

Recent Bryozoan Reefs and Stromatolite Development in Brackish Inland Lakes, SW Netherlands.

With 3 Text-Figures and 4 Plates.

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Abstract.

[BIJMA, J. & BOEKSCHOTEN, G. J. (1985): Recent bryozoan reefs and stromatolite development in brackish inland lakes, SW Netherlands. — *Senckenbergiana marit.*, 17 (1/3): 163-185, 3 figs., 4 pls.; Frankfurt a. M.]

Bryozoan reefs and stromatolites from the southwestern part of Holland are described. The so called "growing stones", first described in 1729, consist of two parts: the center, a more or less spherical colony of the cheilostome bryozoan *Electra crustulenta* and the rind, consisting of stromatolitic limestone. Three modes of occurrence were observed; bryozoan reefs, consisting of small spherical colonies up to megacolonies, one meter high and tens of meters across; bryozoan reefs capped with stromatolites and stromatolite crusts covering various substrates (furnace slags, concrete, bottles and even rubber tires). The apparent substratum preference of the stromatolites for bryozoan reefs may be the result of a high preservation potential of stromatolite crusts on porous bryozoan colonies.

Fossil counterparts of these reefs in man-made environments are the Miocene bryozoan-stromatolite reefs in the Paratethys. They may be compared with the uppermost Jurassic serpulid reefs along the North Sea basin, and the Zechstein reefs in the same region.

Problems in the mechanisms currently invoked for stromatolite growth are reviewed and a new explanation of stromatolite formation is presented.

Kurzfassung.

[BIJMA, J. & BOEKSCHOTEN, G. J. (1985): Rezente Bryozoenriffe und Stromatolithenentwicklung in brackischen Binnenseen, SW-Niederlande. — *Senckenbergiana marit.*, 17 (1/3): 163-185, 3 Abb., 4 Taf.; Frankfurt a. M.]

Untersucht wurden Bryozoenriffe und Stromatolithen in brackischen Binnenseen der südwestlichen Niederlande. Die 1729 zum erstenmal beschriebenen „Wachsenden Steine“ bestehen aus zwei Teilbereichen: A. dem Zentralbereich: einer mehr oder weniger sphärischen Kolonie von cheilostomen Bryozoen der Art *Electra crustulenta*; B. der Rinde aus stromatolithischem Kalk. — Drei Vorkommensweisen wurden beobachtet. 1. Bryozoenriffe, deren

Größe von kleinen sphärischen Kolonien bis zu Megakolonien von 1 m Höhe und mehreren Zehnermetern im Durchmesser reicht; 2. Bryozoenriffe, die von Stromatolithen überwachsen sind; 3. Stromatolithische Krusten auf den verschiedensten Substraten wie Ofenschlacken, Beton, Flaschen und sogar Gummireifen. Die offensichtlich bevorzugte Bindung von Stromatolithen an Bryozoenriffe dürfte ihre Ursache in der guten Erhaltungsfähigkeit der Stromatolithenkrusten auf den porösen Bryozoenkolonien haben.

Diese Riffe in Lebensräumen der Kulturlandschaft haben ihre fossile Entsprechung in den miozänen Bryozoen-Stromatolithen-Riffen der Paratethys. Diese sind wiederum vergleichbar mit den Serpulidenriffen des obersten Jura am Rande des Nordseebeckens und mit den Zechsteinriffen in derselben Region.

Jüngst aufgeworfene Fragen des Wachstumsmechanismus von Stromatolithen werden kritisch betrachtet und es wird eine neue Vorstellung über die Stromatolithenbildung entwickelt.

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Introduction.

Stromatolites, common as they are through the Precambrian, become progressively more rare in the Phanerozoic stratigraphical column. Recent occurrences are scarce; most are found in fresh water environments and some in tropical hypersaline lagoons. When we recognized stromatolites encrusting the "growing stones" known since at least three centuries from backish inland waters in southwestern Holland, this occurrence seemed interesting enough to warrant closer inspection.

"Growing stones" attracted local attention and several names were coined for them, such as "kaaskens" (= little cheese), "ziltsteen" and "zouterik" (= salty stone) and "palingbrood" (= eels' bread). A deep creek that originated 1576 as a result of inundations caused by the Dutch/Spanish war, directly NW of the town of Zierikzee (Fig. 1) is indicated on a 1673 map as the "Kaaskenswater". This inland creek filled with backish water still contains fine occurrences of huge bryozoan colonies lined with stromatolitic crusts. More famous became another inland water "De Waal" near the village of Rockanje (Fig. 1). In a book describing this region, VAN ALKEMADE & VAN DER SCHELLING (1729) are the first to print their astonishment about the petrifying force of these inland waters. A walking stick, thrown into "De Waal", would be completely covered by stone if left alone. A rock had grown in this lake, starting about 1660, from mud that had gradually petrified. BASTER (1762) recognized that bryozoans constructed the "Kaaskens" of his native Schouwen island; he observed that this species had not yet been described by LINNAEUS and coined the Latin name *Eschara lapidescens* for these

ectoprocts. As BASTERS' species is non-Linnean, the objective synonym *Eschara crustulenta* PALLAS 1766 is the valid name. Dr. CUFFEY called our attention to the fact that in the eastern U. S. A. *Conopeum tenuissimum* (CANU) has been confused with the present species. *Conopeum* has an amphiatlantic distribution, and is found in African estuaries. BODDAERT (1768) translated PALLAS and observed that the Rockanje rocks consist of colonies of this species, covered with a crust of coralline nature. An artificial mound was constructed (Pl. 1 fig. 1) from the cauliflower-like colonies, so that the many curious visitors could admire this natural wonder with dry feet. LE FRANCQ VAN BERKHEY (1771) gave a very lengthy description; the bryozoan zooecia would be simulated by trace fossils of boring shells, tunneling in limestone that would be itself a deposit of calcareous particles cemented together by the currents of a former system. The chemical theses of BERGSMAN (1823) and VAN ANROOY (1852) discarded this idea. Studies by LORIE (1896) and BLAAUW (1917) essentially confirmed BODDAERT (1768); these papers provided a wealth of new data, but did not give much more insight. Public wonder about these occurrences of "growing stones" remained. Mud from the Rockanje lake was again chemically analysed in 1913; the presence of much radium was ascertained; radioactivity would be the explanation for the peculiar lithification in the lake. The farm Walesteijn (dating from 1697) was pulled down to make place for a big health spa, Bad Walesteijn, much in favour in the neutral Netherlands when it was impossible to visit foreign balneary stations during the great war. Later analysis failed to detect any appreciable radium content in the mud that filled the Walesteijn tubs. The enterprise had to close in 1918, notwithstanding the fact that the healthy regime cured about half of the well-to-do's that frequented the spa. At Oostburg (Fig. 1) another inland lake, the Groote Gat, was found by J. AB UTRECHT DRESSELHUIS (1839) to contain the same "growing stones" as the Rockanje lake. Here also public wonder about the phenomenon was considerable. In about 1935 a so called Lourdes Cavern was built from these miraculous stones in the garden of the roman catholic hospital.

