

## Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.

With 6 Text-Figures, 4 Tables, and 5 Plates.

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### Abstract.

[HOEKSEMA, B. W. (1983): Excavation patterns and spiculae dimensions of the boring sponge *Cliona celata* from the SW Netherlands. — *Senckenbergiana marit.*, 15 (1/3): 55-85, 6 figs., 4 tabs., 5 pls.; Frankfurt a. M.]

Actuopaleontological aspects of *Cliona celata* from the Dutch Delta Region were investigated. This tunneling sponge occurs abundantly in limestone boulders and in shells of *Ostrea edulis*, *Crassostrea gigas* and *Crepidula fornicata*. Ostial and oscular papillae protrude from the substratum surface through perforations.

All found spicules are tylostyles. The length of the tylostyles prepared from ostial papillae is positively correlated with the diameter of the perforations which contain these papillae. The tylostyle diameter is not correlated with the perforation size.

Reproduction apparently is mainly asexual. Excavation patterns in the substrata are described. Mathematical models of perforation-rates and -patterns are applied to describe the relative age of sponge parts in oyster-shells. Interactions of sponge tunneling with borings of two polychaete worms, *Polydora ciliata* and *P. hoplura*, are studied.

In the Dutch Delta Region only the  $\alpha$ - and the  $\beta$ -stage of *Cliona celata* are found. Therefore the  $\gamma$ -stage was collected near Roscoff, France, to measure tylostyle length and papillae distribution.

### Kurzfassung.

[HOEKSEMA, B. W. (1983): Bohrformen und Spiculae-Formen des Bohrschwammes *Cliona celata* in den südwestlichen Niederlanden. — *Senckenbergiana marit.*, 15 (1/3): 55-85, 6 Abb., 4 Tab., 5 Taf.; Frankfurt a. M.]

Untersucht wurden die Bohrformen des Bohrschwammes *Cliona celata* im niederländischen Deltagebiet. Dieser Bohrschwamm ist ein häufiger Besiedler von Kalkbruchstücken und -geröllen und von Schalen der Austern *Ostrea edulis*, *Crassostrea gigas* und der Pantoffelschnecke *Crepidula fornicata*. Die Bohrgänge der Schwämme münden mit ihren Ostial- und Oscularpapillen an die Oberfläche des jeweiligen Substrates.

Alle gefundenen Spiculae sind Tylostyle. Die Längen der Tylostyle aus den Ostialpapillen sind positiv korreliert mit dem Durchmesser der zugehörigen Bohrlöcher. Der Tylostyldurchmesser zeigt keine Korrelation mit der Bohrlochgröße.

Die Vermehrung von *Cliona celata* ist zumeist ungeschlechtlich. — Beschrieben werden die Bohrlochformen in den unterschiedlichen Substraten. Es werden mathematische Modelle für Bohrleistungen und Bohrungsformen entwickelt zur Bestimmung des relativen Alters von Schwammteilen in Austernschalen. Untersucht wurde auch das Ineinandergreifen der Bohrgänge von *Cliona celata* und der beiden bohrenden Polychaetenarten *Polydora ciliata* und *P. hoplura*.

Im niederländischen Deltagebiet wurden nur die  $\alpha$ - und  $\beta$ -Stadien gefunden. Die  $\gamma$ -Stadien wurden bei Roscoff, Frankreich, untersucht, um Tylostyllängen und Papillenverteilungen zu ermitteln.

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## Introduction.

Sponges of the family Clionidae (Demospongiae) have the ability to excavate hard calcareous substrata. Much attention has been paid to these animals because of their capacity to destroy the shells of commercially important molluscs. Besides bivalves like oysters (OLD 1942; KORRINGA 1951b; HOPKINS 1956; WARBURTON 1958a; KRAKATITSA & KAMINSKAYA 1979) also gastropods like *Haliotis* are attacked by *Cliona* (HANSEN 1970).

Clionids have ecological and geological significance as bioeroders (RÜTZLER 1975; BAK 1976; MACGEACHY 1977). The borings of *Cliona* can be of paleontological importance as trace fossils that may be used as paleoecological guides (FISCHER 1868; BOEKSCHOTEN 1966, 1967; LAWRENCE 1969; BROMLEY 1970; GARGOURI 1982).

The morphology and physiology of boring sponges are of interest because of their specialized substratum tunneling. POMPONI (1980) reviewed the cytological mechanisms of calcium carbonate excavation. GOREAU & HARTMAN (1963) described the water circulation system in *Cliona*.

The eurythermal cosmopolitan species *Cliona celata* Grant has first been described from the coast of Scotland, living in oyster-shells (GRANT 1826). HANCOCK (1849) gave more morphological information on borings and silicious monaxial spicules of specimens from about the same locality. TOPSENT (1887) distinguished three successive forms of *C. celata* from the Calvados coast: boring into calcareous

material, encrusting the eroded substratum and massive without remnants of the original substratum. VOSMAER (1933-1935) called these successive forms later respectively  $\alpha$ -,  $\beta$ - and  $\gamma$ -stage.

The purpose of this study is to provide paleobiological studies of clionids with a firm actuopaleontological basis. The widespread occurrence of *Cliona celata* in the Delta Region of the Netherlands presented an opportunity for this research.

## The Area of Investigation.

During spring and summer of 1981 specimens of *Cliona celata* and their substrata were sampled in two former estuaries in the Dutch Delta Region, SW Netherlands. The Grevelingen Lake (Fig. 1A) has been disconnected from the rivers Rhine, Waal and Meuse since 1964 and from the North Sea since 1971. In 1978 an underwater sluice was opened which allows sea-water inflow from the North Sea (see NIENHUIS 1978). The sea-arm Eastern Scheldt (Fig. 1B) was cut off from river-water supply in 1969; it still opens to the west in the North Sea.

In both waters oysters from oyster-beds were fished with a dredge. The breakwaters, dams and dikes surrounding both waters are for a great part covered with limestone. Here samples were obtained by SCUBA-diving.

## The Substrata.

The first casual observations of *Cliona celata* in the Eastern Scheldt had been made during the 1881-1883 investigations of the Dutch oyster-beds. Afterwards, in 1886, the sponge became a pest there (HOEK 1902). KORRINGA (1951b) found the boring sponge on the oysterbeds only rarely, but he was more successful in finding them in old oyster-shells attached to dikes.

In the Grevelingen Lake (Fig. 1A) most oysters fished were five or more years old, but did not show traces of *Cliona*-infection. Many oyster-shells had a black coloured hinge region. In situ inspected oysters were living with the flat right valve up. The hinge region and a great part of the convex left valve were buried in the mud. As at the locations dredged, the flat valves were covered with epifauna, but did not contain *Cliona*.

Diving near the dike at Dreischor and Scharendijke and on the submerged remains of the drowned town Bommenede (west of Veermansplaat) produced many living specimens of *Cliona celata*. There the boring sponge was common in limestone, in oyster-shells (*Ostrea edulis* L.) and in shells of the slipper-limpet, *Crepidula fornicata* (L.).

Most of the infected oysters lived attached to limestone boulders which were also penetrated by *Cliona*. Only 19 of the 26 infected doublets contained the living mollusc. Six single left valves were collected from the stones. Three living specimens of *Crepidula* were sampled. Infected shells without the living gastropod were gathered between the boulders. In a boulder of white Eocene limestone off Bommenede an affected shell of *Venerupis pullastra* (MONTAGU) was found. Barnacle-shells (*Balanus*) on affected oyster-shells may also become penetrated by *Cliona* (Pl. 5 fig. 22).

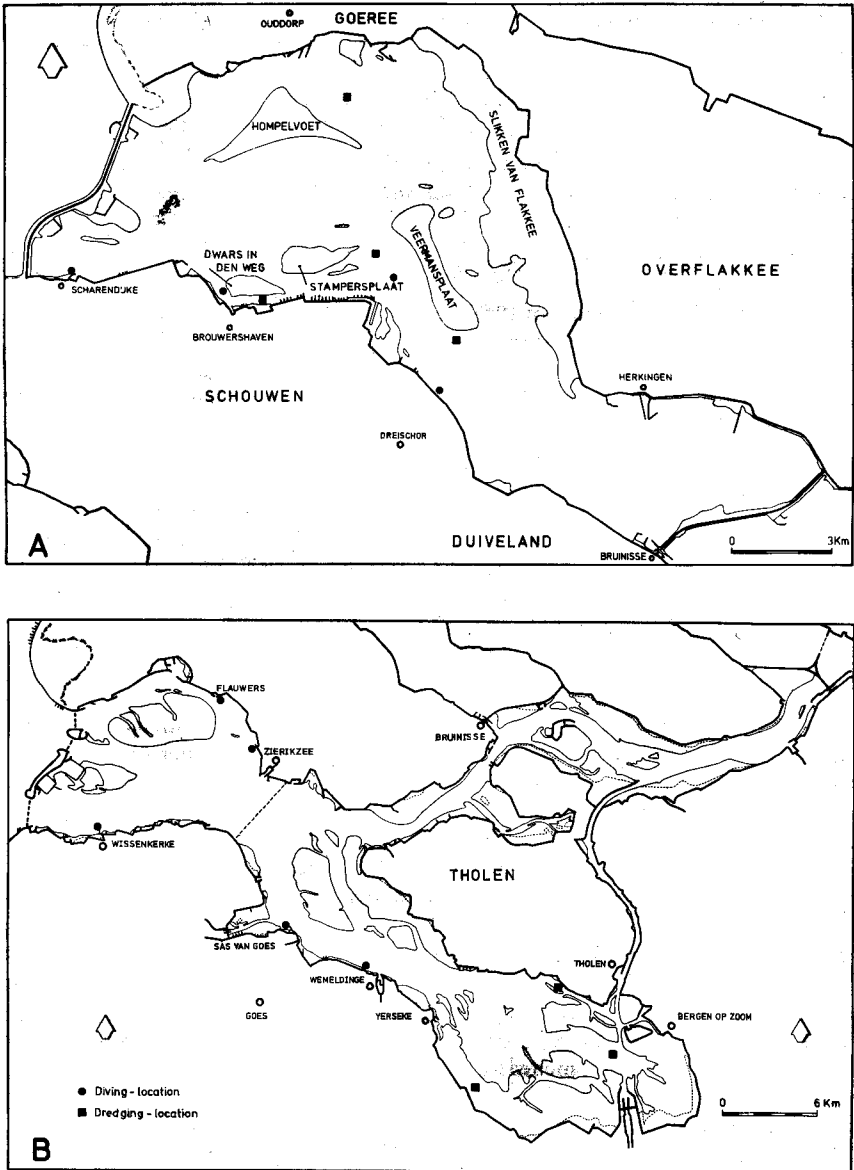


Fig. 1. The locations where oysters were collected by dredging and the places where diving provided data on *Cliona celata*. — A. The Grevelingen Lake. B. The Eastern Scheldt.

Abb. 1. Dredgeproben von Austern und Tauchbeobachtungen an Bohrschwämmen *Cliona celata*. — A. Grevelingen-See. B. Oosterschelde. — ● = Tauchpunkt; ■ = Dredgepunkt.

