacement of bristles. In case of wear the longest bristles are al-

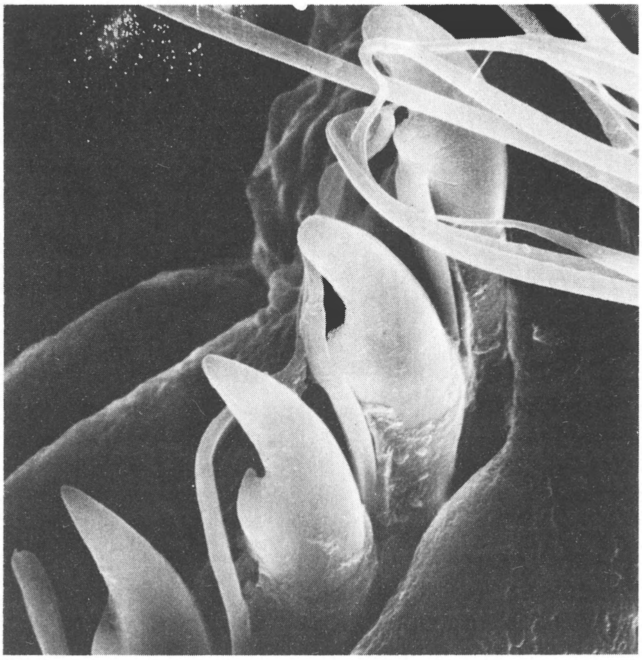


Fig. 18
Scanning electron microphotograph showing the surface of the bore-bristles on the fifth segment of *Polydora ciliata* (2500 X).

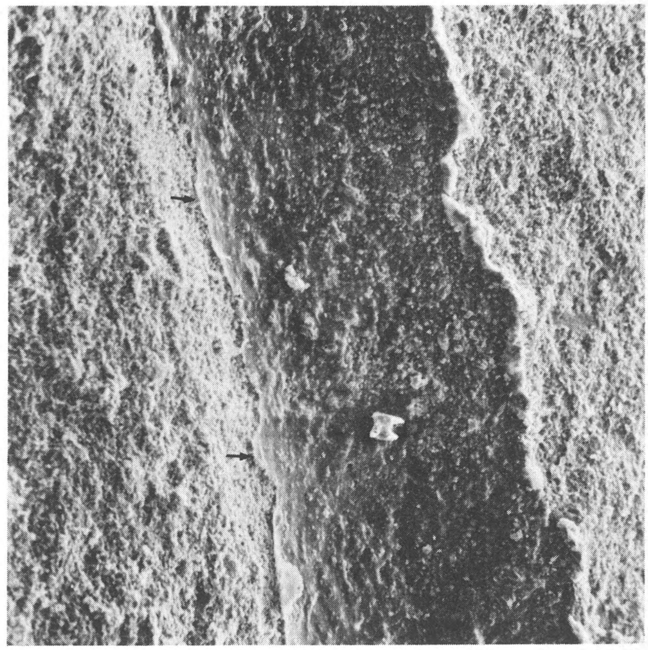


Fig. 19
Scanning electron microphotograph of the inner wall of a burrow of *Polydora ciliata* in sandstone. The arrow indicates the mucus lining (100 X).

ways rounded. The other bristles, particularly the most aboral ones are too short to function in the boring process. Therefore, they are sharp-pointed in all studied specimens.

Surface of bristles

In scanning electron micrographs the surface of the bristles is shown (Fig. 18). In consequence to the movement direction of these bristles scratches corresponding to the movement should be expected. Such scratches would run more or less parallel to each other, as the bristles move only in a plane longitudinal to the axis of the animal. However, only an irregular relief at the top of the bristles was observed.

Inner wall of the burrows

In literature on *Polydora,* little attention has been paid to the mucuous layer covering the inner wall of the *Polydora* tunnel. DORSETT (1961) observed that the mucus covers the entire wall of the *P. ciliata* bore-hole but for a small section at the bottom of the tunnel where the animal deepens the borehole. This mucus, according to EWER & HANSON (1945), was identified as an acid mucopolysaccharide. HANNERZ (1956) observed the weak acid reaction of this substance. Dorsett nor Hannerz did consider this etching quality as a factor in the boring mechanism.

