Beitr. Paläont., **20**:75–87, Wien 1995

# Epibiontic microorganisms as a local control factor of bryozoan distribution and bryozoan "micro-reefs"

## Epibiontische Mikroorganismen als lokaler Kontrollfaktor von Bryozoen-Verteilung und Bryozoen-„Mikroriffen"

by

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SCHOLZ, J., 1995. Epibiontic microorganisms as a local control factor of bryozoan distribution and bryozoan "micro-reefs" — Beitr. Paläont., **20**:75–87, 2 Figures, 2 Plates, Wien.

## Contents

## Abstract

Bryozoan growth and distribution patterns are often regarded as an expression of a biological control factor such as competition or a physical factor like wave energy. An alternative thought to this preliminary concept of the interplay of global, regional and local control factors of bryozoan diversity and distribution patterns is introduced. In this context, the role of microbial communities colonizing living New Zealand and Philippine bryozoans have been studied.

On some calcifying bryozoan species, various benthic diatoms, coccoid bacteria and aquatic fungi are organized in complex microbial ecosystems. This is illustrated by critical point-dried samples of *Chaperiopsis cervicornis* BUSK. Together with the bryozoan as principal "frame builder", these minute ecosystems ("Bryozoan Micro-reefs") show some parallels with larger-sized reefs: Like macroscopic reef structures, micro-reefs are biologically controlled during the formation of the structure. This structure is rigid and shows a laterally restricted topographic relief. The microorganisms themselves exhibit a complex pattern of layering and zonation which appears to be controlled mainly by bryozoan-generated feeding currents. On the other hand, microbial mats and cnidarian nematocysts on orificial spines of *Chaperiopsis cervicornis* evidently increase the ability of the bryozoan to prevent overgrowth by other bryozoans. The bryozoan-colonizing biofilm is the outcome of a symbiotic relationship.

Epibiontic microorganisms, microbial mats and biofilms represent probably the most important **local** control factor of bryozoan distribution.

## Zusammenfassung

Wachstum und Verteilungsmuster von Bryozoen werden häufig als ein Ergebnis des Zusammenwirkens physikalischer und biologischer Kontrollfaktoren (z.B. Wellenenergie/Raumkonkurrenz) interpretiert. In diesem Zusammenhang ist der mikrobielle Aufwuchs rezenter Bryozoen Neuseelands und der Philippinen einer näheren Betrachtung unterzogen worden. Es stellte sich heraus, daß die Annahme einer reinen „Microfouling"-Assoziation dem Systemcharakter der komplex zonierten, teilweise mehrlagigen Assoziationen benthischer Diatomeen, verschiedener kokkoider Bakterien und anderer Mikroorganismen nicht gerecht wird. Am Beispiel von Critical-Point-getrockneten Kolonien der anascen Bryozoe *Chaperiopsis cervicornis* BUSK wird das Konzept eines „Bryozoen-Mikro-Riffes" entwickelt. Wie makroskalische Riffstrukturen unterliegen Mikroriffe einer biologischen Kontrolle der Gerüstbildung. Die „Riff"-Struktur zeichnet sich darüber hinaus durch ein verfestigtes „Riff"-Gerüst aus, auf welchem weitere sessile (Mikro)organismen eine Lebensgemeinschaft bilden, die an das Zusammenleben auf engstem Raum angepaßt ist. Insgesamt erhebt sich die Mikro-Riffstruktur über das Niveau der Sedimentation bzw. des Substrates (hier: Bivalvenschale). Die Bryozoe erfährt in ihrer Eigenschaft als mikrobielles Substrat Vorteile in der Raumkonkurrenz gegen ansonsten dominante Bryozoenarten; hierbei spielen u.a. Nesselkapseln von „Mikroriff"-bewohnenden Cnidariern eine Rolle. Demgegenüber profitieren die mikrobiellen Lebensgemeinschaften von dem erhöhten Wassertransport, wie er durch die strudelnde Aktivität der Bryozoen-Tentakelkronen bedingt ist. Demnach liegt eine symbiontische Beziehung vor.

Epibiontische Mikroorganismen stellen, gemeinsam mit Mikrobenmatten und Biofilmen, den wohl bedeutensten

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lokalen Steuerungsfaktor der Bryozoen-Diversität und ihres Verteilungsmusters dar. Hieraus wird ein vorläufiges Konzept der Bryozoen-Verteilung abgeleitet, welches sowohl globale, regionale als auch lokale Steuerungsfaktoren berücksichtigt.

## 1. Introduction

The various geomorphological reef types such as fringing reefs, barrier reefs or patch reefs exhibit an extraordinary diversity in terms of size and lateral extension. Aside from large topographic structures which reach up to the water surface, some reefs reach only a few meters in extension. This is true, for example, in the scattered occurrence of *Madracis* and *Dendrophyllia* – deep water reefs recorded in the Gulf of Aqaba below the depth of 105 m (FRICKE & SCHUHMACHER, 1982; FRICKE & HOTTINGER, 1983).

Following the definition of reefs of CUFFEY (1977), GEISTER (1983) and KRUMBEIN (1983), a functional reef ecosystem in a broader sense may be defined as a biogenic topographic structure resulting from accelerated growth of frame-builders. The consolidated framework rises above the level of sedimentation and is potentially wave-resistent. Reefs are upwardly growing sedimentary rocks which influence sediment and ecology around them. Reef corals and other frame-building organisms provide numerous ecological niches for a great variety of reef-dwelling marine animals and plants. For example, the spatial occurrence of Philippine reef bryozoan species is quite distinctive that competition with other epibenthic organisms is often effectively avoided. The attraction of settling larvae and success of zoaria, microbial mats and biofilms divides the settling space within the laminar boundary layer and results in a far more complicated pattern, than a surface which is characterized by physical parameters alone. This is one important reason for maintaining a high reef bryozoan diversity (SCHOLZ & KRUMBEIN, 1994).

For quite some time it has been known that the substratum-specific settlement behaviour of larvae may have a considerable influence on whether a certain species occurs and where it occurs. Different microbial mats and biofilms covering the substratum surface may further control the point of final attachment (literature reviewed e.g. by GORDON & MAWATARI, 1992; McKINNEY & McKINNEY, 1993; SCHOLZ, 1993). Thus, taking into account microbial ecosystems results in an expansion of the microhabitat concept for reef bryozoans (CUFFEY, 1970, 1978) towards smaller scales. The interaction with microbiota may also serve to explain morphologic variations and growth forms displayed by reef bryozoans which are not correlatable with fluctuations in particular environmental factors such as water turbulence (CUFFEY, 1972; SCHOLZ, 1991a). In a broader sense, microbial control of reefs and carbonate production may be essential to the understanding of reef evolution through time (FLÜGEL et al., 1993).