In the Eastern Scheldt (Fig. 1B) only five boring sponges were found by dredging. They lived in shells of dead *Ostrea* or *Crepidula*. Living oysters from nearly all oyster-beds were removed earlier to combat the oyster-disease *Bonamia ostrea*.

Diving near the dikes at Wissenkerke, Flauwers, Zierikzee, Sas van Goes and Wemeldinge produced every time *Cliona* in limestone. Near Zierikzee the boring sponge was more abundant than at the other localities. In addition to doublets of *Ostrea*, many single valves were found with *Cliona*. Only 33 of 54 infected doublets contained the living mollusc. Sixty single left valves were detached from the stones, but only three loose right valves were collected with infection. The right valve, if containing *Cliona*, may act as a carrier of the shell disease. As soon as such a valve makes contact with another shell or with a piece of limestone, the sponge is able to infect a new substratum. This may occur several times when the valve is transported by the tidal currents.

Besides *Ostrea edulis*, the Japanese oyster, *Crassostrea gigas* (THUNBERG) was also found. The latter was imported in 1964 for culture experiments. Five living infected specimens and one single right valve with *Cliona* were collected near Zierikzee.

It is seen that the commercial oyster-beds in both waters did not contain *Cliona*-infected oysters. Although the oyster-beds are in general in more shallow water than the oysters attached to the dikes, this probably does not cause the difference in infection. In the Adriatic Sea, near Rovinj, *Cliona celata* is able to live in a broad range of depths (HARTMAN 1957, 1958). It is probable that limestone boulders which contain *Cliona* are a continuous source of infection for the oysters which live in their neighbourhood. Infection of oysters and slipper-limpets is in general the result of direct contact with a calcareous substratum which already was infected before. Most stones containing *Cliona* are not in direct contact; a distance more than one meter between infected stones is not rare. Many oysters on the beds live partially buried in the sediment. This makes direct infection more difficult.

## Spicule Dimensions.

Tissue samples were taken from specimens of *Cliona celata* which were partly in  $\alpha$ -stage and partly in  $\beta$ -stage. Sponges in the  $\gamma$ -stage were collected from the Bay of Morlaix, near Roscoff, France. Tissue in  $\alpha$ -stage was prepared from a tunnel inside an oyster-shell and from perforations containing ostial papillae in the shell surface of *Ostrea* and *Crepidula*. The diameter of each perforation containing a selected papilla was measured ( $\pm 0.02$  mm). The spicules were prepared from the sponge tissue by oxidizing the sponge parts in a warm  $\text{HNO}_3$ -solution (4M).

Only tylostyles were found. Several samples of 100 tylostyles each were taken from a single sponge. From every sample the length of the tylostyles was measured ( $\pm 12.5$   $\mu\text{m}$ ) under a microscope with an ocular micrometer. One sponge was taken to measure the diameter of the middle part of the sampled tylostyles ( $\pm 0.25$   $\mu\text{m}$ ). The obtained data were also used for calculating their length/diameter ratio.

In two selected sponges the length of the tylostyles is linearly correlated with the diameter of the perforations from which they were prepared (Fig. 2). In the *Crepidula*-shell,  $r=0.53$  ( $p<0.0001$ ) and in the shell of *Ostrea*,  $r=0.38$  ( $p<0.0001$ ). Papillae in small perforations contain fewer long tylostyles than papillae in larger perforations. When the tylostyles of the smallest perforation are compared with those of

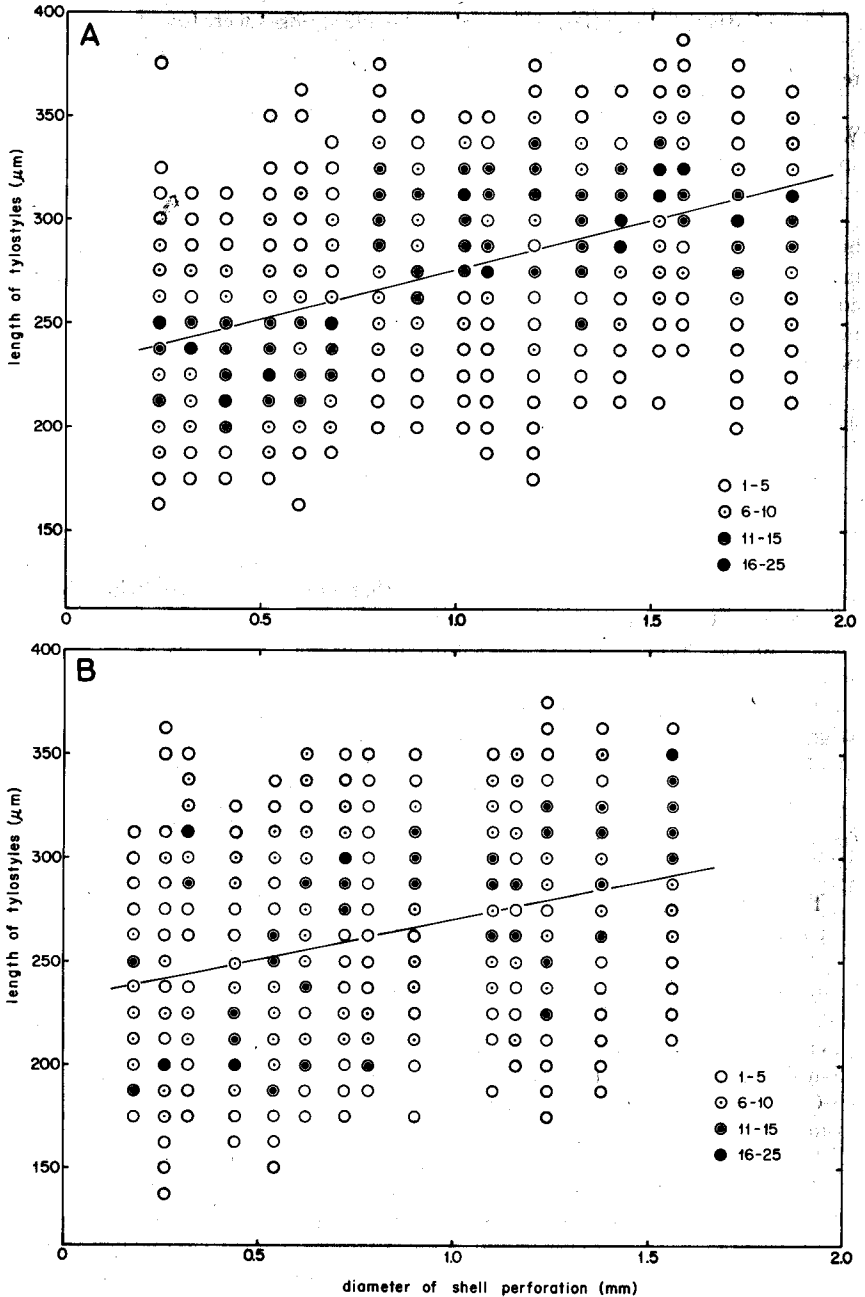


Fig. 2. Relation between tylostyle length and diameter of shell perforation made by *Cliona celata*. — A. Perforations in body whorl of *Crepidula fornicata*;  $y = 48x + 227$ . B. Perforations in flat right valve of *Ostrea edulis*;  $y = 45x + 231$ .

Abb. 2. Verhältnis zwischen Tylostyl-Länge und Bohrlochdurchmesser von *Cliona celata*. — A. In *Crepidula*-Schale. B. In rechter ("oberer") *Ostrea*-Klappe.

Table 1. Lengths of tylostyles in the  $\alpha$ -,  $\beta$ - and  $\gamma$ -stages of *Cliona celata*. — The  $\alpha$ - and  $\beta$ -stages are from the Dutch Delta Region; the  $\gamma$ -stage is from Roscoff, Brittany, France.

Tabelle 1. Längen der Tylostyle in den  $\alpha$ -,  $\beta$ - und  $\gamma$ -Stadien von *Cliona celata*. — Die  $\alpha$ - und  $\beta$ -Stadien aus dem niederländischen Deltagebiet; die  $\gamma$ -Stadien von Roscoff, Bretagne, Frankreich.

Stage	Substratum	Location of investigated sponge tissue	Length of tylostyles, $\mu\text{m}$		
			mean	s. d.	range
$\alpha$	<i>Crepidula</i>	perforation $\phi$ 0.24 mm	240	39	163 - 375
$\alpha$		perforation $\phi$ 1.86 mm	299	33	213 - 363
$\beta$		under internal ledge	361	40	238 - 425
$\alpha$	<i>Ostrea</i>	perforation $\phi$ 0.26 mm	231	52	138 - 363
$\alpha$		perforation $\phi$ 1.56 mm	305	35	213 - 363
$\alpha$		tunnel in shell	354	31	250 - 413
$\beta$		between valves	377	35	263 - 450
$\gamma$	unknown	peripheral region	338	33	238 - 413
$\gamma$		central mass	344	34	225 - 400

the largest, the difference in the mean length is significant ( $p_t < 0.0005$ ) for both substrata (Tab. 1).

Tylostyles from an excavation inside the oyster-shell are on the average longer than those of the largest measured perforation ( $p_t < 0.0005$ ). In both shells the spicules of the  $\beta$ -stage are longer than those of the  $\alpha$ -stage ( $p_t < 0.0005$ ). They are also longer than the tylostyles of a sponge in  $\gamma$ -stage ( $p_t < 0.005$ ). VOSMAER (1933-1935) discovered the same mutual differences in *Cliona celata* from Naples, except that the tylostyles which were investigated by him, were much longer. In the  $\gamma$ -stage the difference in mean length of spicules from the peripheral region and from the central mass is too small to be significant ( $p_t > 0.05$ ).

The mean diameter of tylostyles from perforations in a *Crepidula*-shell (Fig. 3A) is not correlated with the diameter of these perforations ( $r = 0.21$ ,  $p > 0.05$ ). The range of the tylostyle diameter is very broad. The mean length/diameter ratio is relatively small in the papillae of the smallest perforations (Fig. 3B). This is due to the many short spicules there (Fig. 2A).

