

AUTECOLOGY OF STROMATOPOROIDS IN SILURIAN CRATONIC SEAS

by HELDUR NESTOR

ABSTRACT. Stromatoporoids are fossils of problematical affinity that were probably colonial, benthic sessile, or liberossessile marine organisms with a basal ectodermal skeleton. They were most common on carbonate shelves bordering peneplaned continents in low palaeolatitudes. They were rare in shelf seas with a high influx of coarse clastics. Stromatoporoids were absent from seas of the Malvinokaffric Realm and in late Silurian evaporitic epicontinental basins (Michigan basin, Tunguska basin). High-energy carbonate shoal environments were optimal for stromatoporoids, and there they often formed parts of organic buildups (bioherms, biostromes, banks). Their role in reef building increased during the Silurian. Near-shore low-energy environments (lagoons, mud flats, restricted shelf) were less favourable for stromatoporoids, especially when their hydrochemical regime declined from normal marine. Stromatoporoids were typical of low-energy open shelf environments, but their taxonomic diversity and frequency decreased offshore. They lived in normal marine conditions in warm water, at depths up to 70 m. They preferred agitated water and a hard or semi-soft, stable bottom. Ecological differentiation of Silurian stromatoporoid faunas was quite low.

ECOLOGICAL investigations of stromatoporoids are complicated because their nature and relationships with Recent organisms are still a matter of considerable debate. Direct comparisons with modern relatives cannot therefore be applied to explain their mode of life. On the other hand, as the skeletons of stromatoporoids (coenostea) were mostly buried near their habitats, and often even in living position, the nature of the surrounding rocks enables interpretations to be made of such important environmental factors as the character of the substrate, hydrodynamics, hydrochemistry, etc., which are essential aspects of the ecology of marine benthic organisms.

Of various aspects of stromatoporoid ecology, those best-studied to date are their role in forming organic buildups (Hadding 1950; Lowenstam 1950; Jux 1957; Rutten 1958; Klaamann and Nestor 1968; Manten 1971, Philcox 1971, St. Jean 1971, Scoffin 1971, Lesovaya 1977; Nestor and Nestor 1977) and the dependence of shape (morphotype) upon their conditions of life (Broadhurst 1966; St. Jean 1971, Wilson 1975; Kershaw and Riding 1978, 1980; Kershaw 1981). The richest ecological information about Silurian stromatoporoids is given by Mori (1968, 1970) in his papers on the faunas of Gotland. Unfortunately, there is no ecological information of the same value on stromatoporoids from any other region. This review is therefore based to a large extent on my own observations made during field-work in the East Baltic, Gotland, Podolia, and the Siberian Platform. Material obtained through these studies provides a basis for generalizing the data on distribution and ecology of stromatoporoids only in cratonic basins, since evidence from geosynclinal basins is still insufficient.

AFFINITIES AND FUNCTIONAL MORPHOLOGY

Different opinions have been expressed as to the biological nature and affinities of stromatoporoids (see recent review by Bogoyavlenskaya and Boiko 1979). There are three main current views on relationships: cnidarian, spongian, and cyanophycean (cyanobacterian).

According to the cnidarian interpretation (e.g. Carter 1877; Nicolson 1886), the stromatoporoid skeleton (the coenosteum, with a cystose, laminated, or reticulate internal structure) is comparable with the exoskeleton of colonial hydrozoans (e.g. *Hydractinia*, *Millepora*), secreted mostly by the coenosarcal tissue of a colony. The astrorhizae, representing the stellate systems of radiating and branching wall-less channels in the stromatoporoid skeleton, are regarded as homologues of the

hydrorhizae of modern hydroids like *Hydractinia* (Carter 1877) or as traces of anastomosing coenosarcal stolons of *Millepora* (Nicholson 1886) that serve as centres of colony growth. The intense development of astrorhizae at the base of latilaminae supports such an opinion (Lecompte 1956). A cnidarian affinity assumes the presence of polyps in the soft body of stromatoporoids, but this has not been proved since criteria that would allow them to be discerned in the skeleton from other interspaces have not yet been demonstrated.

Assumption of a poriferan affinity of stromatoporoids is based on the great similarity of the astrorhizae to the stellate impressions of the excurrent canal system on the surface of the basal calcareous skeleton of Recent sclerosponges (Hartman and Goreau 1970; Stearn 1972, 1975). Stromatoporoids are regarded by these authors as encrusting sponges, with the basal calcareous skeleton secreted by the ectodermal layer of a thin veneer of soft living tissue confined to the surficial part of the coenosteum. Astrorhizae are considered as traces of an exhalant canal system, which functioned to gather and discharge water from the filter-feeding organism.

A cyanophycean or cyanobacterian relationship for stromatoporoids has been suggested recently by Kaźmierczak (1976, 1980, 1981), who interpreted the granular (maculate or melanospheric) microfabric of some forms as remnants of coccoid cell aggregates of cyanophytes (Cyanobacteria), and concluded that stromatoporoids were stromatolith structures formed by *in situ* calcification of coccoid cyanophycean mats. He explained astrorhizae as traces of young colonies of coccoid cyanophytes that coalesced with older ones.

A cyanophycean affinity of stromatoporoids is as yet less well founded than that of poriferans or cnidarians, since the interpretation of coccoid cell structures in the coenostea is based on only a few examples. The relatively regular reticulate of the stromatoporoid skeleton, with distinct skeletal elements and interspaces, contradicts a cyanophycean affinity, but suggests rather a higher organization of the stromatoporoid coenosteum than is typical of cyanophycean or cyanobacterian mats.