On the other hand, reef surfaces themselves exhibit a complex pattern that follows a fractal geometry (SANDER, 1989) which in turn results in highly complex zonation patterns of biofilms and microbial mats. There are technical adversities one is likely to encounter when conducting in-situ analysis of microbial ecosystems on reef hard substrata (SCHOLZ & KRUMBEIN, 1994). When it comes to the analysis of interrelationships of micro- and macrobenthos, it is advantageous to select a microhabitat which is somewhat isolated from other microhabitats, thereby resembling the controlled conditions of a settlement panel. Numerous studies have been conducted on bryozoan settlement on bivalve shells, the latter being a perfect example of an isolated "habitat island" as mentioned above (e.g., BISHOP, 1988 and WARD & THORPE, 1991; with review of literature). However, the role of microbial mats and biofilms in controlling bryozoan settlement with regard to bivalve microhabitats still remains to be studied. It is important to note that the physiology of microbial mats (such as found to be present on the spines of *C. cervicornis*, see below) represents the most complete system of biochemical reactions of microbiota in intimate relationship and exchange (KRUMBEIN & STAL, 1991).

This study is a part of a larger paper on the ecologic dynamics of 12 bryozoan species and associated sessile microorganisms on disarticulated New Zealand shells. This paper will deal mainly with one selected bryozoan species among the twelf.

## 2. Materials and methods

In March 1993, several hundred detached bivalve shells of the New Zealand species *Paphies australis* GMELIN, *Gari stangeri* GRAY, *Mytilus edulis aoteanus* POWELL, *Aulacomya ater maoriana* IREDALE and other mollusc shells were collected to determine ecologic dynamics of the bryozoan fauna settling. The sampling locality is in the immediate vicinity (200 m north) of the NIWA laboratories located at Greta Point, Evans Bay, Kilbirnie, Wellington. The disarticulated shells were deposited in the shallow nearshore area at a water depth of about 50 cm to 1.5 m below low tide level. Distance from the shore line is only about 1 to 5 meters. The beach front is characterized by the presence of decimeter-sized boulders deposited in a sandy matrix. The shells are deposited in a stable position (convex side up), filling the space between the boulders. Approximately 30 specimens after collection were immediately fixed in 2%-glutaraldehyde solution buffered with borax. After 24 hours, the samples were transfered to ascending alcohol concentrations until they became 100% dehydrated. SEM samples were coated with gold. SEM-Photomicrographs were taken at the EM Unit of

Victoria University, Wellington, and the Department of Geology and Paleontology (Hamburg).

SCHOLZ & KRUMBEIN (1994) have pointed out that spatial distributions and zoarial growth directions of shallow water bryozoans are often controlled by inconspicuous, non-lithified cyanobacterial mats. The latter are rarely recognizable in dried samples. On the other hand, benthic diatoms, sponge spicules and/or trapped sediments still give indication on the extent of substrate coverage by inconspicuous but ecologically important microbial ecosystems on hard substrata (Pl. 2, Fig. 6). Thus, uncleaned samples of well known Philippine bryozoans could be used for comparison with the New Zealand samples (Pl. 1, Fig. 4). Normally such data are not considered in bryozoan research for it is traditionally focussed on bryozoan hard parts. This is due to the fact that only a minority of Recent bryozoan taxa, belonging to the Phylactolaemata and Ctenostomata, are uncalcified. In the vast majority of stenolaemate and gymnolaemate bryozoans, skeleton morphology has traditionally been the basis for taxonomic description, making it necessary for the specimen to be bleached to illustrate the morphological characterizations of the mineralized parts.

## 3. Results

Within the scope of this study, special aspects of the ecology of the bryozoan species *Chaperiopsis cervicornis* (Cheilostomata, Anasca, Chaperiidae) are discussed in detail. This conspicuous and interesting Indopacific species forms encrusting, calcareous sheets of 1–2 cm diameter. Zooids are 0.39 to 0.51 mm long. The pale-brownish colonies are visibly spinose. Around the orifice, a row of 8 slender antler-like spines is present. They overarch the membraneous frontal wall (description: GORDON, 1986:41; GORDON & MAWATARI, 1992: 21).

Air-dried samples of *C. cervicornis* appear to be quite "dirty" when compared to other bryozoan species from the same sampling locality. This "dirt" is caused by the trapping of sediments on top of the spines. SEM-Photographs of the air-dried samples reveal that these sediment particles form a connecting layer, bridging the interspinal space (Pl. 1, Fig.1; Pl. 2, Fig. 3). Diatoms are also present and are found on the frontal membranes and side walls (Pl. 1, Figs. 3, 5; Pl. 2, Figs. 1, 2, 4).

Nearly all live specimens of *C. cervicornis* show also a green "belt" around the colony. This marginal green colour never projects toward the center of the colony (Pl. 1, Fig. 6). In fact it is more conspicuous the larger the bryozoan zoarium has grown. This is an indication of a distinct zonation of this microbial epibenthos.

Critical point (CP) dried samples reveal a complicated distribution pattern of bryozoan-colonizing microorganisms. The vertical layering of different microbial communities is notable and 6 layers can be distinguished from it. Each of these layers is characterized by different abundance of benthic diatoms, bacteria, minute cnidarians, and fungal hyphae. The sediment trapping mentioned above is caused by extensive growth of a slime-interwoven microbial mat. Details are explained by Fig. 1 and illustrated in Pl. 1 and 2. Horizontally, the *layers* occupy only certain *zones* of the bryozoan zoarium. The macroscopically visible green coating is an effect of preferred diatom settlement at the zoarial lateral walls and the top surfaces of the marginal zooids. A multi-species microbial mat becomes more dense towards the center of the colony. Photosynthetic microbial activities dominate at the bryozoan margin, while towards the center, consuming metabolic types and/or mixed photoautotrophic – chemoheterotrophic microbial mats are more prominent.

This distribution pattern continues also on the frontal membranes of bryozoans (the sediment-trapping microbial mat is present only on the upper parts of the orificial spines). In the older zoaria towards the center of the colonies, densely clustered coccoid bacterial cells of various types replace the laminar diatom film common on lateral zooids. Scattered diatoms still occur. The vertical layering is a less variable feature among various *C. cervicornis* specimens than the horizontal zones. The young specimen of *C. cervicornis* illustrated in Pl. 2, Fig. 3 is surrounded by a fungal mycelium which occupies a wider space than the bryozoan colony itself. That means that other epibionts (such as other bryozoans) encountered by *C. cervicornis* would contact not only bryozoan tissue but also the microbial ecosystems at the zoarial margin and on the orificial spines.