It may be that small perforations contain relatively less full-grown tylostyles. Monaxial silicious spicules of the fresh-water sponge *Ephydatia* need a few days to reach their maximum length (WEISSENFELS & LANDSCHOFF 1977). Their formation starts with the production of an organic axial filament, which later becomes surrounded by silicon. In the early stages of spicule growth, deposition of silicon is proportional to the available spicule surface. The growth-rate of the spicule decreases as the spicule elongates (ELVIN 1971). If in *Cliona* the process of spicule formation is the same as that in *Ephydatia*, the maximum length of the tylostyles may depend on the original length of the organic axial filament. This length may be limited by the availa-

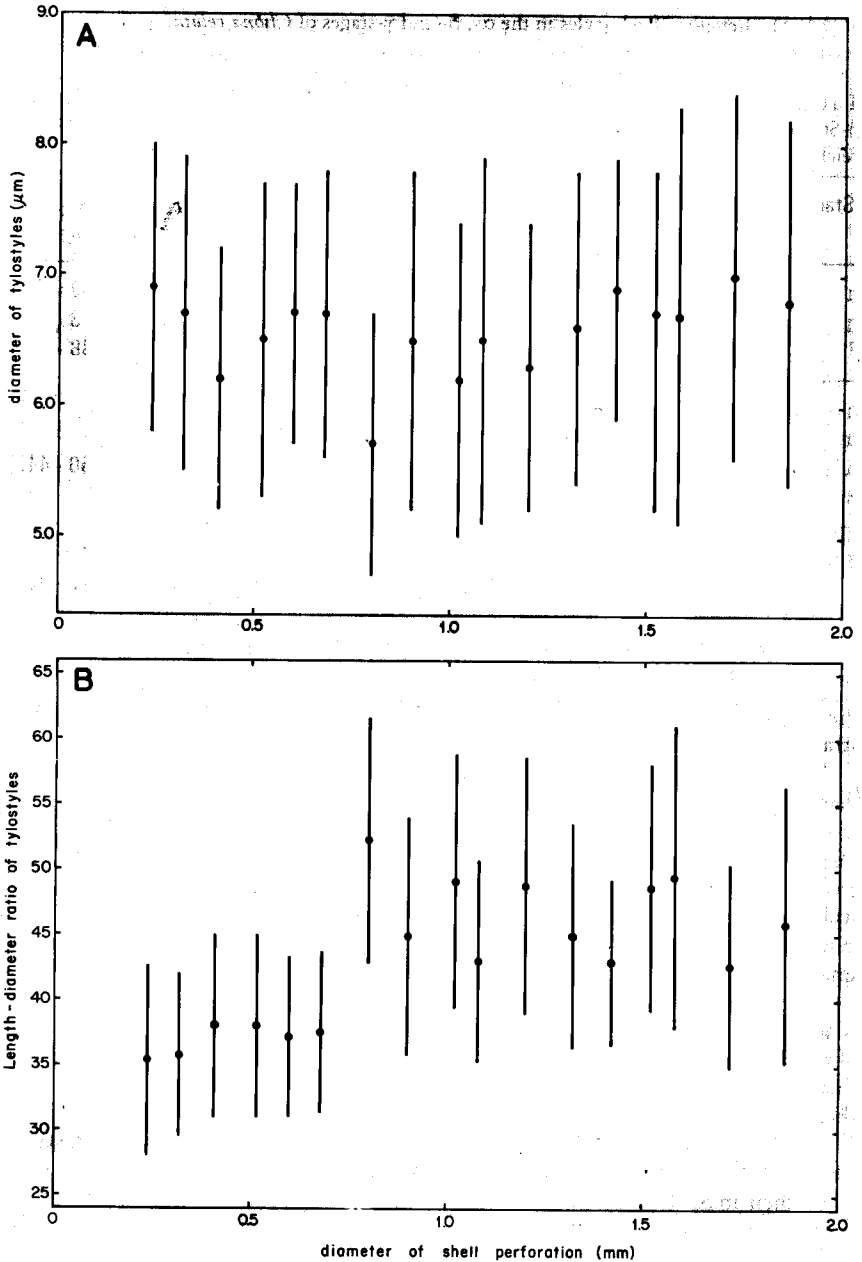


Fig. 3. Tylostyle variables. — A. Mean diameter of tylostyles ( $\pm$  s. d.) of *Cliona celata* tissue in perforations in body whorl of *Crepidula fornicata*. B. Mean length/diameter ratio ( $\pm$  s. d.) of same tylostyles as in Figs. 2 A and 3 A.

Abb. 3. Tylostyl-Variable. — A. Mittlere Durchmesser von Tylostylen ( $\pm$  s) von *Cliona celata* in Schalen von *Crepidula fornicata*. B. Verhältnis zwischen mittlerer Länge und Durchmesser ( $\pm$  s) der Tylostyle in Abb. 2 A und 3 A.

ble space in a perforation. The spicules of *Ephydatia* are formed in moving scleroblasts (WEISSENFELS & LANDSCHOFF 1977). In small perforations the amoeboid scleroblasts of *Cliona* may have too less space for letting the tylostyles reach their potential maximum length. Probably this would not influence the diameter of the tylostyles. In the marine silicious sponge *Hymeniacion* the thickness and the length of the spicules both depend on the available silicate in the water (STONE 1970).

## Reproduction.

*Cliona celata* is known to be viviparous (HARTMAN 1958; WARBURTON 1958b). Therefore, living specimens of *Cliona celata* from the Eastern Scheldt were kept in aquaria in the period from half May until half September and continuously supplied with fresh sea-water. Shells of living oysters, brushed clean of fouling organisms, were presented as potential substrata for sponge larvae. Regular inspection of the sponges for the presence of eggs or larvae did not result in finding any. In the cleaned oyster-shells no traces of infection could be found. Under the supervision of drs. C. BAKKER plankton samples were taken from the Eastern Scheldt during the above mentioned period and controled for the presence of *Cliona*-larvae, but these could not be detected. Sexual reproduction of boring sponges from the Eastern Scheldt thus could not be proved directly.

Many authors give different data on the time of sexual reproduction of *Cliona celata*, but at most studied localities it occurs in mid- or late summer (HARTMAN 1958; WARBURTON 1958b, 1958d; BERGQUIST & SINCLAIR 1973). A possible absence of sexual reproduction in the Dutch Delta Region during the summer of 1981 may be due to an irregular reproduction cycle. According to WARBURTON (1958d) it is not known if the sponges breed every year.

Dispersion of the boring sponge may also be achieved by asexual reproduction. At the beginning of unfavorable conditions gemmules, or internal buds, may be found in the channels of *Cliona*. These pieces of sponge tissue can be ejected into the water via the oscular papillae (OLD 1942).

## Excavation Patterns.

DE GROOT (1977) found that different species of clionids in limestone produce different excavations. LAWRENCE (1969) used fossil borings of *Cliona* in shells for making a paleoenvironmental analysis concerning salinity. Although it is known that the shape of the tunnels strongly depends on the substratum and the age of the different parts of the sponge (VOLTZ 1939), not many details are known about this subject. This makes it less easy to draw conclusions from fossil species as would appear from LAWRENCE (1969).

Therefore, three different kinds of substratum were used for studying the excavation patterns: limestone boulders and oyster-shells from the Eastern Scheldt (Zierikzee) and shells of *Ostrea* and *Crepidula* from the Grevelingen Lake (Dreischor). The dimensions of the boulders present few limitations to boring by the sponge. Most of the shell of *Crepidula* is only 2 to 3 mm thick, which limits the depth to which the

sponge can bore. Oyster-shells are larger, but have a shape and a structure which may influence the boring patterns.

A part of the perforations which contain oscular papillae was marked with pins to compare the tunnels leading to these with those under ostial papillae. In order to study the borings a casting technique was devised. Limestone boulders were sawn in blocks for easy handling. In order to remove sponge tissue, these blocks and the shells were put in an  $H_2O_2$ -solution (30%). The samples which were freed of organic matter were dried in an oven and afterwards impregnated under vacuum during five minutes with a low viscosity polyester resin. A minimal quantity of catalyst was used for extending the hardening time so that all air had time to escape. One day after the impregnation, the tunneled substratum was put in an HCl-solution (30%) until all lime was removed. Some of the casts were studied with a Jeol JSM-35R scanning electron microscope.

### Limestone.

The Belgian Eocene limestone boulders which are found near the submerged town Bommenede are very porous. *Cliona* is able to penetrate more than three centimeters into this substratum (Pl. 1 fig. 1). Its natural porosity and the boring activity of *Cliona* make this material very brittle.

The blocks of Lower Carboniferous limestone from the dikes around the Grevelingen Lake and the Eastern Scheldt are less porous and much better suited for making polyester casts of borings. The excavation pattern of *Cliona* can be described from the observed phases of the boring process.

The tunnels in the blocks primarily show a pattern parallel to the surface of the substratum (Pl. 2 fig. 5). The newest tunnels are thin and have a branch-like appearance. Where they meet each other, they form a network of tunnels close under the surface of the stone. Small branches reach the surface where the sponge makes contact with the sea-water and forms papillae. The perforations of ostial papillae have diameters up to 3 mm. The less common perforations of the oscular papillae have diameters up to 5 mm. The tunnels which lead to both types of perforations are alike, so that they cannot be distinguished from each other.

The network of tunnels gradually becomes more chaotic. The tunnels widen and lose their branch-like appearance. The sponge forms clusters of lobes in the lime. The lobes, which have diameters between 2.5 and 5 mm, finally fuse in such a way, that the original pattern cannot be recognized.

The parts which penetrate more deeply into the substratum form branches which can reach a depth of more than 3 cm (Pl. 1 fig. 4). According to VOLTZ (1939), the penetration depth may be limited by a lack of oxygen. The tunnels remain relatively thin until they reach another side of the stone (Pl. 2 fig. 7). There they form a new network of tunnels with perforations in the surface.

From all branches and lobes of the sponge tiny branches with a spiny appearance penetrate into the substratum (Pl. 2 fig. 6). DE GROOT (1977) calls them rootlets. WARD & RISK (1977) name them pioneering filaments. The density of these little branches increases with the age of the borings. This makes them conspicuous when they originate from old excavations.

Parts of the limestone contain stylolites, suture-like sheets of carbon along fractures (Pl. 1 fig. 2). The presence of these stylolites causes deviations from the above described pattern. The ramifications of tunnels which penetrate deeply into the lime

close to such a stylolite are often orientated in planes parallel to it (Pl. 2 fig. 8). For a *Cliona* which reaches a stylolite, it forms a barrier. Perforations in the surface are visible only at one side of the stylolite, except when the sponge reaches one of the edges, where it bores around the stylolite (Pl. 1 fig. 2a).

The sponge may be able to detect the carbon sheets with its pioneering filaments. These may also detect lime with low density which is easier penetrated than lime with a higher density (WARD & RISK 1977). A filament in lime which is less dense may grow more rapidly and become a new tunnel.

### The Shell of *Crepidula*.

The shell of the gastropod *Crepidula fornicata* is a more restricted substratum for *Cliona* than limestone. The maximum length of the shell is about 6 cm. The oldest part of the shell, the protoconch-area or apex, is thick in comparison with the younger parts, the body whorl and the internal ledge. The latter ones reach a maximum thickness of 3 mm. The thin shell limits the extension of the sponge, resulting in fused lobe-like excavations (Pl. 1 fig. 3c). From the lobes of sponge tissue occupying the excavations many pioneering filaments penetrate into the substratum. In the older parts of the infected shell the fused lobes reach diameters up to 4 mm. The body whorl and internal ledge contain mostly lobes of sponge tissue with a diameter of about 2 mm. If the shell is infected by a young sponge, these parts contain excavations with a branch-like appearance, the farther away from the apex, the thinner the branches.