It is much more difficult to decide whether stromatoporoids belong to the sponges or to cnidarians. Stearn (1972), Mori (1976), St. Jean (1983), and others have stressed the idea that stromatoporoids combine morphological characteristics of these two phyla, and have referred to the possibility of establishing a new phylum intermediate between the two groups. Zhuravleva and Miagkova (1974) even erected a new kingdom for ancient sponge-like organisms, including stromatoporoids.

The main spongian features of stromatoporoids are a striking morphological similarity between the astrorhizae and the exhalant canals of sclerosponges, a similar fibrose and spherulitic microstructures (see Wendt 1983; Stearn 1977), and the lack of definite zooidal tubes in most stromatoporoids. Cnidarian features include the abundance of dissepiments and tabulae in the astrorhizal canals and interspaces, latilaminar and zonal structures of the coenosteum, and the absence of spicules in stromatoporoids.

However, it must be said that none of these features is sufficiently diagnostic to exclude any possibility of a contrary interpretation. Evidently the weakly differentiated skeleton of stromatoporoids, representing only the 'base' of a once-living organism, does not sufficiently reflect such vital functions of a soft living body on which the separation of sponges and coelenterates is based. The sponges are passive filter-feeding organisms that pass water through their bodies to extract planktic micro-organisms. Sessile cnidarians have polyps provided with tentacles for seeking zooplankton, paralysing small swimming animals by means of nematocysts.

In their shape, the astrorhizae of stromatoporoids are very similar to the exhalant channels and osculum of sponges, but they often have partitions (dissepiments or astrorhizal tabulae) that do not accord with the main spongian function—to guarantee a permanent water flow through the organism. It is significant that astrorhizae are absent in the more ancient and primitive stromatoporoid orders Labechiida and Lophiostromatida which, as with most modern sclerosponges, obviously had a continuous sheet of soft living tissue on the surface of the basal skeleton (see Nestor 1974, 1981). Astrorhizae occur in all other more advanced orders of stromatoporoids, which probably had a reticulate soft body (Nestor 1974). Such a positive correlation between the presence of astrorhizae and a reticulate soft body supports the view that they represent stolonial structures.

Phylogenetic relationships between stromatoporoids and certain groups of cnidarians are expressed more clearly than with sponges. In the fossil record, representatives of the Order *Millepora* immediately succeeded the stromatoporoids. The Mesozoic families *Milleporidiidae* and *Sporadoporiidae*, with skeletons containing large tabulated tubes similar to the zooidal tubes of millepores, may be considered as transitional forms between these two groups. Mori (1976) discussed the Japanese Jurassic species *Milleporidium steinmanni* that apparently has zooidal tubes and gross structures very similar to those of the Recent genus *Millepora*. The Triassic genus *Pamiropora* has large tabulated tubes together with typical astrorhizae. Jurassic genera *Coenostella* and *Tubuliella* have large tabulated tubes with reduced horizontal canals resembling a transition from astrorhizae to genuine zooidal tubes (Turnšek 1966).

The appearance of stromatoporoids in the geological record is closely connected with the appearance and rapid diversification of the main groups of Palaeozoic corals (tabulates, heliolitids, rugosans) in the middle Ordovician. In a previous paper (Nestor 1981) I discussed probable relationships based on the great similarity of internal structure of some Ordovician and Silurian stromatoporoids (*Lophiostromatida*, *Labechiida*) and some heliolitids (*Protaraeida*, *Proporida*). Phylogenetic relationships of stromatoporoids and different groups of sponges are still obscure, as linking taxa with Recent sclerosponges are unknown in the fossil record and relationships with fossil groups of sponges are poorly documented.

The general interpretation of the ecology of stromatoporoids also coincides more with the ecology of modern corals than with that of sponges. Stromatoporoids were one of the most important groups of reef-building organisms in the middle Palaeozoic, often associated with corals and calcareous algae. Their role was particularly great in very shallow, open reef environments well exposed to water action and light; they have therefore been considered by some authors as functional counterparts of modern coralline red algae (Heckel 1974). The ecology of Recent sclerosponges is essentially different as they usually live in sheltered, shaded reef caves and channels or on deep reef slopes, being unable to compete with hermatypic corals in open reef environments.

From this discussion it is clear that data available at present do not enable the question of stromatoporoid affinities to be resolved, and other possible interpretations cannot be excluded. Although I favour a cnidarian affinity, under such circumstances it would be speculative to make far-reaching ecological conclusions on the basis of stromatoporoid functional morphology. Therefore in this review I consider only such general functions that are common to the representatives of several groups of lower marine organisms characterized by a basal skeleton and sessile mode of life.