These stromatolites encrust huge colonies of the bryozoan *Electra crustulenta* and, together, form veritable reefs in several brackish inland waters. The geological record shows not a few examples of bryozoan/stromatolite associations. The oldest may be the early Ordovician bioherms in New Foundland, described by PRATT & JAMES (1982). These consist of stromatolites and *Lichenaria*, often interpreted as a primitive tabulate "coral" but more likely a primitive bryozoan. The deposit apparently was formed in very shallow sea water of normal salinity. Spectacular bryozoan-algal patch reefs developed in the Upper Permian around the NW European Zechstein basin (SMITH 1981; FÜCHTBAUER 1980; PAUL 1980). Colonies of the ramose bryozoa *Acanthocladia* and *Thamniscus* were capped by stromatolites in shallow (possibly sometimes hypersaline) water, offshore on a broad shallow marginal carbonate shelf under tropical or subtropical conditions. SMITH (1981) describes saccoliths from the Yorkshire exposures. These consist of a dense network of bryozoan stems in a matrix of dolomite. The saccolith bodies, 0.5 to 1.5 meters across, are remarkably similar to the lithified bryozoan colonies ("kaaskens") found in several Dutch inland lakes (Pl. 2 figs. 5-6).

All but identical with the recent Dutch reefs are the bryozoan reefs that lined the shores of the Late Miocene Paratethys in Rumania, Poland and Russia. Descriptions of these reefs were presented by ANDRUSSOW (1909-12), KARLOV (1937), MARTIN (1943) from the Kertsch and Taman regions along the Eastern Black Sea; by SAJANOW (1968) and VZNUZDAEV (1953) from Moldavia; by GHIURCA (1968) from Rumania; by LISZKOWSKI & MUCHOWSKI (1969) and PISERA (1978) from Poland. Most of these reefs developed in shallow lagoons with restricted salinity. It is hoped that the present paper clarifies some of the problems met with when studying these and other fossil reefs.

Region Studied.

The surface of the northwestern half of the Netherlands consists almost completely of Holocene deposits, of which most were sedimented in lagoons, estuaries and other tidal areas. The most intricate coastline is found in Zeeland where deep

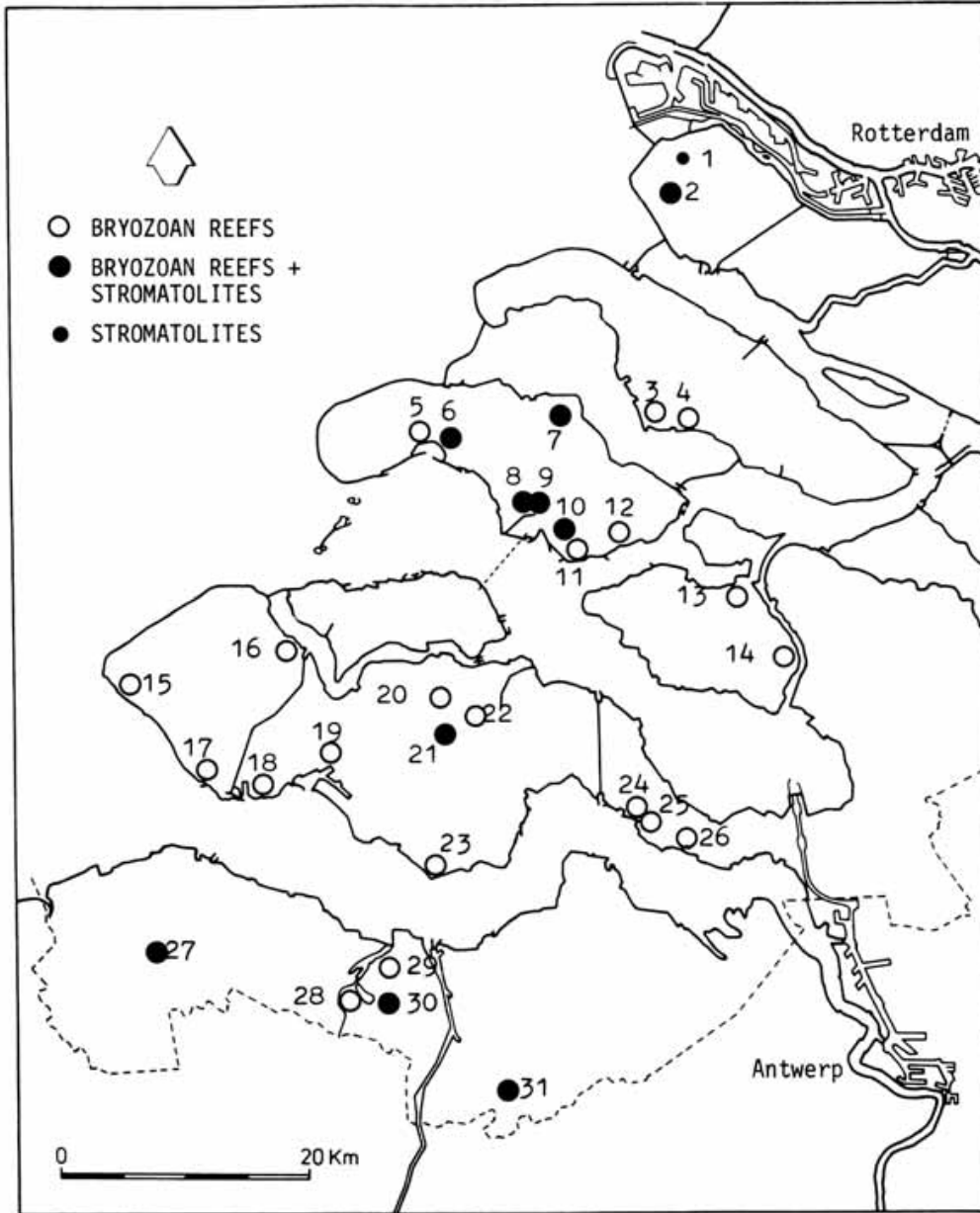


Fig. 1. Locality map of the distribution of *Electra* reefs and stromatolites in brackish inland lakes in the SW Netherlands. — 1. Hekeringen pond. 2. De Wall. 3. Klaasjeswater. 4. Paardegat. 5. Schelphoek. 6. Welgelegen. 7. Kreekzicht. 8. Ronde Weel. 9. Kaaskenswater. 10. Diepe Gat. 11. Eastern channel SE of Ouwkerk. 12. De Guil. 13. Het Stinkgat. 14. Karnemelkpot. 15. Creek near Westkapelle. 16. Creek near Veere. 17. Nollebosch. 18. Rammekenshoek. 19. Sloekreek. 20. Waal near Wolphaartsdijk. 21. Terluchtse Weel. 22. Oosterschenge. 23. Inlaag 1887. 24. Waal near Glerum pumpingstation. 25. Den Inkel. 26. Klaasjes Weel. 27. Groote Gat. 28. Creek Dijkmeester polder. 29. Voorste Kreek. 30. Valput. 31. Lake west of fort St. Joseph.

Abb. 1. Karte der Fundpunkte von *Electra*-Riffen und Stromatolithen in brackischen Binnenseen der SW-Niederlande.

tidal channels cut into pre-existing lagoonal and tidal flat peat, clay and sand. Human settlement in this southwestern half of the Dutch Holocene was dense since the 12th century; with dikes, the shoreline became more or less fixed. Inundations because of storms (1953) and of warfare (1576; 1944) resulted in deep channels incised into the reclaimed inland. These did not silt up because further erosion along such channels was countered by damming. Other inland waters originated by cutting off deep pre-existing channels when new land was reclaimed. Finally, artificial lakes were dug in post-war times for recreational purposes. All these constitute as many permanent brackish water bodies. In 1982, the first author surveyed a large number of these inland waters; localities are indicated on Fig. 1. Because of their origin, most are unconnected with other brackish water bodies and many have rather steep underwater slopes. Natural brackish lagoons more often have flat bottoms and are interlocked with other brackish waters. This means that colonisation by organisms is enhanced and that widely varying circumstances prevail at different zones of the inland water bottoms. It is not surprising, therefore, that only 31 of the 184 surveyed waters turned out to contain the bryozoan and/or stromatolite reefs under discussion. Formerly, this number must have been much larger. Especially after the 1953 flood, most of the area under discussion underwent extensive land-reallocations; one of the aims was to have as much fresh water in the canals as possible. The annual report of the Walcheren water board (BOREEL 1932) contains a chapter dealing with the problems caused by the growth of bryozoan reefs under bridges, along quays and in channels; it was necessary to send gangs of workmen to remove these ongrowths which severely obstructed water movement. Even nowadays, these problems arise (anonymous, 1983).