Three of the nine collected shells contained the living mollusc. At the inside of such shells blisters develop when the shell is under attack by *Cliona* (Pl. 1 fig. 3b). These blisters are found where the mollusc secretes lime to prevent the sponge from making perforations. The lobes of sponge tissue here are larger than in non-blistered parts of the shell. The lobes have diameters up to 4 mm. The shell is weakened and finally it may be impossible for the animal to keep itself attached to the substratum. When loose, it is an easy prey for predators. Finally the animal has disappeared and the sponge may perforate the internal surface of the shell.

The perforations in the external surface of the shell are largest near the apex (Pl. 5 fig. 21), with diameters of 4 mm or (after fusion) even more. In some shells the protoconch-area becomes heavily damaged (Pl. 5 fig. 21). *Crepidula* adheres tightly to its substratum so that this area may touch the substratum. If this substratum contains *Cliona*, an infection may start at this part of the shell. Parts of the shell which have been covered by other slipper-limpets or by barnacles have a smaller perforation density. The diameter of the covered perforations is smaller than the diameter of the neighbouring not covered ones.

### The Shells of *Ostrea* and *Crassostrea*.

Borings in oyster-shells up to four years old differ from those in older ones. Young shells are thinner, so that especially in the flat right valves the sponges have less space. Borings in old shells are similar to those in limestone and excavations in young and thin shells resemble those in *Crepidula*-shells. In general the tunnels in young shells ramify in one plane but sometimes they grow in two parallel levels (Pl. 3 fig. 11c). In old shells the borings are more or less spheric and can be seen in all parts of the shell (Pl. 3 fig. 11e).

Many oyster-shells have structures which influence the boring pattern of *Cliona*. A large part of the shells possesses sheets of conchyolin alternating with layers of lime. The excavation process especially takes place in the lime between the conchyolin. According to TOPSENT (1887) conchyolin of oyster-shells is excavated in the same way as lime. Borings in old oysters from the Eastern Scheldt (Pl. 4 fig. 13) and from eastern Canada (WARBURTON 1958c) show patterns which prove that conchyolin is less easily penetrated than lime. Relatively few borings continue as perforations in the sheets of conchyolin (Pl. 4 fig. 13). Without conchyolin the oysters would probably die sooner.

A majority of the oyster-valves contains chambers filled with seawater. KORRINGA (1951a) discusses the origin of these chambers. Chambered shells with *Cliona* usually have some of these spaces filled with sponge tissue. Two adjacent chambers occupied by *Cliona* are connected with each other by means of perforations in the lime and conchyolin which is situated in between them (Pl. 4 fig. 13, 15).

The boring sponge causes damage to the opening and closing mechanism of an oyster-shell when it reaches, respectively, the hinge-area and the muscle scars. If the sponge grows from one valve to the other, it commonly enters the new one through the hinge (Pl. 4 fig. 14). The lime under the muscle scars becomes very brittle. On the muscle scar itself blister-like structures appear where the mollusc secretes lime to defend itself against the perforating sponge (Pl. 4 fig. 17). If the mollusc fails to defend itself, the sponge succeeds to perforate the internal surface of the shell (Pl. 4 fig. 18). After the death of the oyster the whole internal surface of the shell becomes perforated (Pl. 4 fig. 16).

The abilities of oysters to repair the internal surface of the shell is strongly correlated with the season. In summer the oyster is able to offer resistance to the sponge, but in other seasons the mollusc fails to repair the damaged places (WARBURTON 1958a). Damage to the hinge ligament and to the muscle scars is more difficult to recover and may be fatal.

Most left valves are so heavily attacked, that it is impossible to reconstruct the original excavation pattern. In some left valves it is seen that branching tunnels originate from the area with which they were attached to the limestone substratum. In many right valves the excavations still can be seen to originate from the hinge-area (Pl. 3 fig. 11).

The extent of growth of *Cliona* in the two valves also can be detected from the distribution of perforations over the external surface (Pl. 3 figs. 9, 10). The left valve has an invaded area which includes the area with which the shell was attached to the limestone substratum. In the right valve the perforated area incorporates the hinge (Fig. 4). The perforated area in the left valve is larger than that in the right valve in most doublets (Tab. 2). Shells which contain the living mollusc are less damaged than those without.

HANCOCK (1849) described the earliest borings of post-larval *Cliona* in oyster-shells. Many shells containing the boring sponge show a special area in which the infection started. HANSEN (1970) found that the infection by *Cliona celata* invariably begins in the protoconch-area of gastropods and in the umbonal area of bivalves. These regions are the oldest parts of the shells and most damaged by abrasion. The periostracum is thin or even disappears at these places. This makes settlement by borers easier.

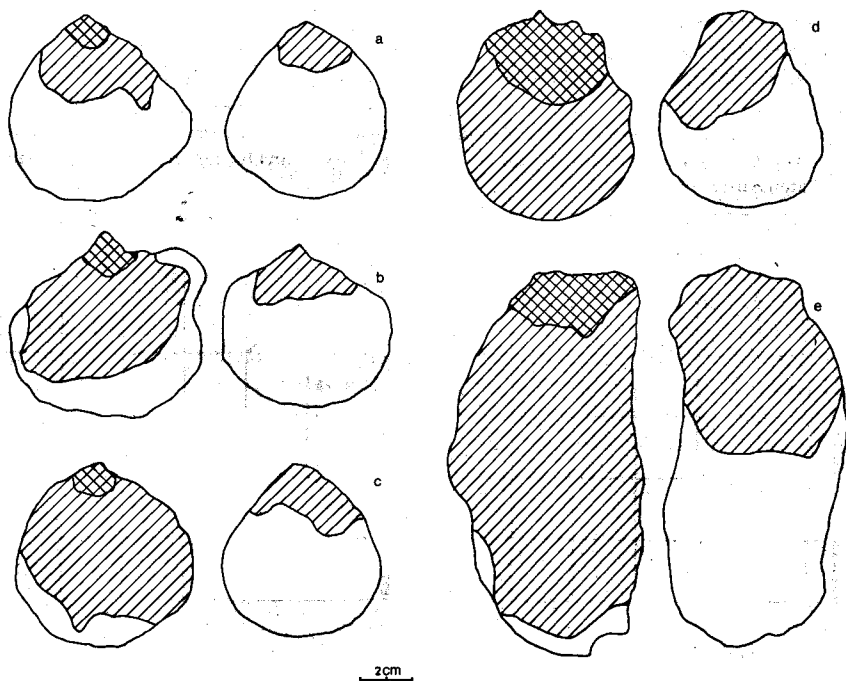


Fig. 4. Perforated area in the external surface of the valves of *Ostrea edulis* (a-d) and *Crassostrea gigas* (e). — Hatched: perforated areas. Cross-hatched in left valves: areas of attachment.

Abb. 4. Klappen von *Ostrea edulis* (a-d) und *Crassostrea gigas* (e) von der Oosterschelde mit Besiedlung durch den Bohrschwamm *Cliona celata*. — Schraffiert: Von Bohrgängen durchsetzter Schalenbereich. Kreuzschraffiert: Anheftungsstelle der linken („unteren“) Austernklappe.

In the shells of bivalves which live attached to a lime substratum or lie on the bottom, the sponge usually starts to attack the attached or the lower valve. When it is in one valve, it may grow to the other.

NESTLER (1960) described *Cliona* in the left valve of Lower Cretaceous oysters (*Pycnodonte vesicularis* (LAM.)). BOEKSCHOTEN (1967) discovered relatively many *Cliona*-excavations in the flat valve of Pliocene *Ostrea edulis*. *Cliona* presence exclusively in the right valve may be a result of infection by larvae.

In scallops the lower valve mostly is more infected by *Cliona* than the upper valve. In the upper valve the excavations are concentrated at the hinge (MEDCOF 1949; EVANS 1969). The lower valve may become infected when it is in direct contact with the boring sponge, eventually after a period of swimming. This is a random occurrence.

Age may also influence the area most infected. The older the part of the shell, the greater the chance of settlement of fouling organisms on or in that part. This was observed in *Chlamys* with *Sycon* and *Styela* as epifauna (ALLEN 1953) and in *Haliotis*

Table 2. Parts of the external surface of oyster-shells (*Ostrea edulis*) which are perforated by *Cliona celata*. — The numbers of shells which contained the living molluscs are placed in the right hand corners above of the squares and the numbers of empty shells in the left hand corners below.

Tabelle 2. Teile der äußeren Oberfläche von Austernschalen (*Ostrea edulis*), die von Bohrlöchern von *Cliona celata* durchsetzt sind. — Lebenden Austern im Diagramm rechts oben, Klappen toter Austern links unten.

		EASTERN SCHELDT					GREVELINGEN				
		right valve, % infection					right valve, % infection				
		0	0-25	25-50	50-75	75-100	0	0-25	25-50	50-75	75-100
left valve, % infection	0	X					X				1
	0-25		1								1
	25-50	1									
	50-75	1	2				1	3			
	75-100	5	3	3	3	13	1	4		4	4
			1	2	1	17	3		2	2	

with *Cliona* as infauna (HANSEN 1970). Why oyster-shells younger than three years mostly do not contain *Cliona*, is discussed by WARBURTON (1958d).

### Interactions With *Polydora* Borings.

In shells of *Ostrea*, *Cliona celata* competes with two polychaetes, *Polydora ciliata* (JOHNSTON) and *Polydora hoplura* CLAPARÈDE. In one flat oyster-valve the three borers have their tunnels at three different places (Pl. 5 fig. 19). The *Cliona*-borings originate from the hinge-area, *P. ciliata* excavates under scales on the external shell surface and *P. hoplura* starts to make its holes in the internal surface, opposite the inhalant chamber of the oyster. The borings of both *Polydora*-species are orientated parallel to the surfaces of the shell. KORRINGA (1951b) gives more information on the tunnelling of both species in oyster-shells from the Eastern Scheldt.

In limestone *P. ciliata* makes its tunnels perpendicular to the surface of the substratum. It is seen that some branches of *Cliona*-borings originate from such tunnels (Pl. 5 fig. 20). It is not probable that the empty tunnels of dead *P. ciliata* become occupied by other worms of the same species (VAN DER PERS 1978). When *Cliona* during its growth reaches such an empty tunnel, it may grow into it and later start to enlarge the tunnel.

In *Crepidula*-shells the borings of *Cliona celata* and *Polydora ciliata* have a very limited space. Most *Crepidula*-shells are occupied by both species (Pl. 5 fig. 21). *Polydora* is able to settle at every part of the shell, while *Cliona* usually starts to bore in the oldest part of the shell and later may grow to the younger parts. When they

meet, it is seen that the excavations of *Cliona* avoid the *Polydora*-tunnels. The *Cliona*-branches grow around them and develop many pioneering filaments (Pl. 5 fig. 23). These filaments can also be observed when two specimens of *Cliona celata* approach each other (BROMLEY & TENDAL 1973).

### The Distribution of Papillae.

The perforations in oyster-shells which contain oscular papillae have a maximum diameter of 5 mm. They are less abundant than the much smaller perforations which contain ostial papillae (Pl. 3 fig. 12). A sponge in a heavily attacked oyster-valve carries four to eleven oscular papillae and more than three hundred ostial papillae.