The mucus lining is demonstrated in figure 19. It is seen that particles of the bore-hole wall adhere to the mucuous tube.

DISCUSSION

Polydora-like trace fossils

Polychaete sedentaria, including *Polydora* and *Dodecaceria,* lack chitinous jaws that may fossilize. As far as these types burrow and bore, only the results of these activities remain as trace fossils under suitable conditions. HÄNTSCHEL (1975) recorded U-shaped boring tunnels as *Caulostrepsis* (CLARKE, 1908) and *Polydorites* (DOUVILLÉ, 1908), which are similar to *Polydora*-borings. These types were found in shells of brachiopods, echinoids and molluscs from Early Devonian and younger rocks.

BOEKSCHOTEN (1967) reported the presence of *Polydora* bore-holes, both U-shaped and mud-blisters, in clam and oyster shells from the Pliocene Tielrode sands of Belgium.

From the Santonian conglomerates from the area north of the Harz Mountains, VOIGT (1970) reported casts of bore-holes, a number of which he identified as *Dodecaceria* sp.

By comparison with boreholes of Recent boring worms one tries to interpret fossil boreholes as traces of animals similar to the living forms. It is rather difficult to apply this method to *Polydora*-like boreholes because of the confused taxonomy of this genus. Here, it is suggested to identify fossil borings in consolidated substrata only as due to Polydorid worms when these show the following features: (1) the opening and cross section of the borehole resemble a dumb-bell (this shape results from the presence of a secondary separation wall – the so-called 'Spreite'-secreted at time the worm

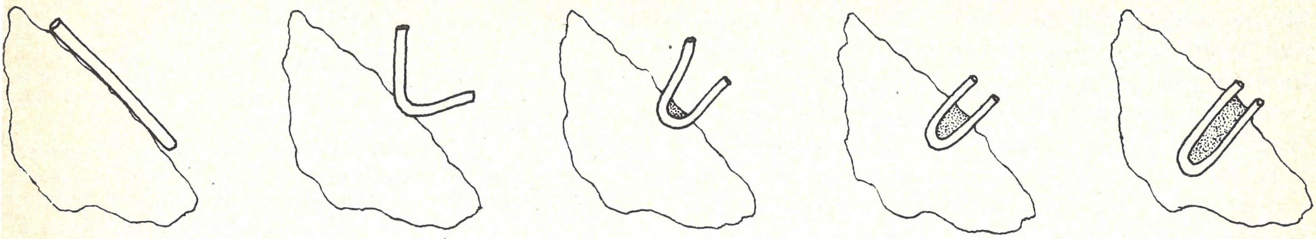


Fig. 20
Stages in the development of the *P. ciliata* burrow in stone. White: stone; dotted: intermediate wall. (after Söderström, 1923).

was living); (2) the length/width ratio of the opening amounts to approximately 2.5; (3) the absence of crossings between adjacent boreholes. As the dimensions of the individuals differ largely and the average size of a population depends on environmental conditions such as salinity (LUNZ, 1941, LOOSANOFF & ENGLE, 1943), food supply and water movements, no definite size is typical for a *Polydora* borehole. Nevertheless, a minimum size is prevented by the dimensions of the juvenile worm at the time it is able to penetrate the substratum.

The smallest borehole measured 0.6 to 0.27 mm in cross section, whereas the largest one measured 2.64 to 0.78 mm. In contrast to the relatively simple borehole in stony substrata the shape of the polydorid tunnels in mollusc shells is more complex. Consequently, no specific determinations are possible on basis of the shape of the borehole of *Polydora.* Besides, there appears to be no relation between the shape of the borehole of *Polydora,* the species of the host, and the quality of the substratum. However, the activity of *Polydora* can provide more insight in the palaeoecology of the infested animals (BOEKSCHOTEN, 1966).

Boring organisms like *Polydora* are also important in bioerosion of limestone coasts (NEUMANN, 1968). This erosion can be intensified when the boring worms are predated by sea-urchins (KRUMBEIN & VAN DER PERS, 1974). According to the X-ray analysis the inner wall of the borehole constructed by *Dodecaceria concharum* appeared to be $CaCO^3$, crystallized as aragonite. Thus, it is possible to recognize a fossil borehole as a structure formed by an organism similar to Recent *Dodecaceria,* provided the aragonite coating is preserved.