Outside the area studied, only a few localities are known to us where *Electra crustulenta* constructed reef-like masses in inland waters: in Holland at the Honds bossche Zeewering (VAN BAREN 1927) and at the eastern side of Texel island (CADÉE, pers. comm.), in Germany, at the island of Pellworm (REMANE & SCHLIEPER 1971). Stromatolites have not been reported from these areas. The development of stromatolite crusts in alkaline saline lakes of the Western U.S.A. (DEAN & FOUCH 1983) may be compared with the Dutch equivalents.

The morphology of the brackish water basins in the area studied also is of importance to their hydrological properties. Because of their relatively large depths as compared with their surface, salinity fluctuations are less important than in brackish lagoons. Water stratification is often present during summer time, because the inland waters are not part of a current system. Surface turbulence and overnight cooling are often insufficient to start circulation in these basins. The different inland waters all have their own hydrological characteristics; these determine the distribution of the reef zones and therefore will be discussed in the reef chapter.

The Reefs.

Biologically, the bryozoan/stromatolite formations can be classified as reefs. The colonies present a suitable substratum for hydroids (*Cordylophora*, *Laomeda*) which are preyed by gastropods (*Embletonia*); the endemic *Semisalsea stagnorum* (GMELIN) is often found grazing on dead surfaces. The reefs provide shelter to

polychaetes (*Polydora*, *Nereis*), sow-bugs (*Sphaeroma*), amphipods (*Gammarus* spp.) and eels (*Anguilla*). Because of the latter aspect, commercial fishermen even try to transplant *Electra* colonies ("eels' bread") to other brackish inland lakes, to enhance the fish crop. The colonies also form a suitable substratum for subaquous plants like *Potamogeton*. In the Terluchtse Weel, the zone of pondweed growth corresponds exactly with the presence of bryozoan/stromatolite solid substratum.

Geologically, the huge bryozoan limestone lenses (up to 1 m high and tens of meters across in the Ouwerkerk channel system) certainly qualify as reef. It is appropriate to discuss the preservation potential (PARK 1977) here of the Dutch examples. However, large they are, the (calcitic) *Electra* colonies never grow very solid; they just support the weight of a human when trodden under foot. If their framework is covered with stromatolitic linings, they become much more solid. Part of the Kaaskenswater reefs are exposed subaerially since water level was lowered, about thirty years ago. These are still well preserved. The saccoliths from which the artificial rock in the Waal lake was constructed, withstood two centuries of subaerial exposure. Yet, no fossil occurrences of these reefs have been encountered during detailed soil surveys and geological mapping in the region studied.

This may be understood when it is taken into account that we found reefal development only in small inland lakes that owe their origin and preservation to human activities. Reasonably limpid brackish water was present here in sufficient time for the reefs to grow. Were the region left to itself, without human interference, no persisting deep bottomed brackish lakes would be available; brackish environments would be restricted to shallow lagoonal and deltaic environment with ever ongoing erosion and sedimentation. River transported clay would be milled around by tidal currents and wave turbulence, thus inhibiting any stromatolite/bryozoan development.

The lagoons lining the shores of the brackish Paratethys in the Upper Miocene, on the other hand were extensive and shallow; tidal movement was practically absent and clastic sedimentation moderate. These circumstances led to the development of the bryozoan reef zones as described by ANDRUSSOW (1909-12) and later authors. It is not to be expected that the recent Dutch examples will be found back in the Dutch Holocene. It is not surprising that many of the organisms in the recent reefs discussed are also present in the Ponto-Caspian region, or are closely related to forms occurring there. The late Miocene Paratethys must have been an ideal region for the evolution of many brackish water organisms.

Bryozoan Constructions.

Electra crustulenta is common in almost any brackish inland lake or creek in the SW Netherlands. Only in some creeks, however, it develops explosively into reefs that are bigger than 10 m. in diameter and more than 1 m. in thickness. The reason why *Electra* is able to form such huge reefs is not understood in detail. *Electra crustulenta* is a species of the Cheilostomata, successful because of a high degree of polymorphism and a welldeveloped mutual communication system. Furthermore the evolution of broodchambers (gonozooids) and heavily calcified cystids make them perhaps less sensitive to predation (RYLAND 1970). Two species of the

suborder Anasca are especially adapted to the brackish biotope. These are *Conopeum seurati* (CANU 1928) and *Electra crustulenta*, possibly because they belong to the few anascans which produce lots of tiny eggs during sexual reproduction as to improve survival rate in the erratic brackish environment. *Conopeum seurati*, however, was not found to produce reefal buildups (HEEREBOUT 1970). The advantage of *Electra crustulenta* in this respect may be its small size. *Electra* is about half as large as *Conopeum* which means that the surface/content ratio is more favourable when neutralizing osmotic differences.

Brackish biotopes are, compared to fresh and salt water systems, very unstable. Salinity fluctuations may be rapid and the extremes can be wide apart (5.8‰-60.36‰ in the Suzanna-inlaag on Schouwen, according to DEN HARTOG 1964). MENON & NAIR (1972) found that *Electra crustulenta* collected before the mouson in the Cochin harbour had a salinity survival range of 16 up to 32‰ whereas samples collected during the mouson could survive in fresh water and in salt water with a chlorinity up to 21‰. This physiological flexibility may explain the ability of *Electra* to develop huge reefal structures. The bryozoan buildups offer shelter and hard substratum not currently available in other brackish lakes, and harbour an associated flora and fauna. Growth habits are different for sheltered and exposed stations: foliate in the former and massive in the latter (Pl. 2 figs. 7-8). Globular colonies were found in mats of filamentous algae in brackish water near Rammekenshoek, Walcheren. Growth rates of the colonies are high. Channels in the 1953 Kreen Ouwerkerk are already filled with *Electra* reefs tens of meters across. VAN BENTHEM JUTTING (1946) reported on the rapid spreading of *Electra* in inundated Walcheren, 1944.

Small *Electra crustulenta* patches are widespread in the Zeeland marine habitats (HEEREBOUT 1970); These were probably already present in places that became landlocked later. Transport from one inland water to another by waterfowl legs is another possibility.