There is some indication that the observed zonation of microrganisms could be related to the feeding currents generated by bryozoans. Thin encrusting cheilostome bryozoan sheets may initially – when they consist only of a few tens of zooids – expel all filtered water along the colony periphery. When the colonies grow larger, filtered water in the middle of the colony is exhausted through chimneys, while that filtered near the colony margin is channelled out along the periphery (COOK, 1977; McKINNEY & JACKSON, 1989). In *C. cervicornis*, the dense uppermost microbial mat layer flourishes where the ex-current chimney occurs (Pl. 1, Fig. 1). On the other hand, the above mentioned small zoarium (Pl. 2, Fig. 3) is marginally surrounded by fungal mycelium probably because the feeding currents are not channelled out centrally. In general, microbial mat growth in the center of *C. cervicornis* becomes more conspicuous the larger the bryozoan zoarium grows. Thus, the microbial mats are probably controlled by the individual water flow patterns of the differently sized bryozoan colonies.

The laminar water transport over the frontal membranes provides a nutrient flux to the diatom clusters on spines and zoarial margins (layers 2, 3 and 5). The accumulation of a microbial mat and captured particles on top of the bryozoan spines also stabilizes the water body in the

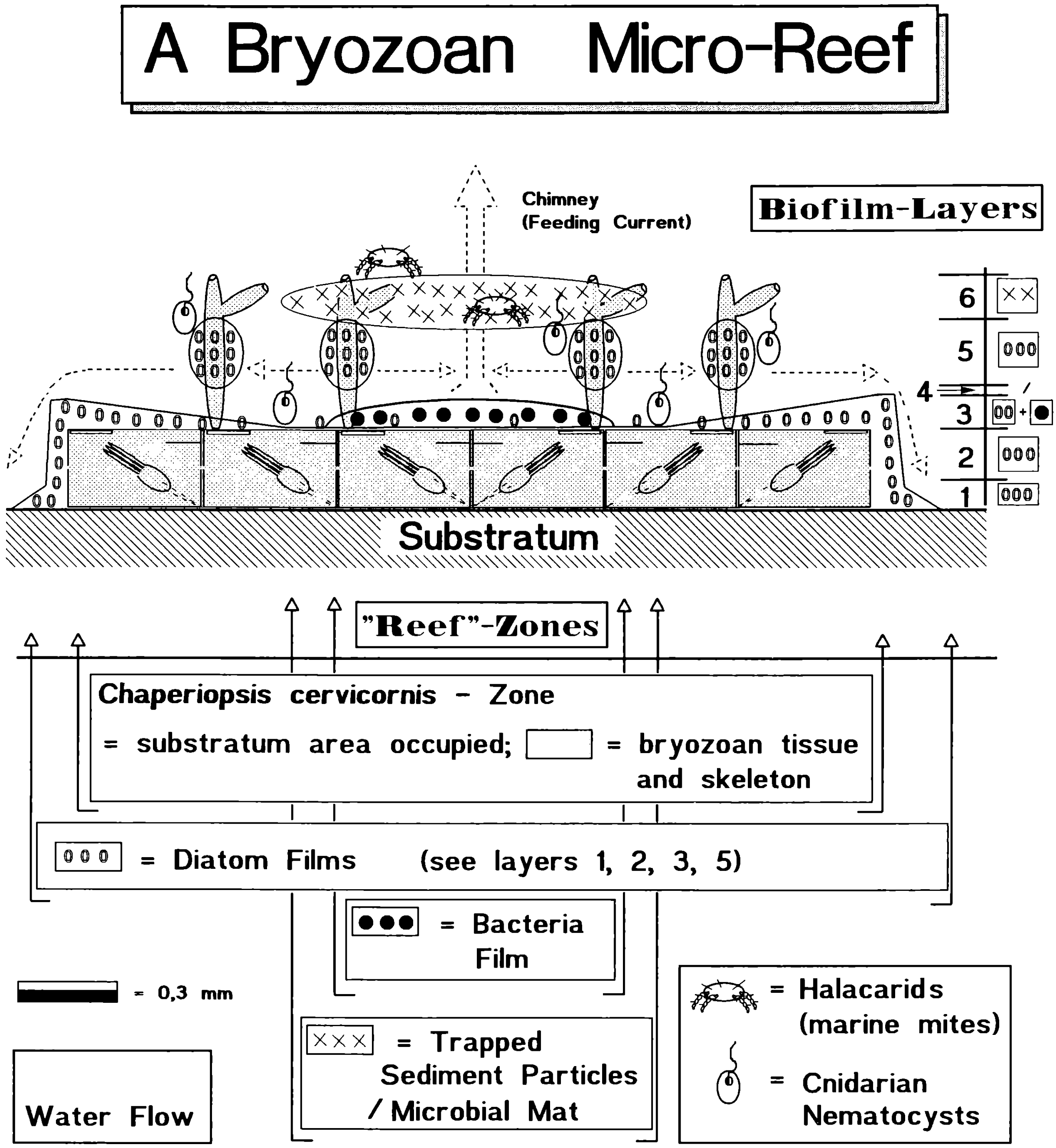

**Figure 1**: Layering and zonation in a bryozoan micro-reef, compiled from the specimen of *Chaperiopsis cervicornis* illustrated in Pl. 1 & 2. Each of the layers has a distinct epibiontic microbial community which can be described as follows:

Layer 1: Clustered benthic diatoms on the substratum surface adjacent to the marginal bryozoan zooids.

Layer 2: A diatom film colonizing the lateral walls of the bryozoan.

Layer 3: Various coccoid (staphylococcoid, monococcoid) bacteria aggregating in the center of the bryozoan colony; scattered diatoms still occur. Layer 3 develops in the area of the bryozoan colony covered by layer 6 (see below).

Layer 4: Basal part of the orificial spines. Not colonized by microorganisms with exception of some isolated diatom cells.

Layer 5: Appr. 30 to 50 µm beyond the level of frontal membrane/basal articulation of the orificial spines, a dense cluster of diatoms occurs. Rarely, a patchy occurrence of coccoid bacteria can be observed, too.

Layer 6: Layer 5 extends continuously into layer 6 which is a slime-interwoven microbial mat, containing trapped sediments. The slime is possibly excreted by diatoms (W.E. KRUMBEIN, Oldenburg, oral comm.);

(not drawn to scale: Thickness of microbial films overexaggerated in relation to the underlying bryozoan as principal frame-builder. Bryozoan polypides shown in retracted position for graphical reasons. Occurrence of cnidarian polyps is not attributed to one of the layers/zones. Patterns of bryozoan-generated water flow adapted from McKINNEY & JACKSON, 1989:136, Fig. 6.12b, showing feeding currents of a sheet-like encrusting cheilostome).

space below. This mat-modified "crevice" may offer quiescent conditions without interrupting permanent nutrient flux, a situation which favours bacterial colonization (GANTZER et al., 1989: 83).

## 4. Discussion and preliminary conclusions: Symbiotic relationships of bryozoans and microorganisms as micro-reef function

Two different conclusions can be deduced from the evidence presented above:

- The first conclusion could be relevant for the ecologic dynamics of patch-like bryozoans such as *C. cervicornis*.