For measuring the diameters and distribution patterns of the perforations in the surface of oyster-shells, only the holes which contain ostial papillae are considered. Per shell one or two areas of about 10 cm<sup>2</sup> are taken for measurements (Tab. 3). The areas show differences in the relative frequency of perforation diameters (Fig. 5). Because borings increase in diameter when they become older, areas with relatively many small perforations contain younger sponge tissue.

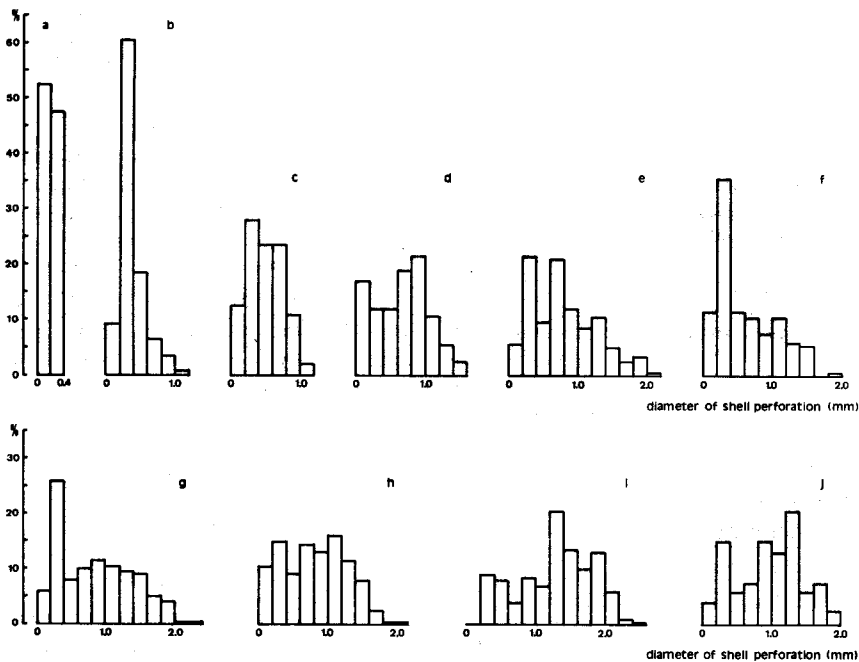


Fig. 5. Relative frequency histograms of perforations containing ostial papillae in 10 areas of oyster-shell surface. — The letters refer to Tab. 3.

Abb. 5. Histogramme der relativen Häufigkeit von Bohrlöchern mit Ostialpapillen in zehn Teilbereichen von Austernschalen. — Die Buchstaben siehe Tab. 3.

Table 3. Values of variables containing the perforating activity and the spacing of perforations as indices for relative age in the  $\alpha$ -stage of *Cliona celata*. — For explanations see text and Tab. 4.

Tabelle 3. Numerische Angaben zur Bohrtätigkeit und Bohrlochdichte von *Cliona celata*. — Erläuterungen der Symbole siehe Tab. 4.

Shell No.	Shell area		Fig. 5	N	P	$\rho$ cm <sup>-2</sup>	$\bar{r}_A$ mm	R	c
	Valve l/r	Inside/outside							
1	r	o	a	173	1.2	25.0	0.74	0.74	6.5
2	r	o	b	89	1.3	7.7	1.40	0.78	4.0
3	r	o	c	111	1.6	6.9	2.02	1.06	1.0
4	r	i	d	152	2.9	6.1	2.39	1.19	3.3
4	r	o	e	177	4.7	7.6	2.31	1.27	5.3
5	r	i	f	198	4.7	10.0	2.04	1.29	6.0
6	r	o	g	213	8.3	9.7	1.85	1.16	3.6
5	r	o	h	222	10.1	13.3	1.69	1.23	5.5
6	l	o	i	218	14.7	9.0	2.30	1.38	7.5
7	l	i	j	199	17.6	18.8	1.58	1.37	10.0

To establish an index of relative age, a calculation with perforation diameter  $\Phi$  and perforation density  $\rho$  can be used. This calculation yields the relative perforation surface  $P$  of a given substratum surface  $A$ ,

$$P = \frac{\sum \pi (\frac{1}{2}\Phi)^2}{A} = \frac{1}{4} \pi (\overline{\Phi^2}) \rho$$

in which a summation of perforation surfaces is related to the used substratum surface. The density of perforations  $\rho$  itself is not a good criterium for relative age because the perforations and their papillae often fuse when they grow (Fig. 6). This makes  $\rho$  very variable, so that substratum areas with a high value of  $\rho$  can have a low value of  $P$  (Tab. 3).

The relative perforation surface  $P$  is an indicator of the perforating activity of the sponge during its life. The older the sponge tissue in a certain substratum area, the more substratum surface is eroded away. In the ideal situation only the perforations of ostial papillae are measured. When the perforations of the larger and scarcer oscular papillae are also measured, the values of  $P$  cannot be compared.

Other indices of relative age can be derived from a model which indicates the dispersion pattern of perforations in an area of substratum surface. Shell-surfaces containing many small perforations show a more irregular pattern than shell-surfaces containing many large holes (Fig. 6). CLARK & EVANS (1954) used the mean distance between nearest neighbours as a measurement of spacing in populations of organisms. When applied to the distribution patterns of perforations or their papillae, some concepts used by these authors have to be adapted (Tab. 4).

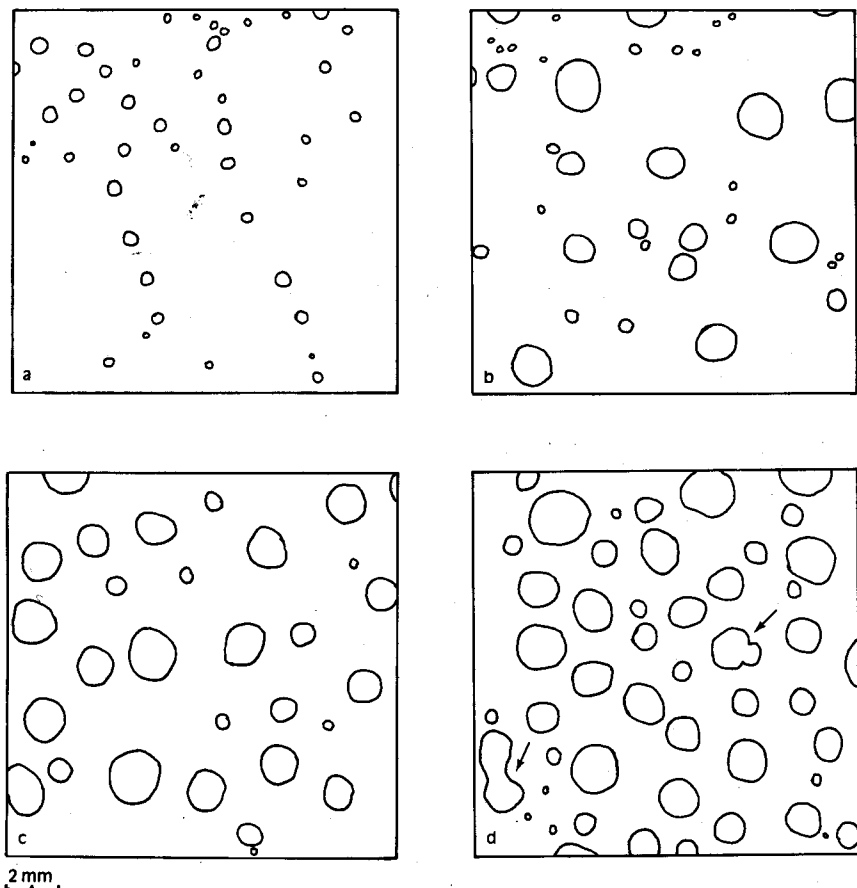


Fig. 6. The spacing of perforations in four areas of oyster-shell containing *Cliona celata*. — The letters a, b, c, d refer to areas 2ro, 6ro, 6lo, 7li of Tab. 3. Arrows indicate clearly visibly fused perforations.

Abb. 6. Räumliche Anordnung der Bohrlöcher von *Cliona celata* in vier Teilbereichen von Austernschalen. — Die Buchstaben a, b, c, d beziehen sich auf Tab. 3: 2ro, 6ro, 6lo, 7li. Die Pfeile zeigen ineinander übergehende Bohrlöcher.

The ratio  $R$  of the observed mean distance  $\bar{r}_A$  to the expected mean distance  $\bar{r}_E$  in an area serves as the measure of departure from randomness. When  $R=0$ , the distribution is completely aggregated and when  $R=1$ , it is at random. In a complete even distribution, all perforations will be equidistant to six other ones and form a hexagonal pattern with  $R=2.15$ .

The  $c$ -values of 1.96 and 2.58 (and their negative values) represent respectively the 5%- and 1%-levels of significance. Shell-areas 1ro and 2ro (Tab. 3) depart significantly from randomness to an aggregated distribution. Shell-area 3ro represents an at

Table 4. Symbols and definitions of concepts used in measuring the spacing of perforations made by *Cliona celata* in substratum surfaces. — Adapted after CLARK & EVANS (1954).

Tabelle 4. Symbole und Definitionen zur Ermittlung der Bohrlochdichte von *Cliona celata* auf der Substratoberfläche. — Nach CLARK & EVANS (1954) abgewandelt.

N	The number of perforations used for measurements in the observed area of shell surface.
r	The distance in any specified units from the centre of a given perforation to that of its neighbour.
$\rho$	The density of the observed distribution expressed as the number of perforations per unit area.
$\bar{r}_A = \frac{\sum r}{N}$	The mean of the series of measured distances to nearest neighbour.
$\bar{r}_E = \frac{1}{2\sqrt{\rho}}$	The mean distance to nearest neighbour expected in an infinitely large random distribution of density $\rho$ .
$R = \frac{\bar{r}_A}{\bar{r}_E}$	The measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbour.
$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma \bar{r}_E}$	The standard variate of the normal curve.
$\sigma \bar{r}_E = \frac{0.26136}{\sqrt{(N\rho)}}$	The standard error of the mean distance to nearest neighbour in an area of randomly distributed perforations with density $\rho$ .

random distribution. The other areas depart significantly from randomness to an even distribution.

P is linearly correlated with R ( $r=0.73$ ;  $p<0.01$ ). This means that the distribution of the perforations becomes more regular after more perforating activity of the sponge. The internal surface of two heavily attacked shells (shells 4 and 5 in Tab. 3) shows a lower value of P than the external surface, but not a lower value of R. Perforations in the inside surface of a shell are younger than those in the outside surface, because the former usually can develop only after the death of the mollusc. The whole shell is tunneled and after the mollusc dies, many small papillae develop with a relatively regular distribution at the inside of the shell. In the external surface of shell 6 both, P and R, have higher values in the left valve than in the right valve. This supports the hypothesis that the sponge is oldest in the left valve.