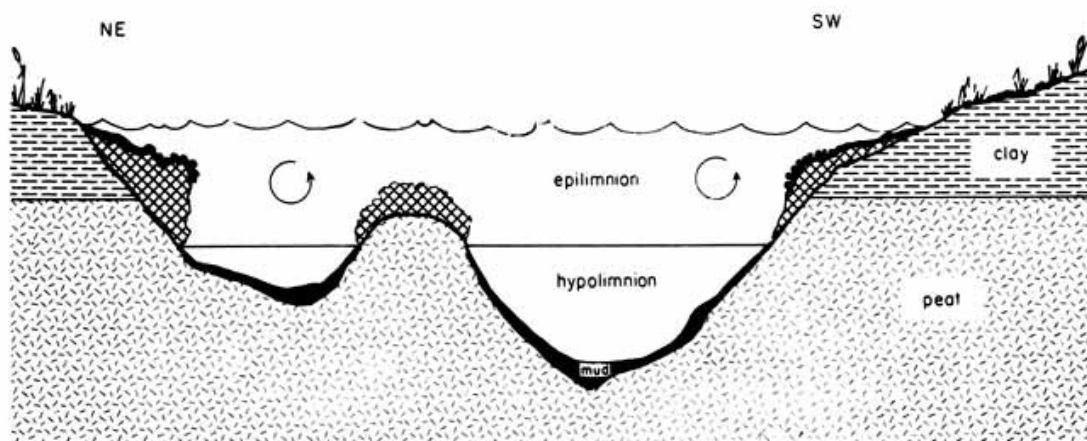


Fig. 2. Cross-section of brackish inland lake, SW-Netherlands. — Bryozoan reefs (indicated as grids) present in the epilimnion down to thermocline; stromatolite laminae (thick line) and columns (cantilevered line) present from water level down to 0.3 m water depth.

Abb. 2. Profil durch einen brackischen Binnensee der SW-Niederlande. — Die Bryozoen-vorkommen (kreuzschraffiert) im Epilimnion; die Stromatolithenbildung (schwarz) vom Wasser-spiegel bis 0,3 m Tiefe.

Distribution of mature colonies is in first instance determined by the larval stages (*Cyphonautus barroisi* LOHMAN). *Electra crustulenta* larvae are drifting in the upper waterlayers (BORG 1947; SILEN 1972).

Windexposure of the creeks may influence the pattern of settlement. The southwestern part of Holland is characterized by a predominantly southeastern wind (80%) resulting in a northwestern transport of the larvae. Larvae sink to the bottom and start exploring the substratum on suitability for settlement. The absence of a microscopic algal film on the substratum may be the key factor determining larval settlement (SILÉN 1972). These factors together result in a distribution pattern that is characterized by predominant development of reefal buildups in the north-eastern part of the creeks and the presence of bryozoan colonies in culverts (absence of light and thus absence of algae) which drain the creeks.

The inland waters are not subjected to tidal influences. Lowering of the man-controlled water levels in the polders results in the emersion of the otherwise submerged colonies. The upper side of the colony then dies, but its lateral faces grow on and extend upward during high water stands. A micro-atoll development thus takes place (Pl. 1 fig. 2).

Vertical Distribution.

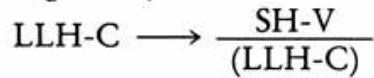
Due to the presence of thermoclines and stagnant water conditions, bryozoan reefs are not normally present below the 2m depth line in the region studied. The depth limitation of these reefal buildups, however, is not narrowly correlated to temperature and chlorinity. HEEREBOUT (1970), RYLAND (1970) and many others stress the flexibility of *Electra* with respect to the parameters mentioned above. At the level of the thermocline the condition of the soil in many inland lakes suddenly changes from firm and sandy in the epilimnion to sapropelium like in the hypolimnion. This may be caused by the turbulent effect of the wind on the upper waterlayer. Because of the watermovement in the epilimnion small particles are kept in suspension. The hypolimnion, however, is effectively isolated from wind-generated waves and currents. In this motionless water mass, organic and inorganic particles settle and cover any potential substrate (Fig. 2). Oxygen uptake and discharge of waste products, which take place by diffusion, will be hampered in motionless water. Moreover there may occur oxygen depletion in the hypolimnion due to microbial activity. The outcome of these circumstances causes the absence of bryozoan constructions in the hypolimnion.

Cyanophyte Stromatolites.

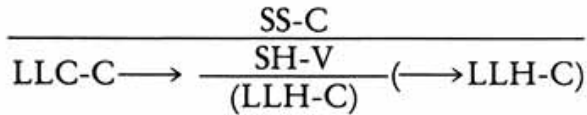
In the Delta-area four types of stromatolites are recognized. LOGAN & REZAK & GINSBURG (1964) typify stromatolites by the arrangement of the hemispheroids. The four types can be specified as follows: LLH-C = closely linked hemispheroids; SH-V = vertically stacked hemispheroids; SS = spheroidal structures.

R = randomly stacked; C = concentrically stacked.

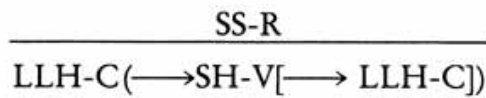
Stromatolitic crusts on top of the *Electra crustulenta* reefs
(Pl. 3 figs. 9-10):



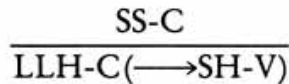
Oncolites (Pl. 3 figs. 11-12; Pl. 4 figs. 13-18):



“growing stone” rinds (Pl. 3 figs. 9-10):



Stromatolitic pipes around rush stems (Pl. 3 figs. 11-12):



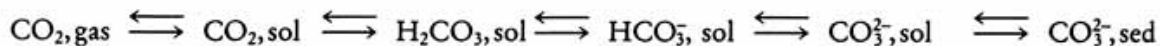
LORIE (1896) called these stromatolitic pipes “tubes de roseau”. As seen in Pl. 3 figs. 11-12 they all show the triangular imprints of the tightly packed triangular leaf-stocks that constitute the submerged part of the rush, *Scirpus maritimus*. The cyanophyte linked to the formation of stromatolitic structures was found to be *Lyngbya semiplena* (AGARD). This species is abundant in many Dutch inland lakes (pers. comm. VAN DEN HOEK); stromatolites, however, are rare. Consequently, stromatolite formation is largely controlled by environmental circumstances. Certain species of blue-green algae calcify in fresh water, whereas they live uncalcified in the marine environment (MONTY 1973).

Stromatolite Formation.

Two mechanisms have been invoked to explain the formation of stromatolites: sediment trapping and binding (involving local cementation), and CaCO_3 precipitation due to CO_2 -fixation during photosynthesis. Carbonate precipitation as a result of photosynthetic activity of bluegreens has frequently been postulated but was never proven (GOLUBIĆ 1973). This explanation meets several insuperable problems. All macro- and micro-algae as well as higher aquatic plants exhibit photosynthesis; only a few, however, deposit CaCO_3 on leaves, thalli or around individual filaments. How does precipitation of CaCO_3 proceed when CO_2 diffusion is hampered by a barrier of calcium carbonate? And how is it possible that the filaments are not completely covered by CaCO_3 , when CO_2 -uptake, resulting in CaCO_3 precipitation, takes place on the entire surface? According to us there must be another mechanism causing local CaCO_3 deposition leaving the younger ends of the filaments free of chalky matter. This can be achieved either by bicarbonate or

even carbonate assimilation (GOLUBIĆ 1973; KRUMBEIN 1979) and/or by CaCO_3 deposition within the mucus sheaths of blue greens (KITANO et al. 1969; CHAVE & SUESS 1970).