The zonation and layering of microorganisms settling on live *C. cervicornis* specimens are too complex to be interpreted as mere microfouling. Fouling species are those which do not display marked substratum specifity (RYLAND, 1971; SOULE & SOULE, 1977). The epizoitic microorganisms show a very distinct distribution pattern. Evidently, the bryozoan provides numerous "Nannohabitats" which can be measured in terms of few µm or mm. In contrast, a Microhabitat as defined by CUFFEY (1978:69) is measured in centimeter to decimeter-scale.

In general, microbial fouling of frontal surfaces has a detrimental effect on anascan bryozoans (WINSTON, 1988; WINSTON & HÅKANSSON, 1989). This may be due to the fact that, in anascans, the frontal wall is not calcified. Contraction of parietal muscles depresses the frontal wall, thereby displacing body fluid and forcing the protrusion of the polypide. Therefore, it is essential that the frontal wall remains flexible. SCHOLZ & KRUMBEIN (1994) have shown that Philippine specimen of the anascan species *Onychocella angulosa* REUSS show extreme reactions of physiologic intolerance when being fouled by cyanobacterial mats. WINSTON (1988) demonstrated that the *Cupuladria doma* even has a molting strategy in order to remove epizoitic filamentous algae. On the other hand, ascophorine species with a calcified frontal shield are probably less sensitive to fouling by epibionts. Dried but uncleaned specimen of *Stylopoma parviporosa* CANU & BASSLER from exposed Philippine forereef substrata are so heavily fouled by diatoms and filamentous algae that the bryozoan (which was still alive and growing) itself appears to be hardly recognisable (Pl. 1, Fig. 4). The fast-growing multilayered photoautotrophic microbial mat partly continues beyond the level of the bryozoan zoarial margin. Due to the presence of an inflatable ascus, the feeding activity of *Stylopoma* is probably not much affected by the microbial epibionts. Moreover, *Stylopoma* is able to grow in an aggressive sheet-like pattern: The margin of the colony is broad, flexible and weakly calcified. The leading edges of the colony can be raised which helps the bryozoan to overgrow the uncalcified microbial mats (Pl. 1, Fig. 4: see arrow). A similar mode of growth is present in *Parasmittina* (SCHOLZ, 1993). For reef bryozoan species, the differential ability to interact with biofilms and microbial mats is probably the most important factor controlling their various distribution patterns and diversity.

Since the New Zealand specimens of *Chaperiopsis cervicornis* was not collected in a tropical region, multilaminar photoautotrophic mats are less abundant. In Philippine subtidal areas the concave interior parts of disarticulated bivalve shells are usually heavily fouled by filamentous, slime-interwoven photoautotrophic mats. Bryozoans are rarely present, and calcifying solitary encrusters such as serpulids tend to encrust the convex exterior part (SCHOLZ, unpublished data). In the temperate environment of *C. cervicornis*, the photoautotrophic mats on the inner valves are absent or scattered in occurrence. Competition with microbial mats is therefore a less important control factor. This makes it interesting that *Chaperiopsis* is overgrown by microorganisms which show increased diversity and abundance compared with bryozoan-free substrate areas. Abundance of benthic microorganisms can be considered as indicator for a favourable microenvironment (MEYER-REIL, 1993). Since filamentous algae and cyanobacteria are not a conspicuous part of the community on *C. cervicornis*, the frontal membrane themselves is probably not very much affected with regard to its flexibility.

I prefer to consider both parts – the bryozoans and the overgrowing microorganisms – as a system which has reached a new level of organization (complexity), thereby exhibiting functions which cannot be found in either bryozoans or epizoitic microorganisms alone. This system is self-controlling due to mutual benefit for both colonized bryozoans and colonizing (micro-)organisms. Microorganisms have mainly to rely on diffusional processes in order to exchange energy and matter. Eukaryotic macroorganisms can organize the fast and active transport of matter more efficiently (KRUMBEIN & SCHELLNHUBER, 1992:358). Thus, it is a common feature that in symbiosis of microorganisms with a larger metazoan partner, the macroorganisms support the metabolic activity of their minute partners by carrying out a transport function (OTT et al., 1991; OTT, 1993). The bacteria on the bryozoan frontal membranes (Pl. 1, Fig. 5) may benefit from the constant supply of food assured by the feeding currents. Benthic microorganisms usually remain deeply immersed within the diffusion boundary layer. Algae are able to achieve a higher level of metabolism when exposed to increased water movement (RIEDL & FORSTNER, 1968: 177). This may explain why diatoms show a peak occurrence not at the base of the spines but ca. 50 µm above the level of the basal spine junction where they are exposed to the bryozoan-generated laminar water flow (Pl. 2, Figs. 1–3).

The benefit to the bryozoan is a probable increase in competitive ability. On the bivalve shell microhabitat, *C. cervicornis* frequently competes for space with other bryozoans (Pl. 2, Fig. 5; in this specific shell microhabitat, other calcifying organisms with exception of serpulids are a less important factor in space competition). Among these competing bryozoans are weedy species such as *Rhynchozoon larreyi* AUDOUIN which is considered to be a highly successful spatial competitor (RISTEDT & SCHUHMACHER, 1985). It could be observed that *R. larreyi*, although being indeed the most superior bryozoan competitor, usually does not grow over the spines of *C. cervicornis*. On the other hand, *R. larreyi* is theoretically able to show rapid vertical upgrowth of colony margins when a "stand-off" reaction in overgrowth competition occurs (RISTEDT & SCHUHMACHER, 1985:169). Therefore, this inability is rather an effect of avoiding microbial mats or some other components of the multispecific biofilm community of *C. cervicornis*.

CP-samples of *C. cervicornis* have also revealed cnidarian tentacles and nematocysts (W.E. KRUMBEIN, Oldenburg, G. JARMS, Hamburg, oral comm.). They are found on both orificial spines and frontal surfaces of the bryozoan colony (Pl. 1, Fig. 3; Pl. 2, Fig. 4).

Bryozoans are known to react sensitively when touching hydroids; discharged nematocysts clearly harm bryozoan zooids of several species (NAMIKAWA et al., 1992:70). The results of bryozoan-hydroid interaction depend on the bryozoan species involved: It is known that certain bryozoan species live in symbiosis with hydrozoans; the hydroid polyps may form a veil above the bryozoan colony, the latter gaining protection of its surface from predation and fouling. This type of mutualistic partnership between hydrozoans and bryozoans has been frequently recorded (RISTEDT & SCHUHMACHER, 1985; BOERO & HEWITT, 1992; PIRAINO et al., 1992, with review of literature). Bryozoans living in symbiosis with hydroids do not show reactions to touches (F.K. McKINNEY, personal comm.).