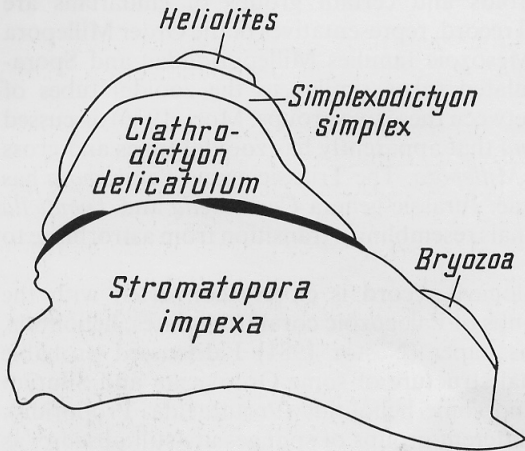
GENERAL MODE OF LIFE

The presence of astrorhizae in a stromatoporoid coenosteum shows that they were probably colonial organisms. They had a benthic mode of life and secreted a basal ectodermal calcareous skeleton that enabled them to hold their colony firmly together and rest on the bottom. A thin layer of living tissue covered the upper surface of the stromatoporoid skeleton, and its protrusions extended between the skeletal elements only in the uppermost part of the coenosteum; lower areas of the skeleton were gradually abandoned as the organism grew upwards.

Stromatoporoid larvae attached to hard-bottoms such as rocks, pebbles, or other skeletal fragments. After fixing on a hard-bottom the colony expanded and encrusted or enveloped it in a truly sessile mode of life. The remarkable encrusting capability of stromatoporoids is comparable with that of algae.

Stromatoporoids often had compound coenostea, consisting of skeletal layers secreted by different species (text-fig. 1). They may also alternate with skeletal layers of tabulate corals (especially alveolitides), bryozoans, and calcareous algae.

Often the object of attachment of a stromatoporoid larva was so small that the organism soon spread over surrounding soft deposits and became free lying (liberosessile—see Jaanusson 1979). Stromatoporoids with a broad laminar coenosteum were able to bind sediments and played an



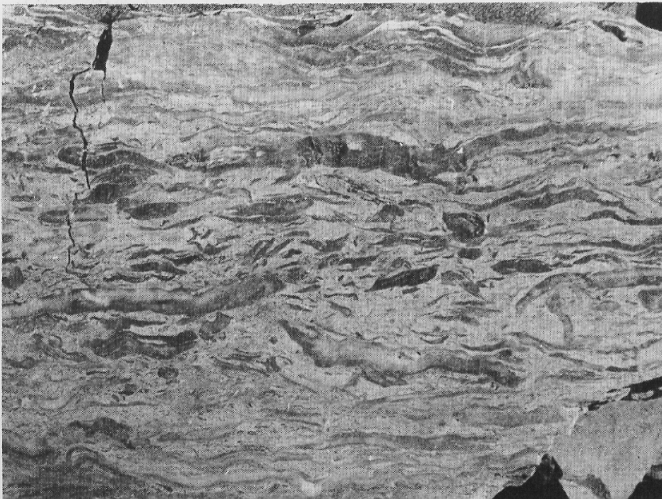
TEXT-FIG. 1. Schematic section of the compound coenosteum of stromatoporoids. Jaani Stage (Wenlock), Suuriku, Estonia.

important role in creating organic buildups (text-fig. 2). Stromatoporoids with massive and dendroid coenostea, growing densely together and partly attaching to one another, were able to form a fairly rigid frame to make up biostromes as well as bioherms. In the Silurian, and particularly in late Silurian times, stromatoporoids were one of the most important groups of reef-building organisms.

FACIES CONTROL OF STROMATOPOROID DISTRIBUTION

Stromatoporoids occur commonly only in carbonate or terrigenous-carbonate sediments, being extremely rare in pure clastic rocks such as clay-, silt-, and sandstones. Silurian carbonate rocks are of comparatively shallow water genesis, mostly as neritic deposits. Various carbonate deposits accumulated in cratonic epi- and pericontinental seas adjacent to stable lowlands. According to sedimentological models (e.g. Anderson 1971; Wilson 1975; Nestor and Einasto 1977) three main hydrodynamic and sedimentological belts could be distinguished in such shelf seas:

1. Near-shore, low-energy belt, including lagoons, mud-flats, and restricted shelf.
2. High-energy shoal belt, which may be represented by shoals, bars, organic banks, or buildups.
3. Low-energy, open shelf below wave base, seaward of the high-energy belt.

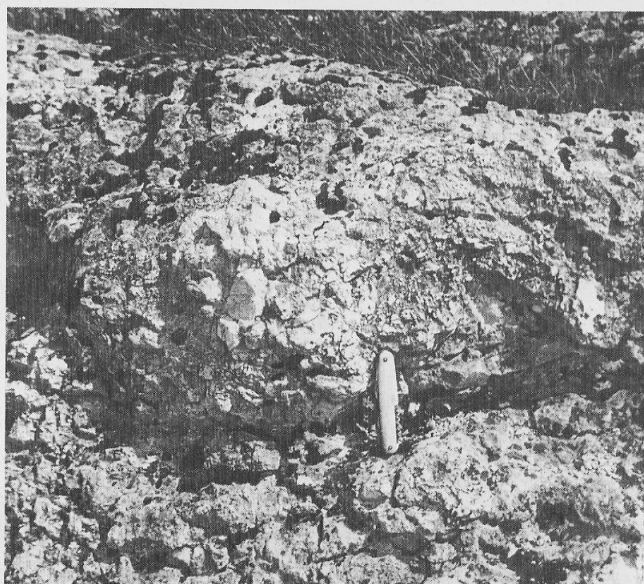


TEXT-FIG. 2. Laminar stromatoporoids forming thick biostrome. Moiero River, Wenlock, Siberian Platform.

Stromatoporoids in high energy facies

The highest concentrations of stromatoporoids were in the high-energy, carbonate shelf shoal belt, where various sparitic and bioconstructed limestones formed; however, the distribution of stromatoporoids in facies of this belt was rather uneven.