The boring mechanism

There are three processes of penetration into solid materials: (1) mechanical, (2) chemical, (3) a combination of mechanical and chemical means. Despite all arguments in favour of a definite mechanism produced by various investigators, *Polydora*-boring remains controversial up to the present time. SÖDERSTRÖM (1920) emphasized mechanical abrasion by the modified bristles of the fifth segment. He demonstrated that the U-shaped borehole resulted from an originally undivided hole in which an intermediate wall of mucus and loose particles was built (Fig. 20). He suggested in that paper that boring was a joint effect of chemical erosion by an acid secreted by the segmental glands, and mechanical abrasion by the bristles of the fifth segment. In 1923, however, he suggested that the bristles were used as a means of support or adhesion during ventilation or feeding, and served as boring tools without chemical preparation. Also HANNERZ (1956) examined the mucus-secreting glands and assumed that the mucus converts the lime into a more easily workable substance which is subsequently eroded by using the bristles. Since the glands of setiger five disappear after the metamorphosis he asserted that boring was accomplished entirely with the aid of the bristles. HEMPEL (1957) favoured mechanical boring of *P. ciliata* by means of the bristles as the bristles of a specimen that bored in a shell were worn in contrast to the sharp bristles of a specimen that built a tube in loose sediment.

Because of the acid reaction of the mucus secreted by the glands in every segment and the musculature of the 'bore bristles', DORSETT (1961) suggested that the boring mechanism is a combination of mechanical and chemical effects. A bristle similar to *Polydora* bristles was applied against a block of limestone for 112 hours with a pressure of 10 g. The rock showed no sign of abrasion, although the bristle was a little shorter. It was concluded that the substance of the bristles of Polychaeta was too soft to excavate in limestone. HAIGLER (1969) even removed the bristles of setiger five of *P. websteri* boring in solid substrata and found that the animal could still bore!

The arguments for mechanical boring are inconclusive because:

(1) the wear of the bristles of the fifth segment varies in a definite substratum and cannot be correlated with the hardness of various substrata;
(2) the top of these bristles is not worn in the direction in which they move and parallel scratches are not visible;
(3) mechanical abrasion of limestone in which *Polydora* bores is facilitated by using diluted acetic acid. In substrates with a high percentage of calcium carbonate the wear of the bristles tend to be less than in substrates containing more material that is insoluble in acetic acid;
(4) if *Polydora* bores with the aid of the bore-bristles only, the process applied by *Dodecaceria* without such bristles would be mysterious unless an acid solvent is assumed.

Notwithstanding the above, *Polydora* also bores into peat as well as into the soft and rotten outer layers of wooden piles (DORSETT, 1966). An acid is useless in the penetration of such materials. Consequently, the boring mechanism has to be imagined as a combination of mechanical and chemical effects.

According to observations of SÖDERSTRÖM (1923) and subsequent authors, the juvenile *Polydora* begins to construct a mucuous tube on the surface of the substratum after settlement, Gradually the substratum is penetrated, the legs of the tube tending to run parallel and the intermediate wall being formed (HEMPEL, 1957). It is evident that deepening is only possible after removal of the mucus layer covering that part of the substratum that is to be abraded. This should be the case in any stage of enlargement of the hole.

Due to the adhesive qualities of the mucuous sheet, particles of the substratum joined to the mucus must be withdrawn during removal of the layer by the worm. In limestone, the weak acid nature of the mucus will facilitate this process. Thus, a small quantity of the substratum is abraded. Subsequently, a new mucus lining is secreted on the fresh wall of the enlarged tunnel. By repetition of this process the bore hole is gradually enlarged. This mechanism is also effective in soft wood, peat and shale. According to the present author, all bristles including the hook-shaped chaetae are active. The modified bristles of the fifth segment serve as scrapers and anchors.

The boring mechanism of *Dodecaceria* should be different, as this polychate does not cover its bore-hole wall with a mucuous film. In case *Dodecaceria* bores in about the same way as *Polydora,* the aragonite layer on the inner wall must also be removed frequently during enlargement of the bore-hole. This is only possible by dissolution of this layer by an acid secreted by the worm. Consequently, *Dodecaceria* must bore in a chemical way in lime-rich substrata.

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