The value of  $\bar{r}_A$  is negatively, linearly correlated with  $q$  ( $r=0.81$ ;  $p<0.005$ ) for the ten areas indicated in Tab. 3. So this variable, like  $q$ , cannot be used as a measurement of relative age in by *Cliona* perforated substratums.

The most even distribution of papillae found in *Cliona* inhabiting the shell of *Ostrea*, is one with  $R=1.38$ . The theoretically most dispersed distribution with  $R=2.15$  cannot be reached in the  $\alpha$ -stage because the relative perforation surface  $P$  also increases when the sponge continues its perforating activity. Before  $R$  reaches its theoretical maximum, the substratum surface will be eroded away.

*Cliona celata* in the  $\gamma$ -stage is studied near Roscoff, Brittany. On sponges with a height up to about 10 cm the few oscular papillae are distributed between the ostial papillae. Bigger sponges often form ridges with the oscular papillae concentrated at the top and the ostial papillae distributed on their sides. One such a big sponge was taken to measure the variables concerning the distribution of the ostial papillae. In a selected area with an apparently even distribution  $N=48$ ,  $q=5.0 \text{ cm}^{-2}$ ,  $\bar{r}_A=4.73 \text{ mm}$ ,  $R=2.03$  and  $c=13.33$ . The value of  $R$  approaches the maximum value very closely. Not all papillae of the sponge in  $\gamma$ -stage are so regularly distributed, but most of them more than in the  $\alpha$ -stage of *Cliona celata*. An even distribution of the incurrent papillae may be more efficient than an aggregated distribution in which the papillae have to compete with each other. The papillae density  $q$  is relatively low in the  $\gamma$ -stage, but this is compensated by the size of the papillae. In the  $\alpha$ -stage they are smaller than those in the  $\gamma$ -stage which are not restricted by the diameter of a perforation in a lime substratum.

### The $\alpha$ -, $\beta$ - and $\gamma$ -Stages.

After the death of an infected mollusc the internal surface of the shell may become perforated. In a shell of *Crepidula* the space between the internal ledge and the whorl may be filled with  $\beta$ -tissue (Pl. 1 fig. 3a). If the valves of an oyster stay tightly closed after its death, *Cliona* may develop  $\beta$ -tissue in between them. No  $\gamma$ -stage *Cliona celata* is found in the SW Netherlands.

In the summer of 1982 the  $\gamma$ -stage of *Cliona celata* was studied in the Bay of Morlaix, near Roscoff, France. Also sponges in  $\alpha$ -stage are found in the shells of *Haliotis*, *Ostrea* and *Pecten*.

In the direction to the sea the  $\gamma$ -stage becomes more abundant. In the direction to the river Penzé the massive forms become scarcer and smaller. In the sea the big ones form long ridges. Sometimes the sponge fills long, narrow crevices in the granite but usually it lives on the rocks. Then the original substratum cannot be identified, but sometimes pieces of shell can be found in the basis.

It seems that shelter in shells is one of the conditions for the presence of the  $\beta$ -stage in the Eastern Scheldt and the Grevelingen Lake. GUIDA (1976) found that animals, such as gastropods, crustaceans and echinoderms, are able to eat *Cliona*. Predators may prevent the development of *Cliona* into  $\beta$ -stage by eating the encrusting material. Attacked *Cliona* in the  $\alpha$ -stage may save its papillae by drawing them temporarily back into the substratum. EMSON (1966) has reported that the papillae can contract. The  $\gamma$ -stage may only occur where there is a shortage of predators.

It is also possible that the  $\beta$ - and the  $\gamma$ -stages are more sensitive to fine particles in the sea-water. In the cavity of a shell the sponge is better protected against silt and

clay, what correlates with the results of DRISCOLL (1967) and of NICOL & REISMAN (1976). These authors were studying the  $\gamma$ -stage of *Cliona celata* when they determined that the sponge prefers environments with low clay-silt contents.

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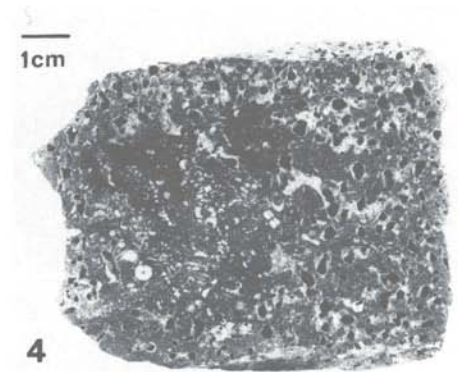
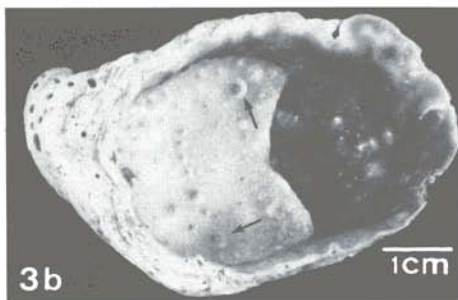
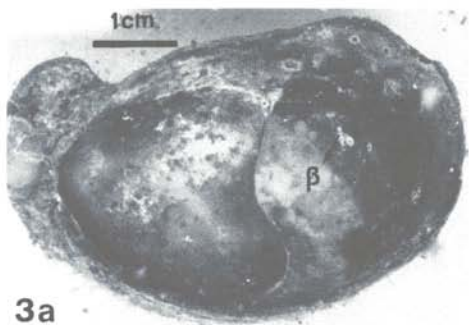
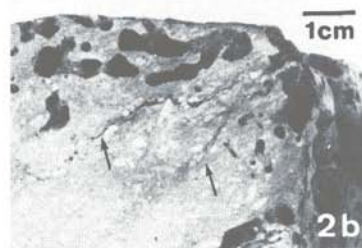
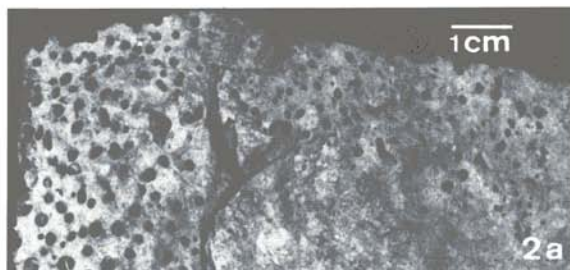
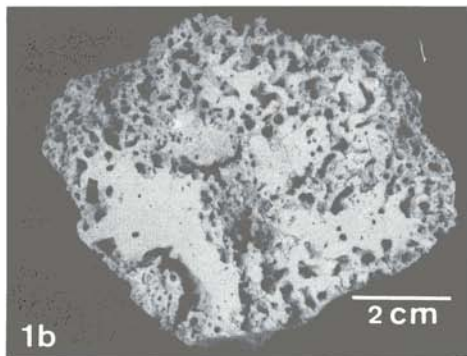
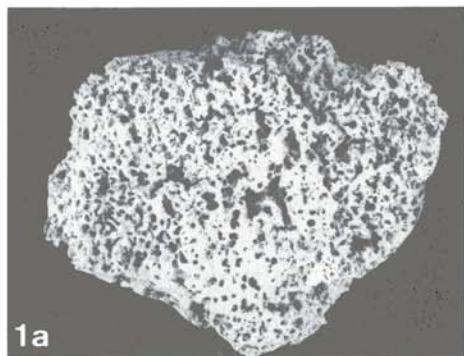
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Plate 1.

- Fig. 1. Belgian Eocene limestone found near the submerged town Bommeneede in the Grevelingen Lake.  
 a. Surface of a boulder attacked by *Cliona celata*.  
 b. The same boulder in cross-section.
- Fig. 2. Lower Carboniferous limestone containing stylolites.  
 a. Surface of a boulder with perforations made by *Cliona celata*.  
 b. Cross-section of a piece with tunnels of *Cliona celata* (arrows).
- Fig. 3. Shells of *Crepidula fornicata* attacked by *Cliona celata*.  
 a. Living sponge in  $\alpha$ - and  $\beta$ -stages,  $\alpha$  in the lime and  $\beta$  under the internal ledge of the shell.  
 b. A shell after removal of organic tissues by H<sub>2</sub>O<sub>2</sub> (arrows indicate blisters).  
 c. Polyester resin cast of borings in shell of fig. 3b (arrows indicate edge of internal ledge).
- Fig. 4. Cross-section of a boulder of Lower Carboniferous limestone containing deeply penetrating tunnels made by *Cliona celata*. — The stone was found near Zierikzee.



B. W. HOEKSEMA: Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.

## Tafel 1.

- Fig. 1. Belgischer Eozänkalk aus dem Grevelingen-See. —  
 a. Kalkbruchstück mit Besiedlung von *Cliona celata*.  
 b. Dasselbe Bruchstück im Schnitt.
- Fig. 2. Unterkarbonkalk mit Stylolyten.  
 a. Oberfläche mit Bohrlöchern von *Cliona celata*.  
 b. Schnittbild-Detail mit Gängen von *Cliona celata* (Pfeile).
- Fig. 3. Schalen von *Crepidula fornicata* mit Besiedlung von *Cliona celata*.  
 a. Lebender Schwamm;  $\alpha$ -Stadien in der Schale,  $\beta$ -Stadien im Septum.  
 b. Schale nach Zerstörung des Schwammgewebes mit  $H_2O_2$ . Pfeile: Blasenabdeckungen von Bohrlöchern.  
 c. Kunstharzausguß der Bohrgänge. Pfeile: Rand des Septums.
- Fig. 4. Unterkarbonkalk mit Bohrgängen von *Cliona celata*. Schnittbild. — Fundort bei Zierikzee.
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## Plate 2.