Stromatoporoids played an essential role in creating organic buildups in Silurian cratonic seas. The most detailed studies have been carried out on middle Silurian (Niagaran) bioherms in the mid western states of the U.S.A. south of the Great Lakes (e.g. Lowenstam 1950; Ingels 1963; Textoris and Carozzi 1964; Philcox 1970) and on Gotland (e.g. Hadding 1950; Jux 1957; Rutten 1958; Manten 1971). Buildups of the same type are known from Anticosti, Estonia, Podolia, the Welsh Borderland,



TEXT-FIG. 3. (*Above*), topmost part of a coral-stromatoporoid bioherm. Juuru Stage, Hilliste Member (Llandover), Pusku, west Estonia; (*right*) detail of coral-stromatoporoid framestone in the bioherm. Photos. U. Veske.

Siberian Platform, Tuva, and other regions. Silurian cratonic reefs are mostly mound-like, lenticular or irregular bodies from some metres to some tens of metres thick and from a few metres to some hundreds of metres in diameter (text-fig. 3). Smaller bioherms were relatively homogenous. Their composition depended on depth and hydrochemical conditions. In bioherms formed in well-agitated water of normal salinity, stromatoporoids were either main frame-building organisms (e.g. in Holmhällar-type bioherms of Gotland they formed up to 60% of the rock volume—Mori 1970; Manten 1971) or they occurred together with corals, calcareous algae, or bryozoans, making up not more than 25% of the rock volume (see Mori 1970). In larger buildups having several growth stages (e.g. 'fully developed middle Silurian ecological reefs' of Wilson 1975; Upper Visby and Höglint reefs on Gotland) the earlier growth stage took place in quieter water conditions below wave base, when main reef-builders were fasciculate or catenulate corals and bryozoans; stromatoporoids at this stage were less common and were represented by laminar colonies. In later growth stages when upward organic growth reached into the zone of wave activity, the role of stromatoporoids in frame building increased progressively, reaching up to 50% in the topmost part of the Höglint reefs (Mori 1970). Smaller and simpler bioherms are also often capped by stromatoporoids (text-fig. 4).



TEXT-FIG. 4. Upper surface of a coral-stromatoporoid bioherm with numerous bulbous and irregular coenostea of stromatoporoids. Muksha beds, Wenlock, mouth of Muksha River, Podolia.

It is apparent that there was an increase in relative importance of stromatoporoids in reef building through Silurian times. In some Llandovery bioherms of north-west Estonia, coenostea made up only 5–8% of the rock, which is three times less than that of tabulate corals (Nestor and Nestor 1977). In the Wenlock bioherms of Gotland, Shropshire, and the Great Lakes area the role of stromatoporoids in different types of buildups and within different parts of the structures was rather changeable but rarely exceeded 25% (see Mori 1970). In late Silurian bioherms the role of stromatoporoids was generally very high. According to Mori (1970), in some Hemse and Sundre examples it exceeded 60%, and bioherms, dominated by stromatoporoids, also occur in the Paadla Stage of Estonia and in the Malinovtsy Stage of Podolia.

A particular feature of Silurian cratonic stromatoporoid and coral-stromatoporoid buildups was that obviously they did not form true barrier reefs at the shelf edge, but the reef belt, if it existed, was situated in the middle or inner part of the shelf, separating the so-called open shelf from the restricted shelf or lagoons (Nestor 1977; Klaamann and Einasto 1982). Some bioherms were also scattered across the open shelf (see Lowenstam 1950; Wilson 1975; Klaamann and Einasto 1982). In the

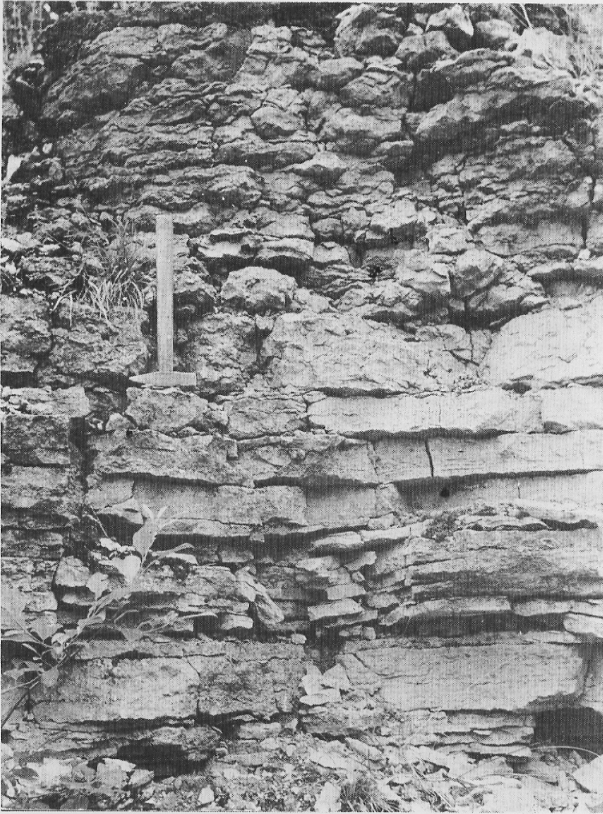
TEXT-FIG. 5. Stromatoporoid rudstone (conglomerate) beside a small bioherm; Wenlock, Moiero River, Siberia.