Carbonate in natural waters is present as a phase in a temperature and pH dependent buffered equilibrium;



BATHURST (1971) mentions six equilibria relating the dissolution and precipitation of CaCO_3 in water to the invasion or evasion of CO_2 . CaCO_3 precipitation can be facilitated by environmental circumstances as temperature increase, evaporation, pH increase, increase of Ca^{2+} , CO_2 evasion, salinity decrease, the absence of crystal poisons and the presence of nucleation particles. If environmental conditions favour CaCO_3 precipitation, this can actually be triggered by HCO_3^- or even CO_3^{2-} uptake by cyanophytes. This process is restricted to stagnant environments with high pH (exceeding \pm pH 8) (PRINS & O'BRIEN & ZANDSTRA 1982). As a matter of fact many cyanophytes thrive under these condition (GOLUBIĆ 1973). HCO_3^- fixation in aquatic vascular plants often involves OH^- excretion in order to maintain electrical balance. These two processes are separated in space. The leaves of *Potamogeton* and *Elodea* assimilate HCO_3^- at the morphologically lower side of their leaves and excrete the resulting OH^- at the upper side. HCO_3^- uptake is accompanied by a lowering of the pH from e. g. 8 to 6. The excreted H^+ drives the CO_2 out of the $\text{HCO}_3^- \cdot \text{OH}^-$ excretion results in a pH increase of up to three units or even more. Under conditions of this raised pH the availability of CO_3^{2-} becomes significant (BATHURST 1971). If we assume a comparable spatial separation of the two processes mentioned above in certain cyanophytes, we overcome the problem met with when CO_2 assimilation is supposed to be the key factor triggering stromatolite formation. In the growth direction HCO_3^- is fixed. The resulting pH decrease keeps this micro-area free of CaCO_3 deposition. In the lower parts of the cyanophytes OH^- is excreted.

The equilibrium shifts towards CaCO_3 precipitation when Ca^{2+} is available. According to MITTERER (1968) organic matrices cause formation of CaCO_3 either by concentrating the appropriate ions on charged sites on the protein of the mucus or by providing a set of specific templates upon which the CaCO_3 nucleates. It has been suggested that the acidic amino acids in the protein of mineralized tissues are important in concentrating calcium because of their polar side groups (MITTERER 1968). Some blue greens are known to be able to concentrate Ca^{2+} ions forming a CaCO_3 deposition. In this way stromatolite formation should be seen as a necessary consequence of an evolutionary trend of the blue greens to assimilate HCO_3^- under stagnant high alkalinity conditions.

Surface processes and, possibly, the periphyton on submerged *Scirpus* leave undersides apparently further lime precipitation; submerged *Phragmites* stems, omnipresent in our stromatolite occurrences are never encrusted with lime. Somehow, *Phragmites* surfaces deter the process, more than rubber tires, asphalt, glass bottles, brick, concrete and even peat surfaces.

The buildup of oncolites is also an open question. Well-developed oncolites (Pl. 4 figs. 13-18) are found at places without any appreciable turbulence, on soft mud. The current idea (MITTERER 1968; FÜCHTBAUER & MÜLLER 1970; GOLUBIĆ

1973) that oncolites originate by spasmodical reorientation of their core cannot apply in this case. It is obvious that our stromatolites also grew in very dark spots (compare upper and lower side of doublet of *Scrobicularia plana*; Pl. 3 figs. 11-12). The fact that the stromatolitic pipes, which we found as long as 16 cm, have the same thickness throughout, also proves that light intensity is but one factor in stromatolite genesis.

We observed a difference between the hardness of freshly collected stromatolites. Those from Hekeringen (Fig. 1: locality 1) are quite hard, all others are soft and lithify later on. GOLUBIĆ (1973) explains this by differences in the degree of inclusion of foreign matter in the calcareous crust, and variation in rates of precipitation.

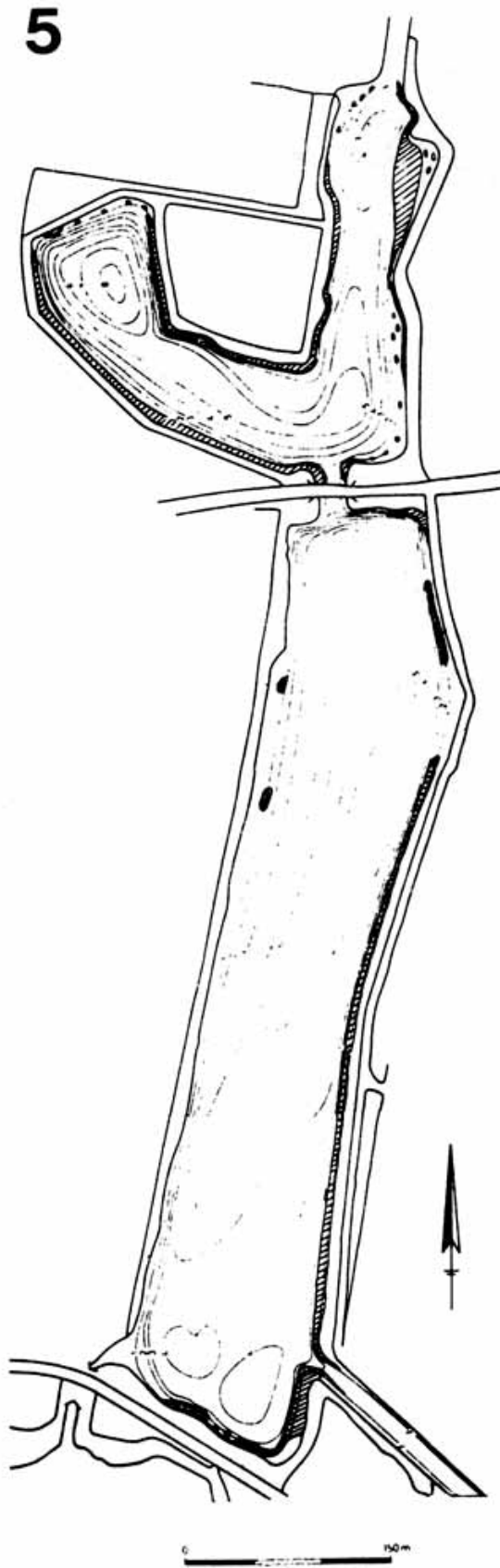
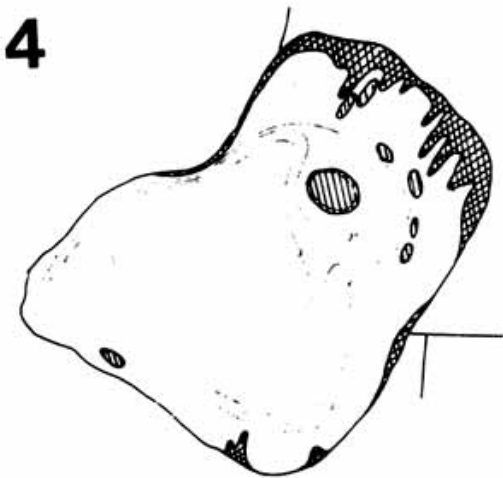
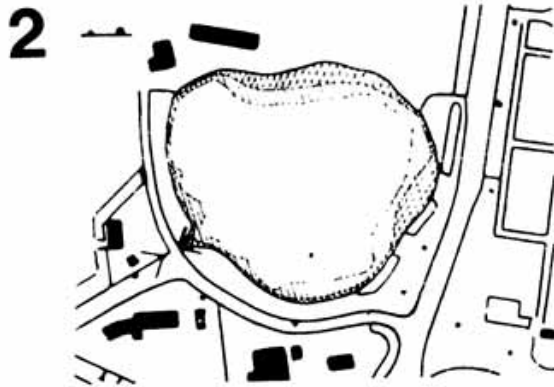
Main Sites.

Hekeringen pond (Fig. 1: locality 1); a man-made pond in a suburb, dug in the fifties. No environmental parameters available. *Electra* not found. Laminae stromatolites coat bricks and concrete down to 25 cm water depth. The stromatolites are up to 5 mm thick. This ornamental pond is surrounded by trees, the shadow of which may explain the absence of stromatolites in this sector of the pond (see Fig. 3) because water and substratum are not different from other sides of the pond.