Extensive spine growth of bryozoans has an important function in modifying the laminar boundary layer in order to allow the protrusion of the lophophore (RIEDL & FORSTNER, 1968). Spines can also be interpreted as a "breeding ground" for microbial mats and other epibenthos, thereby providing protection from overgrowth. Similar observations were made on a Philippine specimens of *Chaperia acanthina* LAMOUROUX, an anascan species related to *Chaperiopsis cervicornis*. The zooids of the Philippine species show 8 to 9 orificial spines which are up to 0.4 mm high. A further similarity to the New Zealand evidence is that the spines of the dried specimens collected from a Philippine reef flat substratum are often coated by trapped sediments, the latter being a possible indication of a microbial slime production. The most aggressive bryozoan competitor for space in Philippine shallow water environments, *Parasmittina parsevalii* AUDOUIN, shows a remarkable inability to grow over the spines of *Chaperia acanthina* despite the ability of the species to bridge considerably large vertical distances while advancing over porous coral skeleton substrata (SCHOLZ, 1991a:281).

- Secondly, a new way of looking at reefs in reference to scale and microbial control can be made.

The bryozoans themselves are too small to rise significantly above the level of sea bottom on a macroscopic scale. However, from a microorganism's point of view (rather than from the geologic perspective of optical dominance), they rise considerably above the local level of the substratum. This micro-topographic feature is supported by the rigidly calcified lateral walls of *Chaperiopsis cervicornis*. When neglecting the diameter/size of this micro-ecosystem, there are parallels to "regular" reefs like coral reefs.

Individual reefs are often understood as a structure which measures from under one to several miles across (CUFFEY, 1978:69), and reach up to the water surface (SCHUHMACHER, 1988:12). Such a definition would not allow the application of the term "reef" on the microbial ecosystem described above. On the other hand, it displays a prominent environmental zonation within themselve which fits into the criterium for reefs, too (CUFFEY, 1978). In the terminology of FLÜGEL & FLÜGEL-KAHLER (1992) who gave an up-dated data base on the study of reef evolution, the bryozoan-microorganism structure could be considered as a reef.

"*To follow reef development over geological time, 'reefs' have to be defined in a very broad and rather simple way .... For ancient reefs it therefore seems to be reasonable to designate all those structures as 'reefs' which are characterized by at least the following features: Biological control during the formation of the structure (especially by sessile organisms), rigidity of the structure and laterally restricted topographic relief*" (FLÜGEL & FLÜGEL-KAHLER, 1992:170).

Previously, the term "micro-reef" has already been introduced by WENDT (1969:185) while studying minute, pillar-like structures consisting of successions of sessile Foraminifera. These fossil (Triassic) Foraminifera-reefs range in height from a few millimeters to two centimeters. Like in the bryozoan-micro-reef, a complexly zoned community of reef dwellers is present. Unlike these Foraminifera-reefs and macroscalic reefs, the non-lithifying microbial communities present on *C. cervicornis* do not play a constructional role by contributing only trapped sediment particles but no calcareous skeletal material to the "reef" mass. At rare occasions, the absence of binding epibionts is also observed in macroscalic reef structures such as rudist reefs (KAUFFMAN & SOHL, 1974:401). An important difference to macroscalic reefs is that the bryozoan micro-reefs can include a single colony while larger reef structures usually become cohesive through the growth of more than one clone.

With these views in mind, bryozoan/microorganism ecosystems in reefs can also be seen as a "Reef in a Reef"

A comparison can be made to the knowledge of interrelationship of macroscalic, mesoscalic and microscalic systems such as applied in weather-forecast; single clouds are defined as a microscalic system while frontal systems are mesoscalic and the general circulation of earth-atmosphere is macroscalic (KURZ, 1992:100). The interplay of micro- and macrosystems has been interpreted by JANTSCH (1992:297) in a most general way. He developed a hypothesis on the co-evolution of interrelated self-organizing micro- and macrosystems within the scope of "evolutionary hierachy of structures" According to JANTSCH, such features of co-evolution are essential for the development of complexity in dissipative structures. Bryozoans may be instrumental in illustrating such system interlinks. Most of the background information applied to *C. cervicornis* were from our previous studies in the Philippines. For example, the bryozoan-micro-reef concept itself is derived from earlier observations on symbiotic relationships of erect (bush-like) reef bryozoans and epibiontic filamentous algae. The latter are raised over the stagnant boundary layer while the bryozoans gain protection from being overgrown by other bryozoan species (SCHOLZ, 1993:115). This in turn could make the concept of "bryozoans as micro-reefs" applicable to reef environments *sensu stricto*.

It has been shown already that bryozoan biodiversity and community structures in the Philippines is linked for example to global control factors such as monsoon seasonality (SCHOLZ, 1991a, b). Monsoons are a factor of global earth atmosphere circulation, thereby representing a macroscalic system. Plate tectonics as a global control factor has contributed to the partial similarity of the Philippine and New Zealand bryozoan faunas, being a part of the former Tethyan realm (GORDON, 1984, and oral comm.). Regional control factors which select bryozoan growth forms in certain coastal environments of the Philippines are abrasive sand waves due to terrigene sediment flux (SCHOLZ & CUSI, 1991) and hydrographic fronts in dependence of regional topographic features (SCHOLZ, 1991 b, c). The interrelationships of bryozoans and various types of microorganisms illustrate another size-step down: as a microenvironment, they are influenced by **local** control within the diffusion boundary layer on the substratum surface. "Microenvironments" are measured in millimeter-scale or smaller (MEYER-REIL, 1993: 39). In accordance with this definition, the range of local control can be measured in mm- or µm-scale.

The total bryozoan biodiversity for example of the Philippines is an expression of global control, while the association found in a specific sampling site is rather influenced (= selected) by regional control and finally, the selection of bryozoan microhabitats such as the New Zealand bivalve shells constitute local control (Fig. 2). As a microenvironment, bryozoan surfaces provide nannohabitats for microorganisms.

The interplay of local, regional and global control of bryozoans still remains to be studied in detail; on the other hand, the introduction of this concept is essential for the definition of the term "micro-reef". In order to provide a more precise definition, the attribute "local" for the