Silurian Baltic Basin, shelf-margin bioherms, consisting mostly of stromatoporoids, appeared for the first time in the late Ludlow (Ventspils Formation in north-west Latvia and central Lithuania). Shelf-margin stromatoporoid reefs seem to have become common in the Devonian.

As Silurian cratonic bioherms were mostly of fairly modest size and occurred in the more coastal part of the shelf, they lacked extensive reef talus. Nevertheless, close to the bioherms there are sometimes lenses of reef-derived conglomerates and breccias, consisting mostly of pebbles of stromatoporoids and other frame-building organisms (text-fig. 5). Silurian bioherms are often surrounded by pelmatozoan grainstone that formed from rather coarse-grained well-washed skeletal sand accumulated in a high-energy environment. The grainstones contain coenostea of stromatoporoids in various concentrations, but they are mostly dislodged, overturned, and sometimes abraded; they can also occur rarely in living position, forming small accumulations that can be regarded as embryonic bioherms. Stromatoporoids are virtually absent in well sorted skeletal grainstones that represent deposits of skeletal-sand bars and are not directly connected with bioherms. They differ from the reef-flank pelmatozoan grainstones in the presence of micro-, graded-, or cross-bedding.

In addition to bioherms, stromatoporoids often formed biostromes, either themselves or together with corals. Some typical biostromes have been described from the Wenlock of the Siberian Moiero River sequence (Miagkova *et al.* 1976) and from the Ludlow Hemse Beds of Gotland near Herrviken and Kuppen (Manten 1971, Kershaw 1981). The thickest of the Moiero Wenlock biostromes (9 m) is traceable for at least 3 km. It consists of wavy laminar coenostea in a skeletal sand matrix (text-fig. 2). Biostromes were often built by nodular or bulbous stromatoporoids (text-fig. 6).



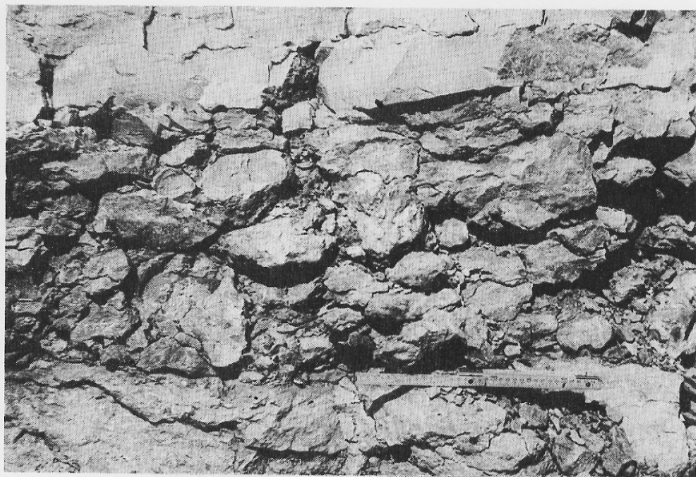
TEXT-FIG. 6. Coral-stromatoporoid biostrome (upper part of section) lying above flaggy pelletal limestones; Raikküla Stage, Llandover, Pakamägi, Estonia.

Apart from genuine biostromes with predominantly *in situ* coenostea, there are often stromatoporoid or coral-stromatoporoid banks in which a considerable part of or all coenostea were moved or overturned; there were probably lateral transitions from true biostromes to bank-type accumulations. I have observed such a feature in Estonia in stromatoporoid limestones forming the basal bed of the Karinu Member (Llandover, Juuru Stage). In the stratotype Karinu quarry, the basal layer of the member is a 30–40 cm thick biostrome, formed of densely packed nodular coenostea in life position (text-fig. 7). At the same horizon in many of neighbouring borings, stromatoporoid conglomerates are developed, consisting of completely rounded coenostea. It seems that stromatoporoid biostromes could form in the lower-energy coastal part of a broad shoal belt or even within the restricted shelf, while on the higher-energy seaward side their coenostea were subjected to retransport and abrasion that led to the formation of conglomerate beds.

The coenostea of stromatoporoids were mostly rather light because of their high porosity, and being liberossessile they were easily subjected to transport by waves and currents. Banks of stromatoporoids therefore often represent secondary accumulations of coenostea that had even higher densities than biostromes of *in situ* coenostea. Distinctive bank-type stromatoporoids form these masses, consisting of cylindrical fragmentary coenostea lying with axes parallel to the bedding plane (text-fig. 8). The mode of life and burial of cylindrical forms is still enigmatic.

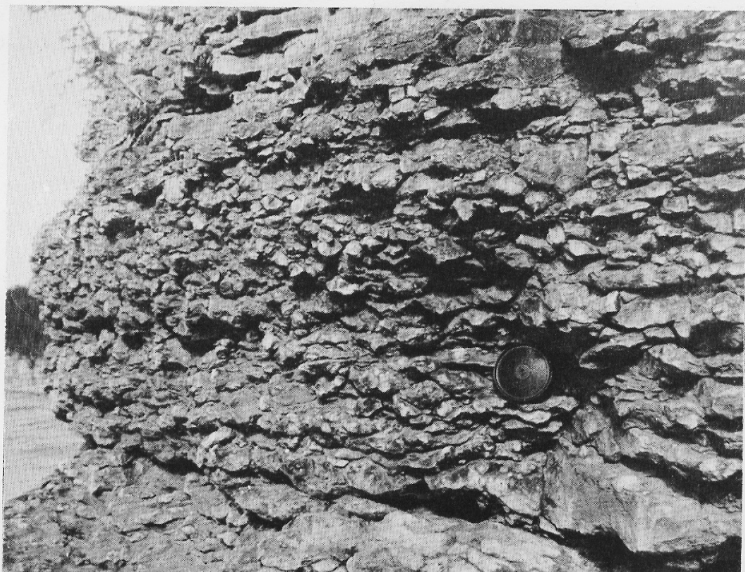
Stromatoporoids are rather atypical in coquinoid grainstones that accumulated in shoal environments. An exception is in brachiopod- and bivalve-limestones consisting of large shells and distributed over a wide area (e.g. the *Pentamerus* and *Borealis* banks in the Llandover of Estonia). Such banks are characterized by a relatively monotonous content of other fossils, while massive stromatoporoids and some types of corals (*Favositida*) are quite common.