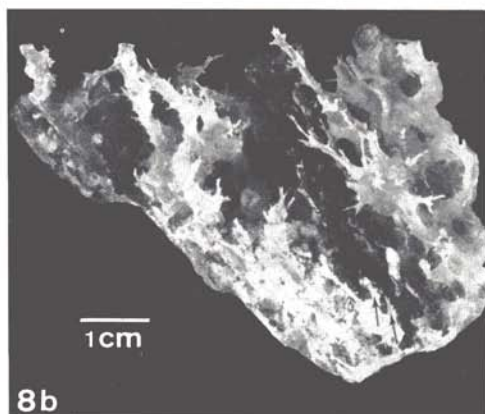
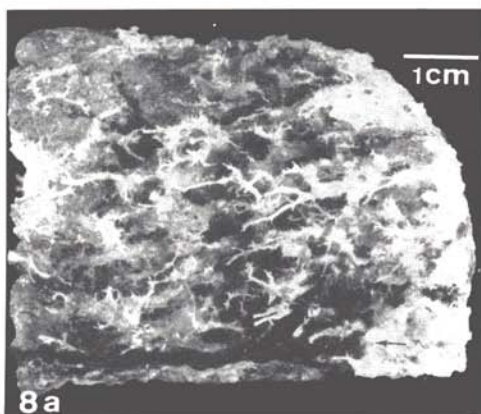
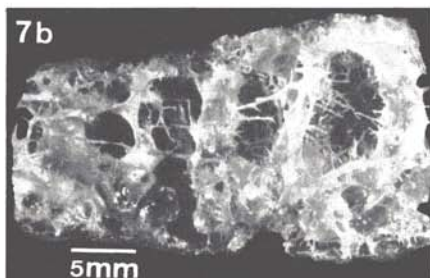
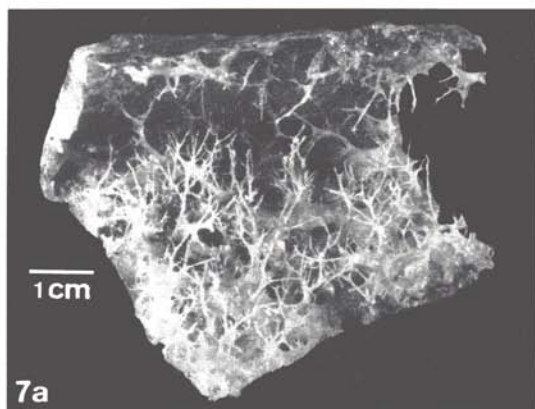
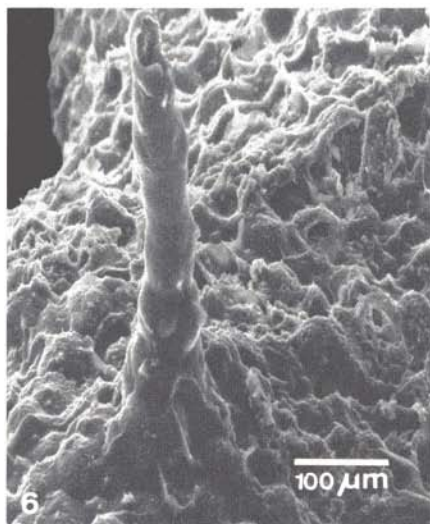
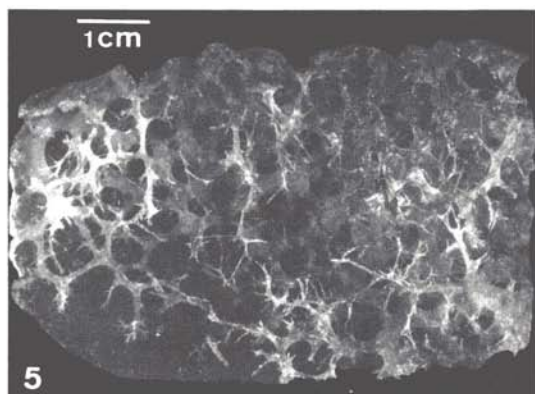
Polyester resin casts of *Cliona celata* borings in Lower Carboniferous limestone found near Zierikzee, Eastern Scheldt.

- Fig. 5. Excavations under the surface of a boulder with branching tunnels penetrating more deeply (in the photograph pointing to the spectator). — The newest borings, that are close to the surface, can be seen in the lower left hand corner.
- Fig. 6. SEM-photograph of pioneering filament.
- Fig. 7. Tunnels between two sides of a boulder fragment.  
 a. A young stage in which the borings recently reached the surface visible at the top.  
 b. Older excavations in a thin piece of stone.
- Fig. 8. Excavations most of which are orientated in parallel planes.  
 a. Recent borings parallel to a stylolite (arrow).  
 b. Older borings with a stylolite (arrows) in the middle of the cast.

## Tafel 2.

Kunstharzausgüsse von Bohrgängen von *Cliona celata* in Unterkarbonkalk. — Fundorte bei Zierikzee, Oosterschelde.

- Fig. 5. Bohrgänge in einem Kalkbruchstück mit den jüngsten feinverzweigten Gängen im Innern des Gesteins (Vordergrund links unten).
- Fig. 6. Vorstoß-Filament einer *Cliona*-Bohrung. — REM-Aufnahme.
- Fig. 7. Bohrgänge im Innern von Kalkbruchstücken.  
 a. Jüngere Bohrungen.  
 b. Ältere Bohrungen.
- Fig. 8. Bohrgänge in paralleler Orientierung zu Stylolit-Strukturen (Pfeile).  
 a. Jüngere Bohrungen.  
 b. Ältere Bohrungen.



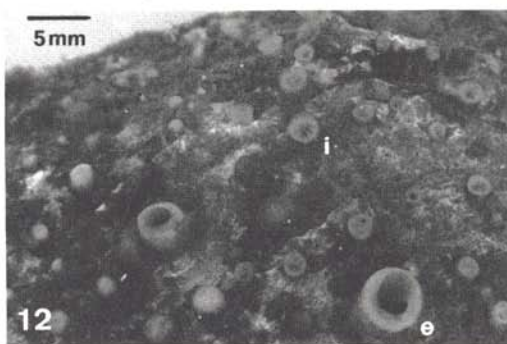
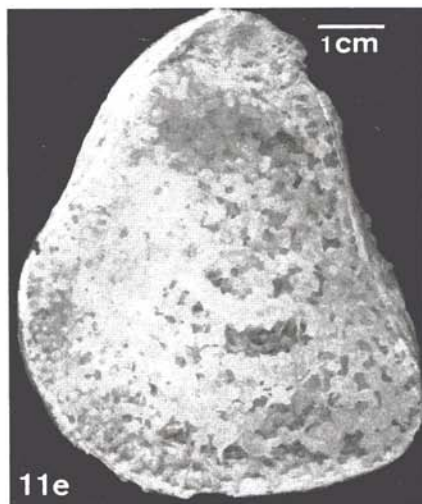
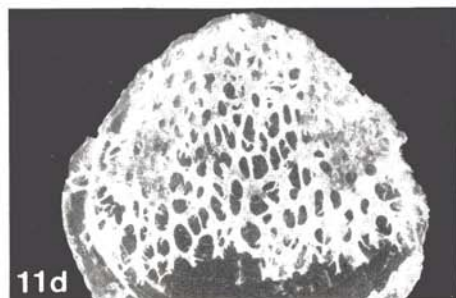
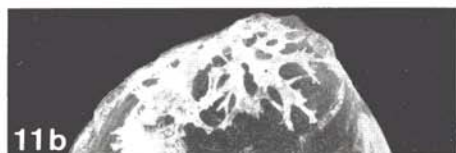
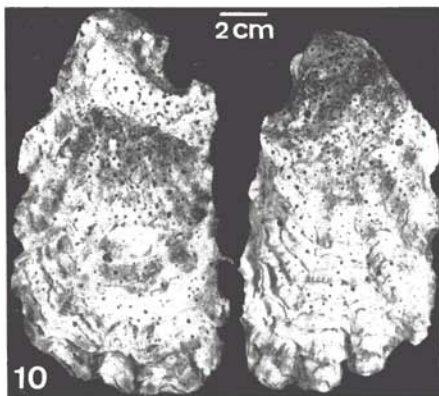
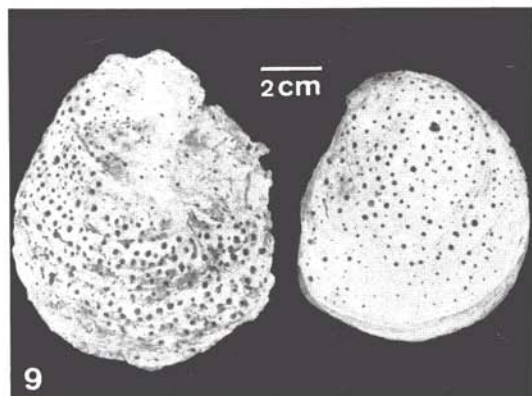
B. W. HOEKSEMA: Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.

## Plate 3.

- Fig. 9. Both valves of a specimen of *Ostrea edulis* excavated by *Cliona celata*. Sponge tissue is removed.
- Fig. 10. A doublet of *Crassostrea gigas* after removal of the sponge tissue.
- Fig. 11. Polyester resin casts of borings of *Cliona celata* in flat right valves of *Ostrea edulis* in successive stages of infection.  
 a-c. Tunnels branching from hinge-region.  
 d. Sponge throughout whole valve.  
 e. Excavations in every part of the shell.
- Fig. 12. Papillae of *Cliona celata* protruding from the surface of a shell of *Ostrea edulis*. The large papillae (e) with one opening are excurrent or oscular papillae. The small papillae with many pores are incurrent or ostial papillae (i).

## Tafel 3.

- Fig. 9 *Ostrea edulis*, beide Klappen mit Bohrlöchern von *Cliona celata*.
- Fig. 10. *Crassostrea gigas*, beide Klappen mit Bohrlöchern von *Cliona celata*.
- Fig. 11. Kunstharzausgüsse von Bohrlöchern von *Cliona celata* in rechten („oberen“) Klappen von *Ostrea edulis* in fortschreitender Besiedlung.  
 a-c. Frühe Besiedlung im Schloßbereich der Auster.  
 d. Besiedlung weit fortgeschritten.  
 e. Bohrgänge durchsetzen die ganze Austernklappe.
- Fig. 12. Papillen von *Cliona celata* an der Schalenoberfläche von *Ostrea edulis*. — Große Papillen (e) = Oscularpapillen. Kleine Papillen (i) = Ostialpapillen.