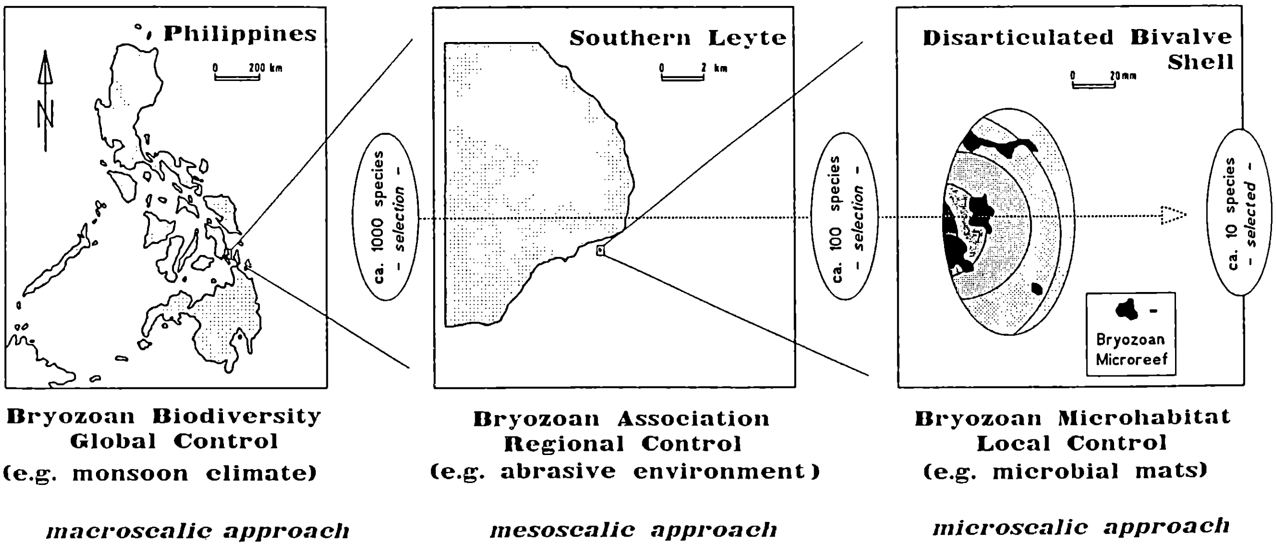

**Figure 2**: In weather forecast, an interplay of micro-, meso- and macroscalic systems has been identified (KURZ, 1992). In an analogous way, (reefal) bryozoan distribution patterns can most profitably be considered at several different scales (CUFFEY, 1978).

Bryozoans are controlled by macroscalic (= global), mesoscalic (= regional) and microscalic (= local) control factors. Microreefs are highly complex systems controlled mainly by local factors of short range. Yet, in a fractal way, microreefs bear similarities to coral reefs developing under regional and global control.

As a function of scale, the diversity of bryozoan species controlled by global, regional and local factors, decreases along this line (dotted arrow). On the other hand, the diversity of control factors increases in opposite direction, resulting in a multiplication of available bryozoan habitats from global level (such as: tropical monsoon seasonality) to regional level (e.g. abrasion-resistant bryozoans of ahermatypic hard substrate associations; "macrohabitats" in the language of CUFFEY, 1978) to local level (e.g. bryozoans of the microhabitat: convex exterior side of disarticulated bivalve shells). The bryozoans themselves provide nannohabitats for microorganisms (not illustrated).

dominating controlling factors is important to distinguish micro-reefs from regionally and globally controlled reef structures such as coral reefs (FLÜGEL & FLÜGEL-KAHLER, 1992). Since the term "micro-reef" refers to the scale of the structure and the range of the main control factors, "micro-reefs" are clearly different from "microbial reefs" The latter are frequently reported from fossil to Recent (e.g., GERDES et al., 1985:247). Microbial reefs are commonly built by prokaryotes such as cyanobacteria (formerly misnamed as blue-green-algae; KRUMBEIN, 1979) and chemoorganotrophic bacteria. The latter significantly contribute to carbonate precipitation (KRUMBEIN, 1983). In contrast, vertically growing microbial structures which do not lithify (and therefore are not reef-like) are called "stromatolitoids" (WESTPHALEN, 1993). The termini "Micro-Reefs" and "Microbial Reefs" do not exclude each other, only that the latter refers to the size of the reef builders rather than to the scale of the reef structure. Due to the size limitation of their zooids, bryozoans grow where the microscalic and the macroscalic world are interlinked. Thus, a point of departure for the development of a general understanding of bryozoan biodiversity should also start at a scale where one of the most important perspectives to consider is that from a growing and feeding bryozoan's point of view— the scale of bacteria and microbial mats.

### Acknowledgement

I would like to express my thanks first to Dr. D. P. GORDON (Wellington, New Zealand), whose generous gift of time and insight made this study possible. He also critically read the manuscript. Furthermore, I am grateful to Prof. Dr. R. J. CUFFEY (Pennsylvania State University, U.S.A.) and Prof. Dr. F. K. McKINNEY (Boone, USA) for their very valuable and constructive review. I am indebted to Prof. Dr. W. E. KRUMBEIN (Oldenburg), Prof. Dr. J. OTT (Vienna), Prof. Dr. E. FLÜGEL (Erlangen), and Prof. Dr. G. HILLMER (Hamburg) for helpful comments. My sincere thanks are extended to Mr. R. THOMPSON (Victoria University, Wellington) for assistance in the analysis and Ms. J. B. GERRA-SCHOLZ for her support. Prof. Dr. W.-Chr. DULLO (Kiel) provided the illustration for Pl. 1, Fig. 2.

I am indebted to the DEUTSCHE FORSCHUNGSGEMEINSCHAFT (DFG-Schwerpunkt "Biogene Sedimentation", Hi 273) for providing the funding of the bryozoan project.

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## PLATE 1

Fig. 1. A reef on micro-scale: The New Zealand bryozoan *Chaperiopsis cervicornis*, rising above the level of sedimentation/substratum: a disarticulated shell (inner surface) of *Paphies australis*. At the lower right, the cardinal teeth of the bivalve are visible. The center of the bryozoan colony is densely covered by a microbial mat, appearing white. This microbial mat may flourish due to increased transport of organic matter (see text). This nutrient flux is provided by ex-chimneys which are part of the bryozoan-generated feeding currents (marked by perforations in the microbial mat). (SEM-microphotography of CP/critical point dried-specimen; x 15).

Fig. 2. A reef on macro-scale: A bioherm formed by the stony coral *Madracis interjecta* rising above the level of sedimentation. Gulf of Aqaba; depth 150 m. Description: FRICKE & HOTTINGER, 1983. Photograph courtesy of W.-Chr. DULLO (Kiel).

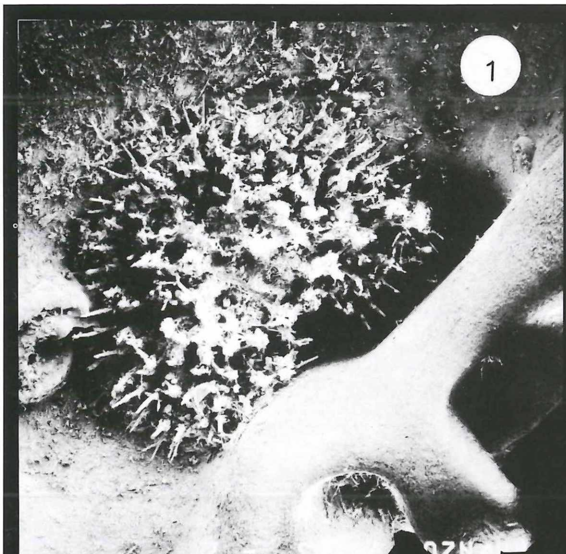
Fig. 3. A single spine of *C. cervicornis* from a young autozooid growing at the margin of zoarium; note the various types of benthic diatoms and cnidarian nematocysts (below) (SEM-microphotography of CP-specimen illlustrated in Fig. 1; x 300).