De Waal near Rockanje (Fig. 1: locality 2); possibly a natural lake that originated when a former outlet of the Meuse river became disconnected from the main stream, in 1350 (BLAAUW 1917). Present-day chlorinity is 1.2‰ Cl (STRAATHOF, pers. comm. 1975) sixty years ago it was 1.5‰ Cl. (VAN BAREN 1927). No stromatolite buildups and live bryozoans are formed nowadays, and BLAAUW (1917) could not find stromatolite pipes being formed in 1916. This was the classical locality of "growing stones" in the 18th and 19th centuries and the first described (VAN ALKEMADE 1729). *Electra* and stromatolites (the latter up to 3 cm thick) were apparently restricted to a small area of about 20/20 m at the middle of the northwestern bank. Nowadays a nature reserve.

Ronde Weel near Zierikzee (Fig. 1: locality 8) originated whilst the surroundings of the town were inundated during the Spanish siege, 1576, but looks pondlike now. Its waters are eutrophied by sewage from sports accommodation. Both *Electra* colonies and *Lyngbya* mats thrive here (Fig. 3; Pl. 1 fig. 3). Large ectoproct cauliflower-like structures are found down to 2 m depth; stromatolite development is restricted to the uppermost half meter (crusts up to 1 cm). The culvert that drains the Ronde Weel westward is half filled with foliaceous *Electra*; the bryozoan and the stromatolites also line the sides of the ditch leading from the culvert.

Diepe Gat W of Ouwkerk (Fig. 1: locality 10) dates from ± 1200 , possibly a pothole due to an inundation, comparable to the Ronde Weel. Chlorinity is 4.25 ± 0.21 ‰ (DE MUNCK et al. 1978). The subsoil of the lake consists of peat, which is covered by clay. This salty peat was exploited during the Middle Ages for its ashes. Colonies of *Electra* with observed diameters of up to 7 m live offshore. Stromatolite outgrowths occur from 50 cm upward; the laminae variety is found at the shallowest depth. These crusts are found on bryozoan colonies as well as on a variety of human artefacts such as bottles, bricks and furnace slags (Fig. 3).



Channel system SE of Ouwerkerk (Fig. 1: locality 11) originated because of stream scouring during the 1953 flood. Chlorinity is $11.57 \pm 0.289\%$ (DE MUNCK et al. 1978). No stromatolites, but huge *Electra* colonies up to 1 m high and tens of meters long lining the borders of these very young brackish water bodies (Fig. 3).

Terluchtse Weel W of Goes (Fig. 1: locality 21); no exact age known, but a late medieval pothole that is now shallow (its deepest point 1.9 m). Here, as in the Diepe Gat, traces of medieval peat exploitation for salt are still visible. Chlorinity (according to DE MUNCK et al. 1978) is $8.72 \pm 1.24\%$. The mud covering its bottom is rich in lime (VAN DER BOOG 1982); brackish water molluscs such as *Cerastoderma glauca* (POIRET) are present. Massive *Electra* colonies are found in the shallower parts of the lake (Fig. 3; Pl. 1 fig. 4) and stromatolite crusts cover these, with thicknesses up to 1.5 cm.

Groote Gat near Oostburg (Fig. 1: locality 27); part of the formerly very extensive Zwin creek finally dammed in the later 18th century. Chlorinity (according to DE MUNCK et al. 1978) is $1.77 \pm 1.026\%$ Cl.; in 1953, it was (VAN OYE 1961) 1.5%. Known as a growing stone locality since AB UTRECHT DRESSELHUYS (1839). The extensive growth of *Electra* reefs has stopped, and only isolated foliated colonies were observed by us. Thin stromatolite crusts still grow around discarded bottles and other refuse on the lake's bottom. Fresh massive colonies with stromatolite crusts (as figured in Pl. 3 figs. 9-10) were still growing in 1966 in the area indicated on the map.

Acknowledgements.

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◀ Fig. 3. Maps of main sites of bryozoan reefs and stromatolites in the SW-Netherlands (cf. Fig. 1). — Hatched: bryozoan reefs; cross-hatched: stromatolites. — 1. Locality 1: Hekeringen pond. 2. Locality 8: Ronde Weel. 3. Locality 21: Terluchtse Weel. 4. Locality 10: Diepe Gat. 5. Locality 11: Channel systems SE of Ouwerkerk.

Abb. 3. Die Hauptvorkommen von Bryozoenriffen und Stromatolithen in den SW-Niederlanden (vgl. Abb. 1). — Schraffiert: Bryozoenriffe. Kreuzschraffiert: Stromatolithen. — 1. Vorkommen 1: Hekeringen Teich. 2. Vorkommen 8: Ronde Weel. 3. Vorkommen 21: Terluchtse Weel. 4. Vorkommen 10: Diepe Gat. 5. Vorkommen 11: Kanalsystem SE von Ouwerkerk.

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Plate 1.

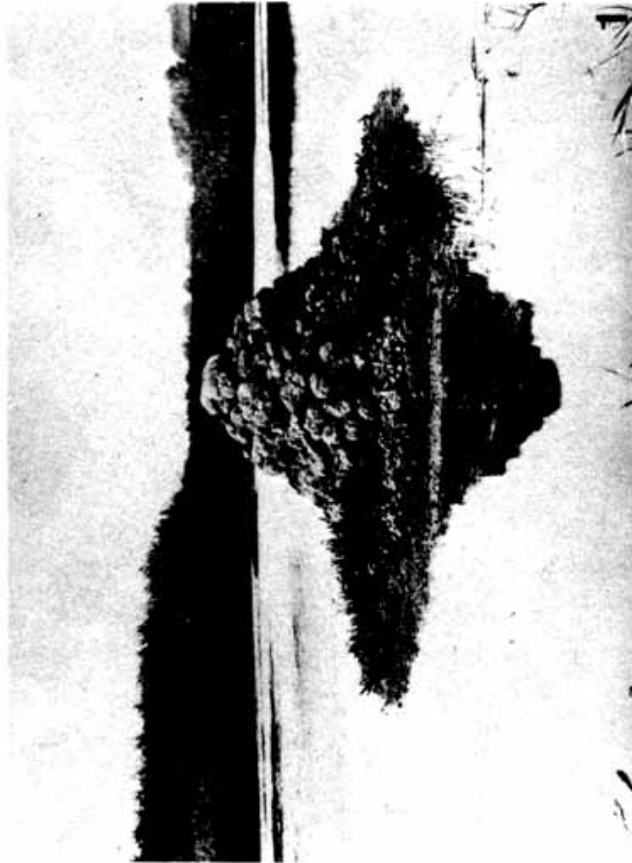
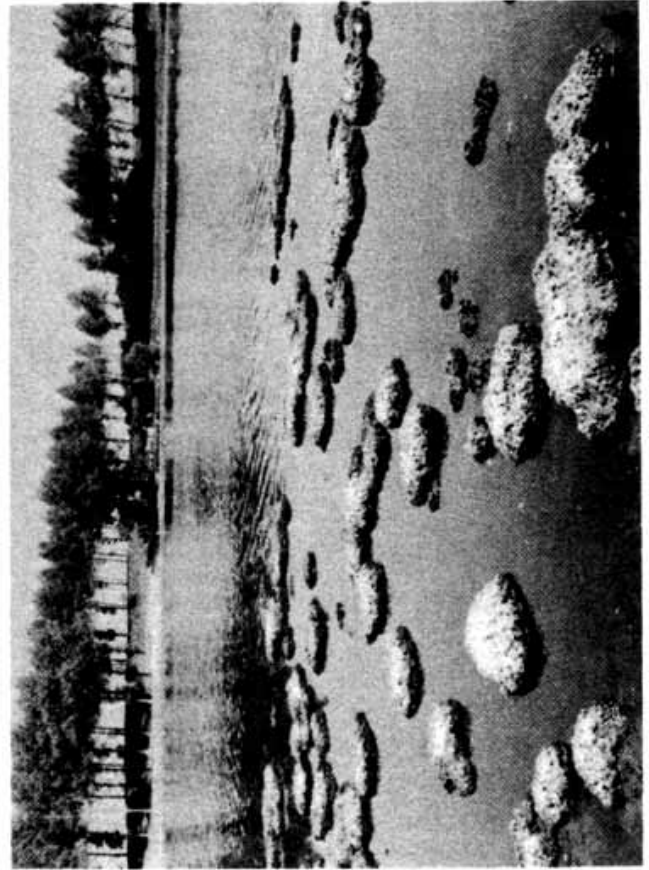
Growth patterns of bryozan reefs and stromatolites in brackish inland lakes of SW-Netherlands.