TEXT-FIG. 7. Thin stromatoporoid biostrome consisting of nodular coenostea, lying above a massive *Borealis* bank, and covered with peloidal grainstone. Karinu Member, Juuru Stage, Llandovery, Karinu quarry, Estonia. Photo U. Veske.



The presence of stromatoporoids in oolitic and coated grainstones that formed in very shallow, warm, agitated water is somewhat exceptional. I have observed such a phenomenon in the Halla Beds of Gotland, where the Bara oolite facies rarely contains small assemblages of stromatoporoids that probably could develop into bioherms. In a few cases stromatoporoids have been found with oncolites—for example, in the lowermost part of the thick Wenlock biostrome on the Moiero River, mentioned above. The possibility cannot be excluded that the stromatoporoids and oncolites were from different areas and were brought together by wave or current activity.

At the transition from the high-energy facies belt to the near-shore low-energy belt, or on restricted marine shoals, pelsparites and peloidal grainstones were developed (see Wilson 1975; Nestor and Einasto 1977). In Estonia, where such facies occur in the Karinu Member of the Juuru Stage (Llandovery) and in the Lümända Limestone of the Paadla Stage (Ludlow), my observations show that stromatoporoids occur in these facies in moderate abundance and they are often somewhat



TEXT-FIG. 8. Stromatoporoid bank consisting of cylindrical fragmentary coenostea of *Neobeatricea nikiforovae*, Wenlock, Moiero River.

abraded. On the other hand, according to Dr. V Jaanusson (pers. comm.) pelsparites and peloidal grainstones are widespread as inter-reef deposits of the Högklint reefs of Gotland, particularly in their topmost part; this suggests a close paragenetic relationship between pelletal and reef limestones.

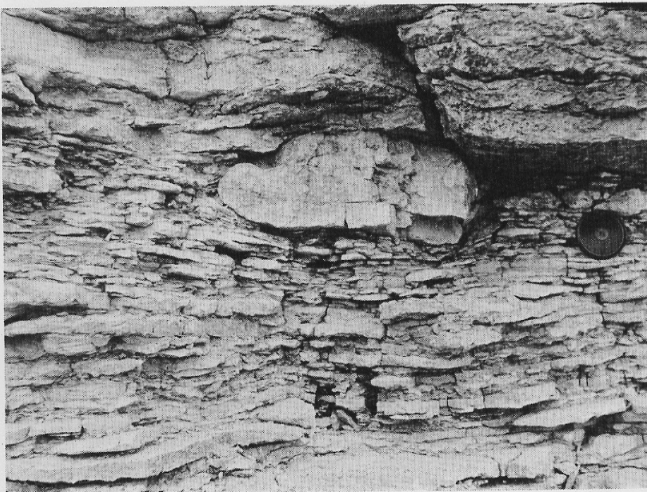
Stromatoporoids in low energy facies

Near-shore low-energy environments were much less favourable for stromatoporoids than high-energy zones. Such conditions of restricted water circulation arise in shallow, flat, epicontinental seas coastward of the zone of wave subsidence (Anderson 1971) or behind the shoal or reef belt that acts as a topographical barrier. As a rule, typical lagoonal and tidal flat facies of Silurian intracratonic seas, such as dolomitic mudstones, algal-laminated mudstones, laminated bioturbated pelletal lime mudstones, etc., do not contain stromatoporoids. One exception is represented by amphipora-limestones, consisting of very thin cylindrical coenostea of a specific group of stromatoporoids in a bituminous calcareous mudstone matrix; they are characteristic of the Devonian and have been considered as sediments of stagnant lagoons (e.g. Lecompte 1970; St. Jean 1971, Elloy 1972). In geosynclinal basins of the Urals and Central Asia, amphipora-limestones already occur in the upper Silurian. In Podolia they are known from the Zvenigorod beds of the Skala Stage (Přídolí).

In less isolated (semi-lagoonal) calm-water facies, stromatoporoids may be more common. For example, they occur in various concentrations up to biostrome levels in massive, slightly bituminous pelleted mudstones and wackestones that are widespread in the Hakom Formation (Wenlock) of the Siberian Moiero River section (Miagkova *et al.* 1976), and in Rashkova beds of the Skala Stage in Podolia (see Nikiforova and Predtetschensky 1972), where they alternate with lagoonal and shoal facies. In such sediments, stromatoporoids are usually represented by domical or irregular coenostea, mostly buried in life position. Argillaceous wackestones in the Kuusnõmme beds of the Rootsikõla Stage of Estonia formed under similar conditions (Einasto 1968) and contain small, nodular, algal-coated coenostea of stromatoporoids.