Fig. 4. *Stylopoma parviporosa* CANU & BASSLER from a Philippine forereef environment (Marigondon, Cebu; depth: 20 m). The bryozoan is completely covered by epibionts but obviously not much affected (Arrow: the leading edges of the bryozoan colony have been raised in order to grow over the uncalcified microbial mat). Filamentous algae are more common than in the microbial community on *C. cervicornis* (air-dried specimen; x 27).

Fig. 5. Coccoid bacteria dominate the microbial communities on frontal membranes of older *C. cervicornis* zooids which occupy the center of the colony (SEM – microphotography of CP-specimen illlustrated in Fig. 1; x 810)

Fig. 6. A disarticulated shell of *Gari stangeri* GRAY with encrustations of *Chaperiopsis cervicornis.* Virtually all bryozoan specimen show a green coating on the zoarial margin, appearing grey on the photograph (arrow). This coating is an effect of high abundance of diatoms = microreef layers 1 and 2 in Fig. 1 (macro-photography of a sample preserved in glutaraldehyde/alcohol; x 2.2).

# PLATE 1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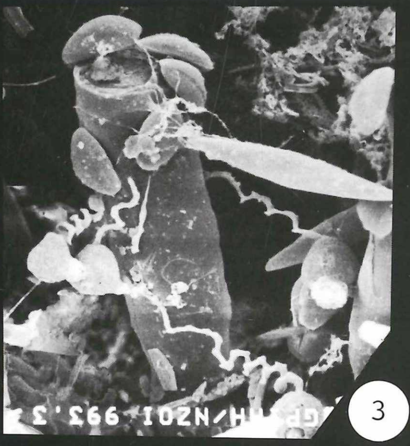

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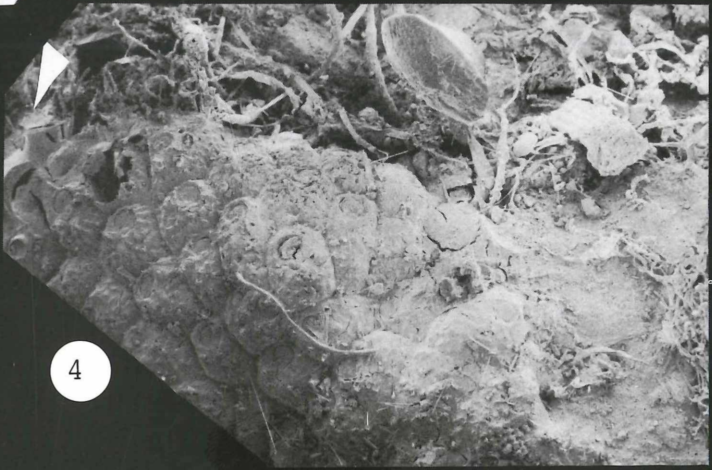
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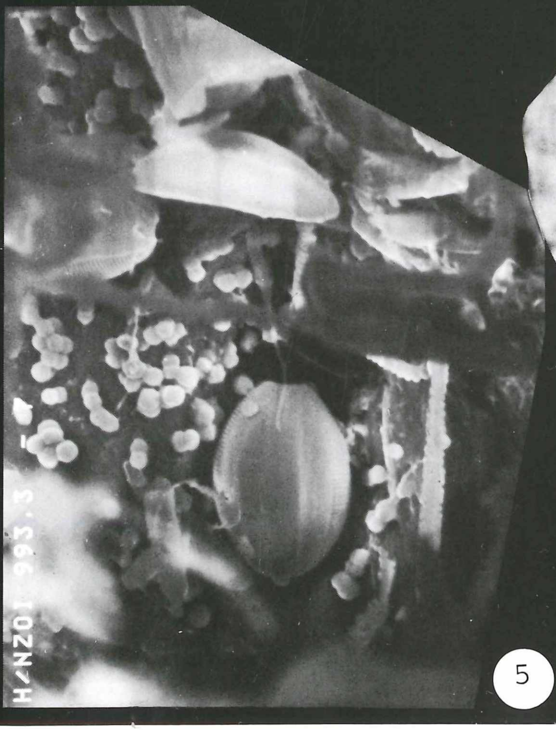

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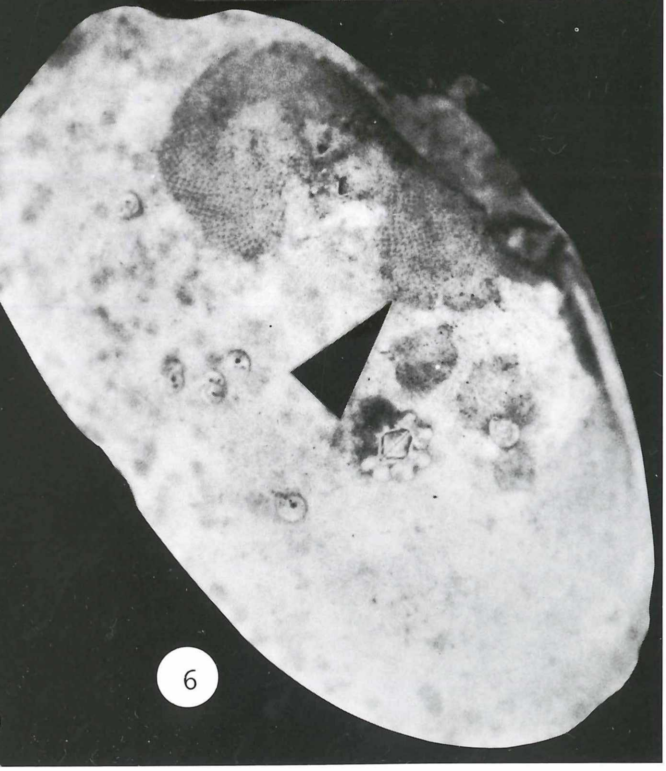
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## PLATE 2

Fig. 1. A microbial garden, colonizing the advancing growth front of *C. cervicornis* (SEM-microphotography of CP-specimen illustrated in Pl. 1, Fig. 1; x 90)

Fig. 2. Zoarial margin of the early astogenetic colony of *C. cervicornis* illustrated in Fig. 3. Diatoms accumulate in the middle part of the spine (microreef layer 5). (SEM-microphotography of CP-specimen; x 230).