- Fig. 1. Artificial mound composed of "Kaasken", i. e. cauliflower-like colonies of bryozoans. — Waal lake, Rockanje (from BLAAUW 1917).
- Fig. 2. Micro-atoll: a byozoan reef with marginal stromatolitic cover. — Kaaskenswater.
- Fig. 3. Bryozoan reefs capped with stromatolites. — Ronde Weel.
- Fig. 4. Bryozoan reefs capped with stromatolites. — Terluchtse Weel, 1976. — Photo: RENE KLEINGELD, Delta Inst. Hydrobiological Research, Yerseke.

Tafel 1.

Wuchsformen von Bryozoenriffen und Stromatolithen in brackischen Binnenseen der SW-Niederlande.

- Fig. 1. Künstliche Hügel aus „Kaasken“, d. h. blumenkohlförmigen Bryozoenkolonien. — Waal-See, Rockanje (aus BLAAUW 1917).
- Fig. 2. Mikroatoll eines Bryozoenriffs mit stromatolithischer Randbedeckung. — Kaaskenswater.
- Fig. 3. Bryozoenriffe, überdeckt mit Stromatolithen. — Ronde Weel.
- Fig. 4. Bryozoenriffe, überdeckt mit Stromatolithen. — Terluchtse Weel, 1976.



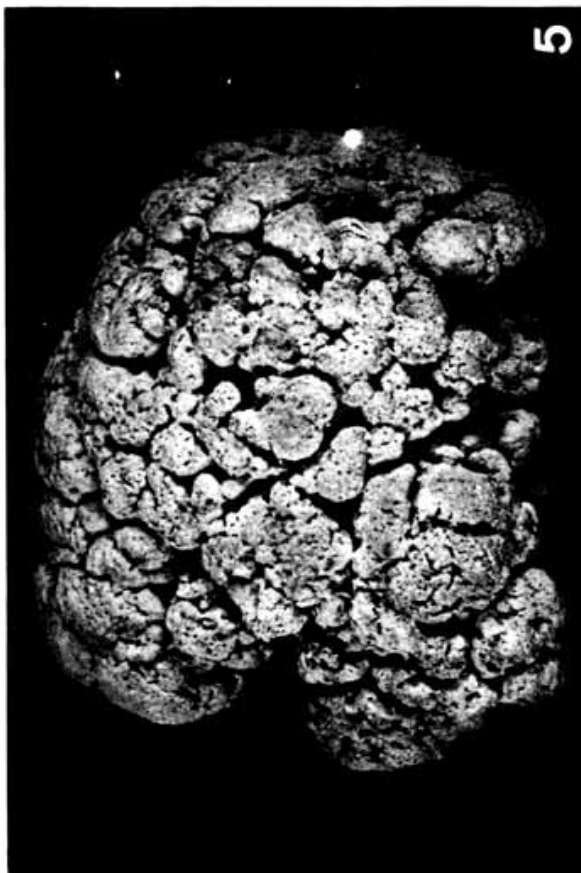
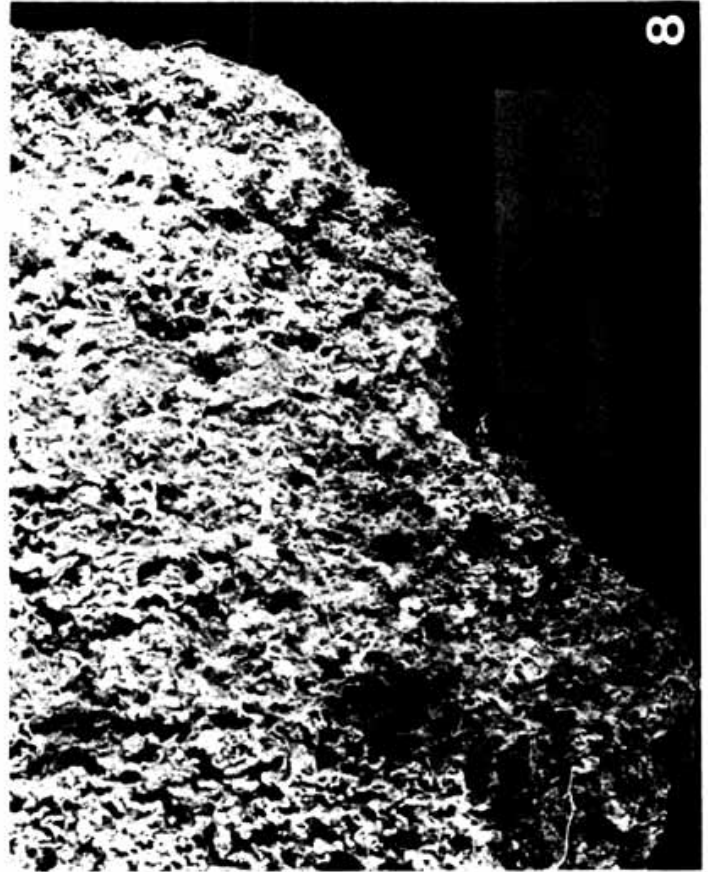
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Recent Bryozoan Reefs and Stromatolite Development
in Brackish Inland Lakes, SW Netherlands.

Plate 2.

- Fig. 5. "Kaasken": foliate bryozoan colony with stromatolitic crust. — Width of structure is 8 cm.
- Fig. 6. Cross-section of the sample from fig. 5.
- Fig. 7. Foliate growth structure of bryozoan reef.
- Fig. 8. Massive growth structure of bryozoan reef.

Tafel 2.

- Fig. 5. Ein „Kaasken“, d.i. eine Bryozoenkolonie in blättriger Wuchsform mit stromatolithischer Kruste. — Durchmesser ca. 8 cm.
- Fig. 6. Querschnitt der Probe von Fig. 5.
- Fig. 7. Bryozoenriff in blättriger Wuchsform.
- Fig. 8. Bryozoenriff in massiger Wuchsform.