The comparatively low diversity of biota in these beds and their position between lagoonal dolomites may indicate somewhat abnormal environmental conditions, but in general, excluding upper Silurian amphiporids, one can conclude that Silurian stromatoporoids probably could not stand considerable departures from normal marine salinity.

In low-energy open shelf sediments, stromatoporoids are much more common than in restricted shelf facies. Open shelf facies are represented by bioclastic or whole fossil wackestones (see Wilson 1975), usually intercalating with thin, wavy layers of marls that give the rock a nodular structure. This facies was widespread in Silurian intracratonic basins (e.g. Upper Visby Marls of Gotland, nodular limestones of Varbola, and Rumba formations of Estonia). They contain a rich and diverse shelly



TEXT-FIG. 9. Low-domical coenosteam of a stromatoporoid in open shelf thin-bedded bioclastic packstone intercalated with marls. Upper Llandoverly, Moiero River.

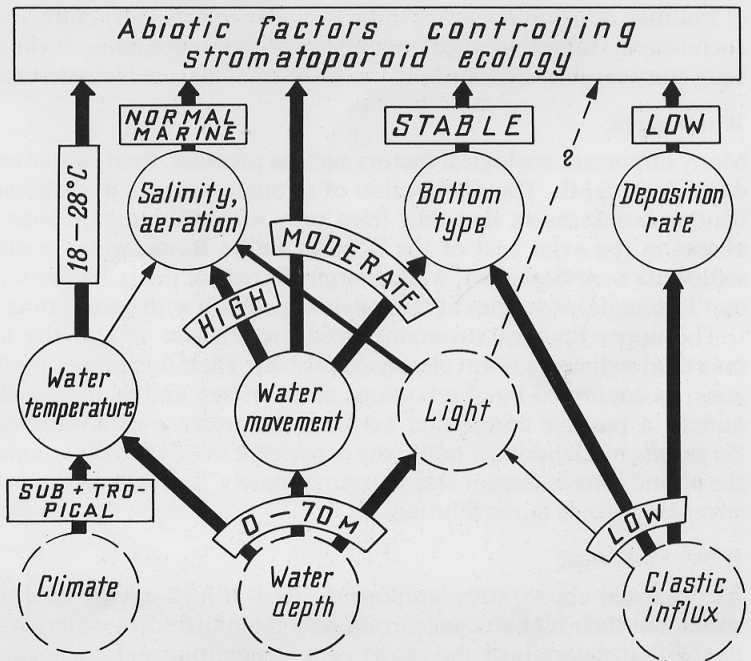
fauna in which stromatoporoids are represented by relatively large, domical, low-conical, laminar, or nodular coenostea (text-fig. 9). Compound coenostea are also fairly common. Stromatoporoids were especially numerous in that part of the open shelf bordering on the high-energy shoal belt. Many thin intercalations and lenses of grainstone occur in sections of this area. Stromatoporoids were occasionally so abundant that they formed biostromes and small bioherms. The growth of the larger 'ecological reefs' might have started in such open-shelf facies.

In open shelf nodular wackestones, coenostea of stromatoporoids are sometimes partly abraded and encrusted with pyrite. Kershaw (1980) has described the process of scouring in the vicinity of domical and conical coenostea in the open shelf environment, indicating the presence of moderate currents in this region.

In Silurian pericontinental basins the belt of open-shelf wackestones was followed offshore by a belt of comparatively monotonous marls and claystones, sometimes with nodules of micritic limestone, forming a transition between the carbonate shelf and basinal graptolitic shales and mudstones (Nestor and Einasto 1977). Stromatoporoids were practically absent in all these deeper-water argillaceous sediments. They were also virtually absent from clastic continental shelves, as, for example, in the Silurian sequences of the Oslo Region and the Welsh Borderland, where carbonate rocks with stromatoporoids occur only at restricted stratigraphical levels (7a-b, 7c β , 8c-d, 9b in Norway; Much Wenlock Limestone in Welsh Borderland). In siltstones and sandstones of the same sequences they are almost completely unknown. Stromatoporoids are also absent in evaporitic deposits of isolated epicontinental basins (e.g. the late Silurian Michigan Basin and Tunguska Basin).

ESTIMATE OF MAIN ABIOTIC ECOLOGICAL FACTORS

The main abiotic ecological factors affecting benthic marine organisms are water temperature (climate), salinity, aeration, water depth, water movement, bottom type, rate of sedimentation, light, and pressure, all of which directly or indirectly control their distribution and adaptation to different environments. Using data from stromatoporoid distribution in different facies, an estimate is made here of the effect of these factors in Silurian cratonic seas (text-fig. 10).



TEXT-FIG. 10. Diagrammatic representation of abiotic ecological factors controlling stromatoporoid distribution. Favourable conditions are shown in quadrangles.

Climate and water temperature

As reef-building organisms, stromatoporoids have mostly been taken to be inhabitants of tropical and subtropical climatic belts. Only St. Jean (1971), pointing to the low taxonomic diversity of certain Silurian and lower Devonian stromatoporoid biostromes, has suggested that they might have formed not at low but at high palaeolatitudes, in cold water conditions. The following factors support a thermophilic mode of life for stromatoporoids: (1) their association with carbonate deposits, particularly with such lime sediments as ooids, grapestones, peloids, lime mud accumulations, reef boundstones, that form today only in tropical and subtropical seas. (2) The skeleton of stromatoporoids obviously consisted mainly of impersistent aragonite as indicated by relict fibrous and spherulitic microstructures and their poor preservation as fossils (Wendt 1975, 1983; Stearn 1977). (3) The absence of stromatoporoids in the Silurian Malvinokaffric palaeobiogeographical realm. (4) Sequences in the Michigan and Tunguska Basins that are rich in stromatoporoids are replaced by evaporites.