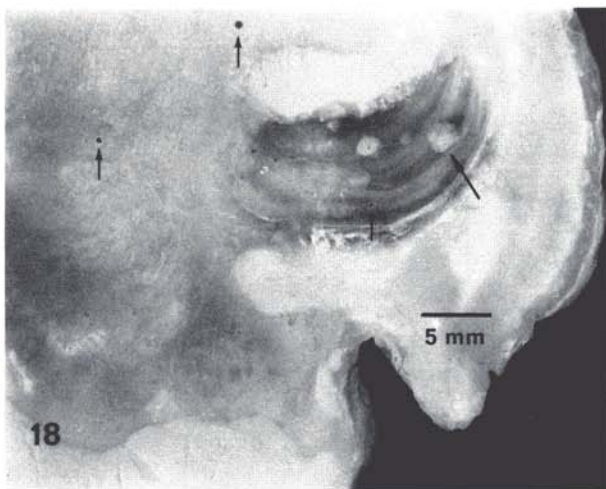
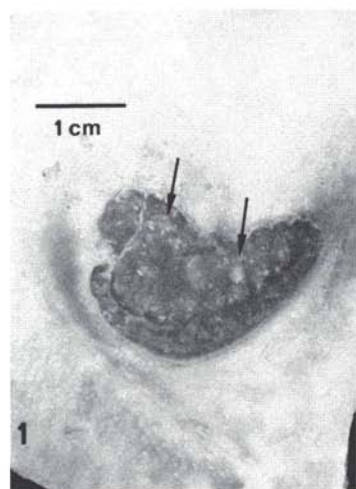
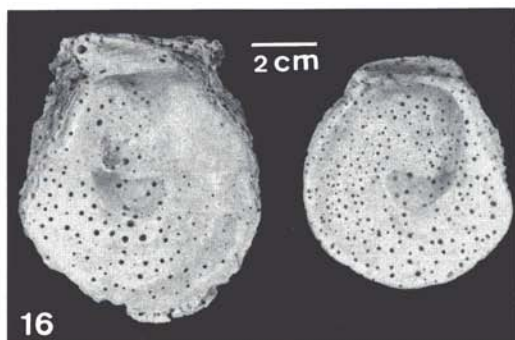
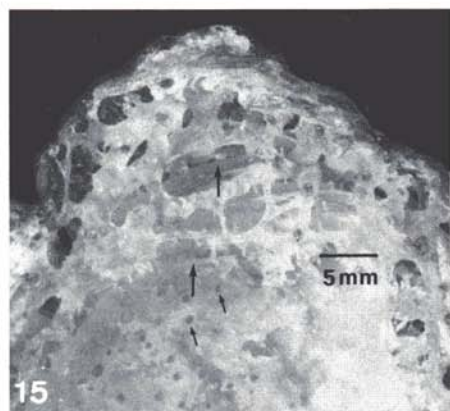
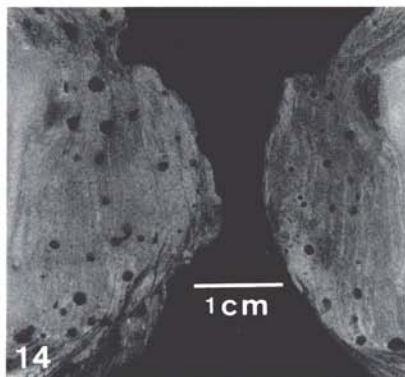
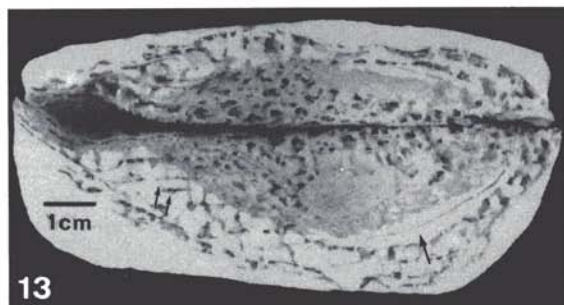
B. W. HOEKSEMA: Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.

## Plate 4.

- Fig. 13. Longitudinal section of a white polyester resin cast of the excavations of *Cliona celata* in an old doublet of *Ostrea edulis*. — The left valve is the lower. The hinge is at the right. (Little arrows: borings in lime between sheets of conchyolin. Big arrow: two adjacent chambers connected by *Cliona*-borings.)
- Fig. 14. Hinge-area of a shell of *Ostrea edulis* perforated by *Cliona celata*.
- Fig. 15. Transparent polyester resin cast of the hinge-area of a left valve of *Ostrea edulis* (see fig. 14). (Big arrows: borders of chambers. Little arrows: perforations in the lime between two adjacent chambers.)
- Fig. 16. Perforated internal surface of a shell of *Ostrea edulis* after removal of sponge tissue.
- Fig. 17. Muscle scar in a right valve of *Ostrea edulis* with blisterlike structures (arrows) made by the oyster attacked by *Cliona celata*.
- Fig. 18. Muscle scar in the right valve of a *Crassostrea gigas*. — Blisterlike structures in muscle scar (big arrow) and small perforations around it (little arrows). This damaged shell was removed from a living oyster.

## Tafel 4.

- Fig. 13. Kunstharzausguß der Bohrgänge von *Cliona celata* in einer Doppelklappe von *Ostrea edulis*. — Linke Klappe unten, rechte Klappe oben, Schloß rechts.
- Fig. 14. Schloßbereich von *Ostrea edulis* mit Besiedlung von *Cliona celata*.
- Fig. 15. Kunstharzausguß von Bohrgängen von *Cliona celata* im Schloßbereich einer linken („unteren“) Klappe von *Ostrea edulis*.
- Fig. 16. Bohrlöcher von *Cliona celata* auf den Innenseiten von Austernklappen. — Linke und rechte Klappe des gleichen Exemplares.
- Fig. 17. Muskeleindruck einer rechten („oberen“) Klappe von *Ostrea edulis* mit Blasen-Abdeckungen gegen die *Cliona*-Bohrungen.
- Fig. 18. Muskeleindruck einer rechten („oberen“) Klappe von *Crassostrea gigas*. — Großer Pfeil: Blasenartige Abdeckungen. Kleine Pfeile: Durchgedrungene Bohrlöcher. Klappe von einem lebenden Exemplar.



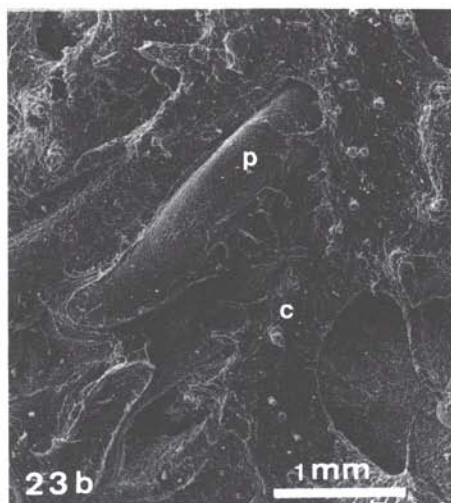
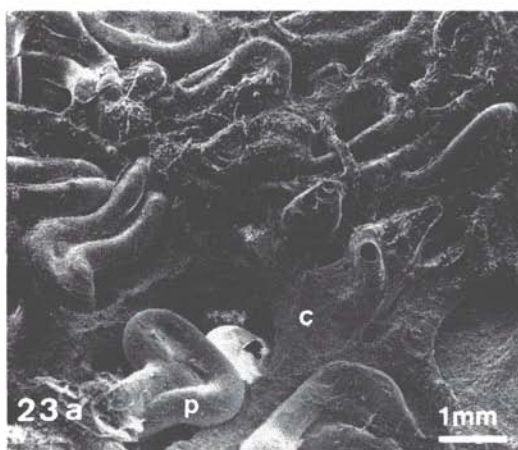
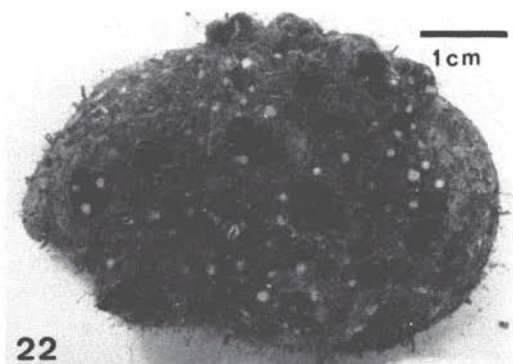
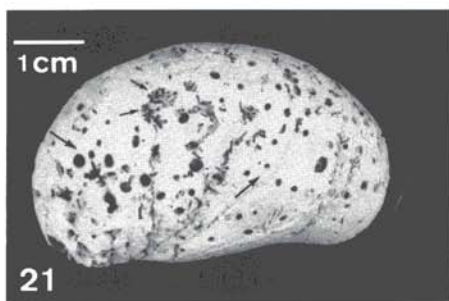
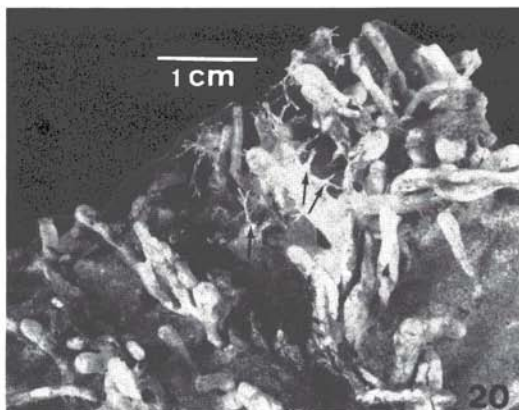
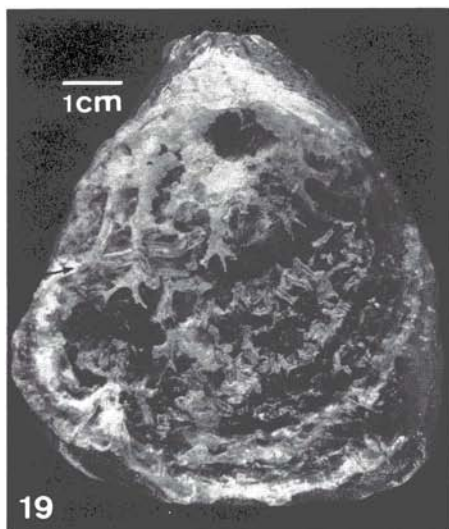
B. W. HOEKSEMA: Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.

## Plate 5.

- Fig. 19. Polyester resin cast of borings in a right valve of *Ostrea edulis*. — Borings of *Cliona celata* branching from the hinge area; Tunnels of *Polydora hoplura* in direction of arrow; Tunnels of *Polydora ciliata* originating from growth lines of shell.
- Fig. 20. Polyester resin cast of young borings of *Cliona celata* (arrows) originating from old *Polydora ciliata* tunnels in Lower Carboniferous limestone.
- Fig. 21. Shell of *Crepidula fornicata* with external surface perforated by *Cliona celata* (big arrows) and by *Polydora ciliata* (little arrows). The apex is destroyed by the sponge.
- Fig. 22. Shells of *Balanus* on body whorl of *Crepidula*-shell with living *Cliona celata*.
- Fig. 23. S.E.M.-photographs of a polyester resin cast of borings made by *Cliona celata* (c) and *Polydora ciliata* (p).  
 a. Overall picture.  
 b. Detail with pioneering filaments branching from the *Cliona*-excavation.

## Tafel 5.

- Fig. 19. Kunstharzausguß von Bohrgängen in einer rechten („oberen“) Klappe von *Ostrea edulis*. — Bohrgänge von *Cliona celata* vom Schloßbereich aus verzweigend bis Mitte der Klappe. Bohrgänge von *Polydora hoplura* in Pfeilrichtung. Bohrgänge von *Polydora ciliata* von den Anwachsstreifen in die Klappe vordringend (untere Bildhälfte).
- Fig. 20. Kunstharzausguß von jungen Bohrgängen von *Cliona celata* (Pfeile), ausgehend von alten Bohrgängen von *Polydora ciliata* in Unterkarbonkalk.
- Fig. 21. Schale von *Crepidula fornicata*, Außenseite, mit Bohrlöchern. — Große Pfeile: *Cliona celata*. Kleine Pfeile: *Polydora ciliata*.
- Fig. 22. Schale von *Crepidula fornicata* überwachsen von *Balanus*-Gehäusen, beide durchsetzt von *Cliona*-Bohrungen.
- Fig. 23. Kunstharzausguß von Bohrgängen von *Cliona celata* (c) und *Polydora ciliata* (p). — REM-Aufnahmen.  
 a. Umbiegungen der *Polydora*-Gänge besonders deutlich (p).  
 b. *Cliona*-Bohrungen mit vorstoßenden Filamenten.



B. W. HOEKSEMA: Excavation Patterns and Spiculae Dimensions of the Boring Sponge *Cliona celata* from the SW Netherlands.