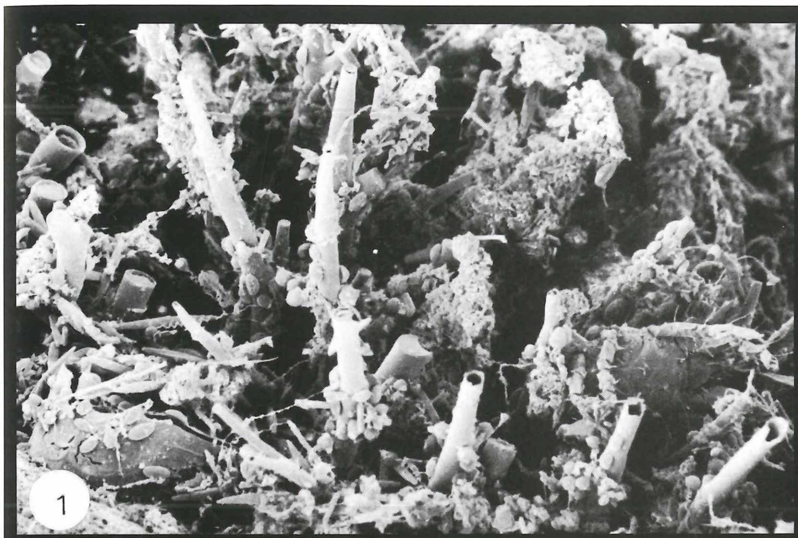
Fig. 3. A specimen of *C. cervicornis*, representing an earlier astogenetic stage than the one illustrated in Pl. 1, Fig. 1. A similar but thinner layer of slime-interwoven microbial mat is present. Arrow: fungal mycelium at the zoarial margin. Since this colony is probably too small to generate ex-chimneys, filtered water is forced out along the periphery. Performing a consuming metabolism, the mycelium shows a correlation with this water flow patterns (probably providing nutrients; further explanations: see text). (SEM-microphotography of CP-specimen, x 80).

Fig. 4. A microbial community on *C. cervicornis* spines in the center of the colony (microreef layer 6). The mat is produced by diatoms, extracellular slimes and trapped sediments. See, for comparison, Pl. 1, Fig. 3. Arrow: cnidarian nematocyst. (SEM-microphotography of CP-specimen illustrated in Pl. 1, Fig. 1; x 315).

Fig. 5. *C. cervicornis* (left) versus the bryozoan competitor *Calloporina angustipora* HINCKS (right; D. P. GORDON, oral comm.); (SEM-microphotography of air-dried specimen; articulated spines of *C. cervicornis* not preserved; x 55).

Fig. 6. A microbial mat similar to the one illustrated in Fig. 4; spines of an air-dried specimen of *C. cervicornis*. Though details on the microbial community cannot be recognized, the former extension of the dried spine-coating mat is indicated by trapped sediments (SEM-microphotography; x 270).

# PLATE 2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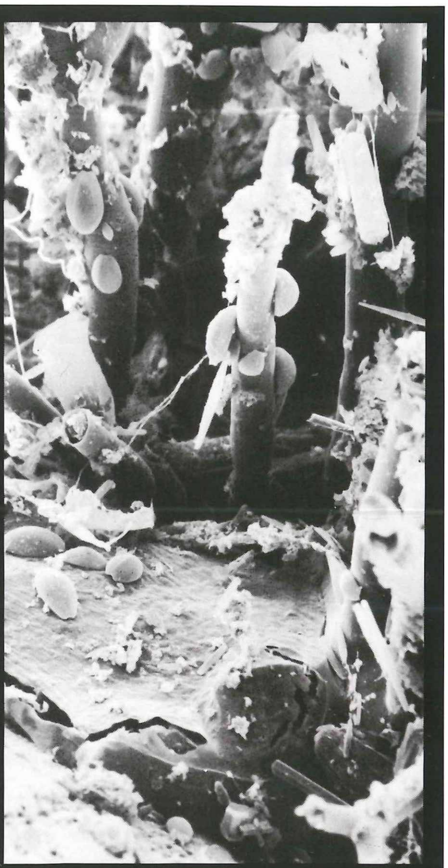
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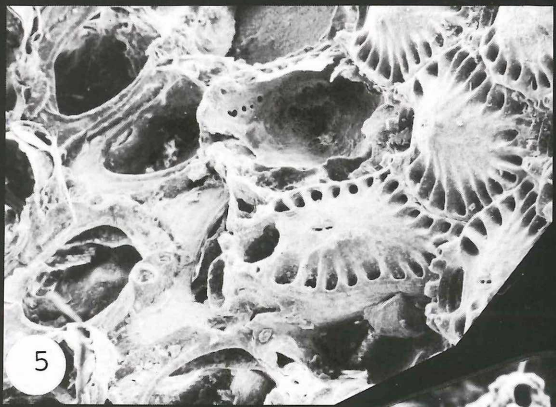
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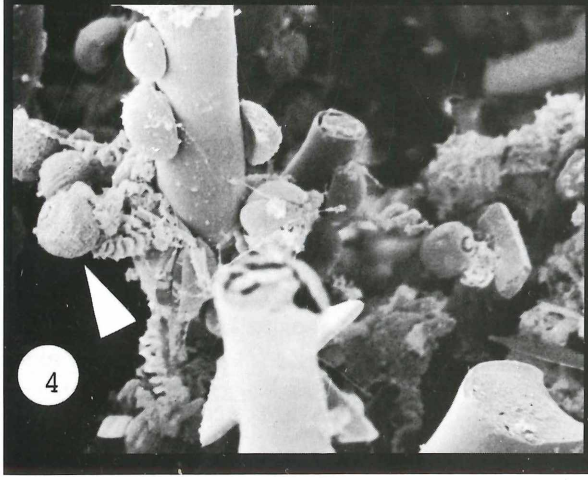
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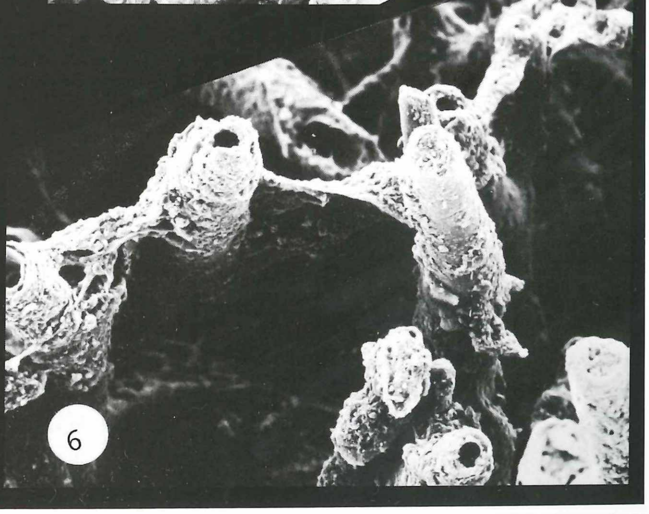
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Zeitschrift/Journal: Beiträge zur Paläontologie

Jahr/Year: 1995

Band/Volume: 20

Autor(en)/Author(s): Scholz Joachim

Artikel/Article: Epibiontic microorganisms as a local control factor of bryozoan distribution and bryozoan "micro-reefs" 75-87