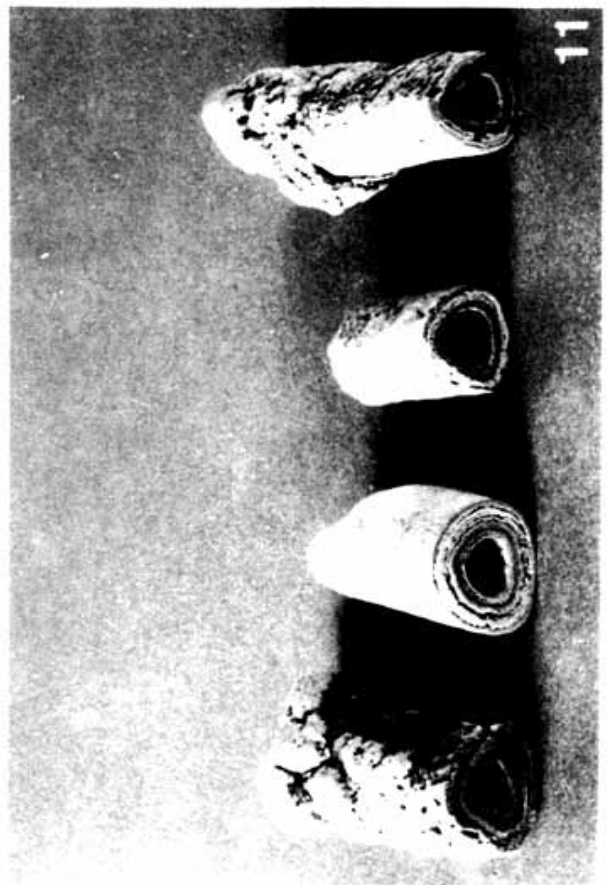
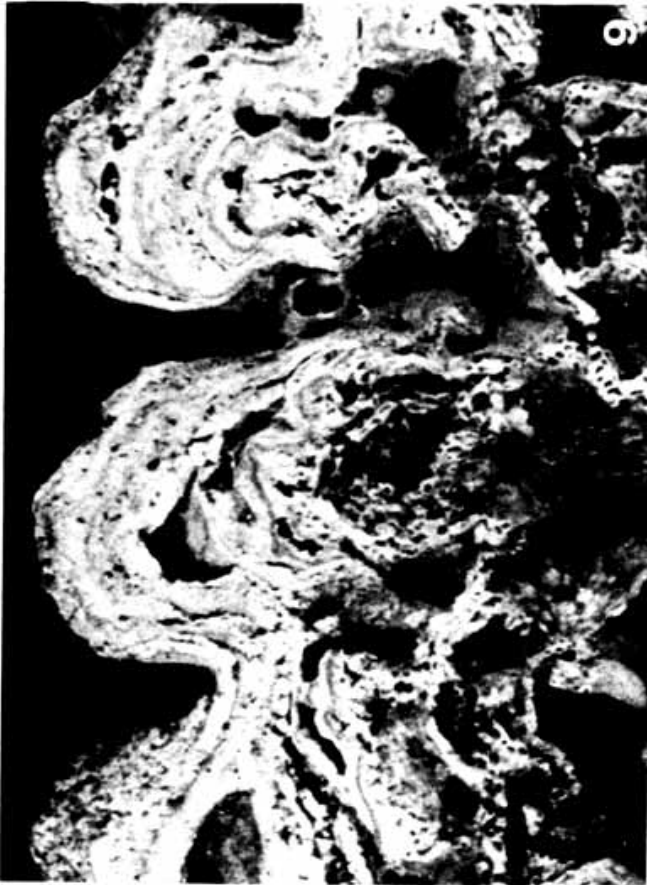
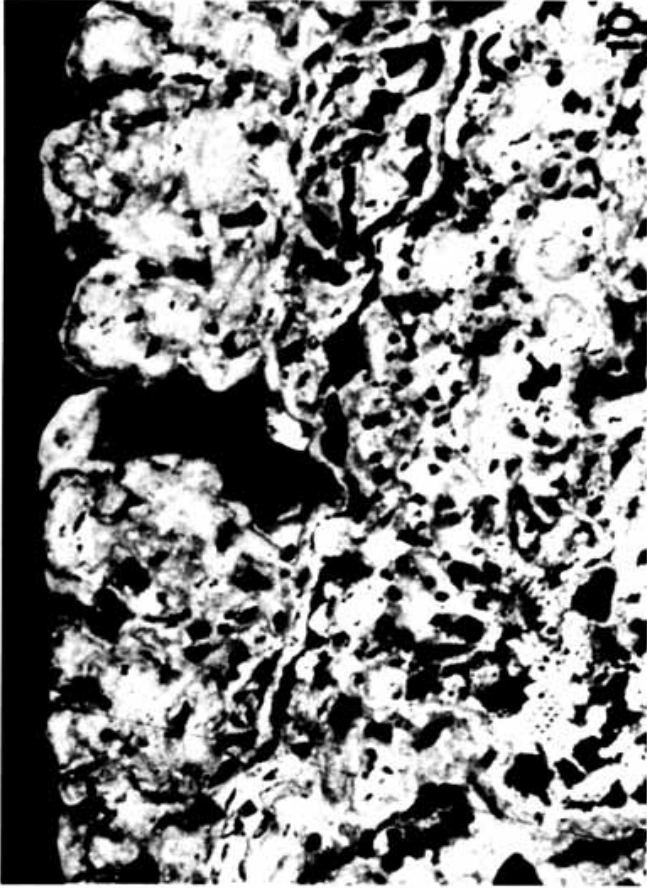
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Plate 3.

- Fig. 9. Stromatolitic crust on top of the *Electra crustulenta* reefs. — Terluchtse Weel. — 2.5 ×.
- Fig. 10. "Growing stone" rind. — Groote Gat. — 2.5 ×.
- Fig. 11. Stromatolitic pipes with triangular imprints of the leaf-stocks of *Scirpus maritimus*. — De Waal. — 0.25 ×.
- Fig. 12. Oncolite; stromatolites encrust the skull of *Anas platyrhynchos*. — De Waal. — Natural size.

Tafel 3.

- Fig. 9. Stromatolithische Kruste auf einem *Electra crustulenta*-Riff. — Terluchtse Weel. — 2,5 ×.
- Fig. 10. Rinde eines „Wachsenden Steines“. — Groote Gat. — 2,5 ×.
- Fig. 11. Stromatolithische Röhren mit dreikantigen Blattstengeln von *Scirpus maritimus*. — De Waal. — 0,25 ×.
- Fig. 12. Onkolith: Stromatolithisch überkrusteter Schädel von *Anas platyrhynchos*. — De Waal. — Nat. Gr.



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Plate 4.

- Fig. 13. Stromatolitic crust around *Scrobicularia plana*. — De Waal. — 1.3 ×.
 Fig. 14. Cross-section of sample in fig. 1 (arrows). — 1.3 ×.
 Fig. 15. Stromatolitic crust around *Cerastoderma glaucum*. — De Waal. — 1.3 ×.
 Fig. 16. Cross-section of sample in fig. 1. — 1.3 ×.
 Fig. 17. Stromatolitic crust around *Cerastoderma glaucum*. — De Waal. — 2 ×.
 Fig. 18. Cross-section of sample in fig. 1. — 1.3 ×.

Tafel 4.

- Fig. 13. Stromatolithische Kruste um *Scrobicularia plana*. — De Waal. — 1,3 ×.
 Fig. 14. Querschnitt der Probe von Fig. 1. — 1,3 ×.
 Fig. 15. Stromatolithische Kruste um *Cerastoderma glaucum*. — De Waal. — 1,3 ×.
 Fig. 16. Querschnitt der Probe von Fig. 1. — 1,3 ×.
 Fig. 17. Stromatolithische Kruste um *Cerastoderma glaucum*. — De Waal. — 2 ×.
 Fig. 18. Querschnitt der Probe von Fig. 1. — 1,3 ×.