Recent coral reefs grow in seas where the minimum water temperature does not fall below +18.5°C (Kukal 1971). On the other hand, the chemical or biochemical precipitation of aragonitic sediments starts at about +25 to +27 °C. Thus a temperature interval from +18 to +28 °C was presumably favourable for stromatoporoids associated with those types of deposits.

Salinity and aeration

Since stromatoporoids are often associated with diverse biota, they are mostly considered as normal marine organisms. Like many other groups, apart from stenohaline forms, they also had euryhaline representatives. Among stromatoporoids to be considered in the latter category are slender, cylindrical amphiporids (genera *Amphipora*, *Paramphipora*, *Clathrodictyella*, *Stellopora*) that appeared in the late Silurian and are widespread in Devonian deposits. It is possible that representatives of some other genera were also able to tolerate poorly aerated semi-lagoonal conditions somewhat below normal marine salinity, because often in very shallow water sequences there are interlayers containing skeletons of only one or two species of stromatoporoids almost without any other fossil. Examples of such forms are *Araneosustroma stelliparratum* from the Rootsiküla Stage of Estonia (Nestor 1982) and *Stromatopora dzvenigorodensis* and '*S.*' *gukovensis* from the Skala Stage of Podolia, which have a very fine, irregular internal structure and a nodular or irregular laminar coenosteum. Lithological characteristics of the surrounding rocks suggest that there could not have been considerable departures from the normal marine hydrochemical regime.

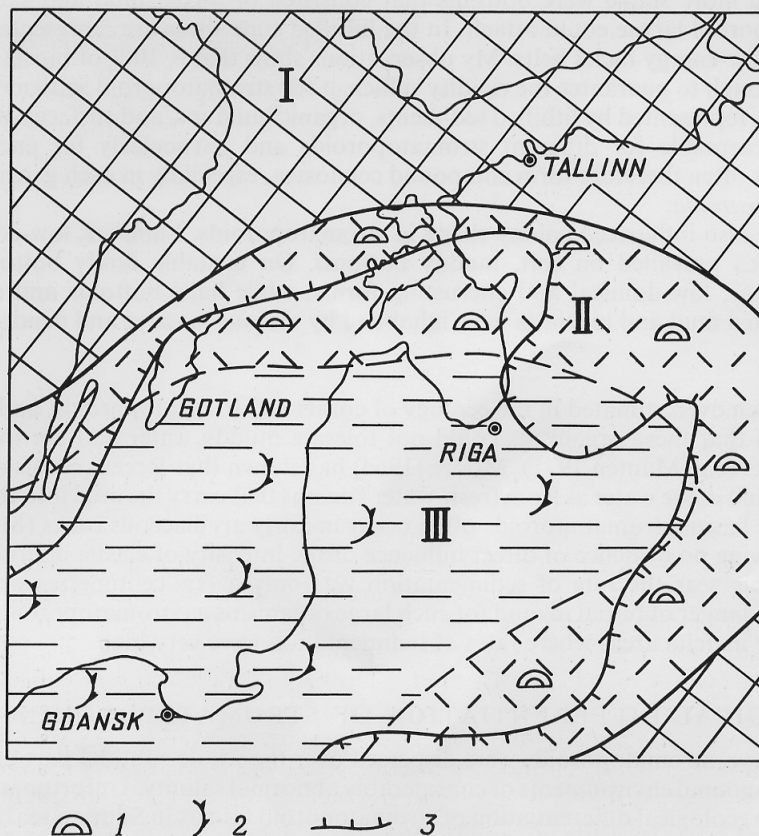
Water depth

Many important ecological factors such as pressure, light, water temperature, and water movement depend on depth. The distribution of stromatoporoids in carbonate facies with a rich and diverse benthic fauna shows that they lived only within the neritic zone. For example, they were totally absent in the axial part of the Silurian Baltic Basin, where deeper-water argillaceous graptolitic sediments were deposited, while marginal areas of the same basin (Gotland, central Estonia, south-east Lithuania) were sites of carbonate deposition with a rich fauna of stromatoporoids (text-fig. 11).

The upper limit of stromatoporoid distribution was at the low tide level—their presence in intertidal sediments is not clearly confirmed. Their maximum depth was near the limit of the photic zone, as confirmed by observations of Lauritzen and Worsley (1974) in the Oslo area, where they noticed a positive correlation between the presence of stromatoporoids and the calcareous alga *Girvanella* in Llandovery rocks; my experience in other areas confirms this observation. The depth of the photic zone in Recent seas is approximately 70 m, which can be taken as the maximum depth for stromatoporoids in the Silurian.

Water movement

As discussed above, stromatoporoids lived in high-energy environments as well as in low-energy zones, but their highest concentrations were in turbulent water. Water movement was an important factor that determined the shape of a stromatoporoid coenosteum (St. Jean 1971; Stearn 1975;



TEXT-FIG. 11. Schematic palaeogeographical map of the Baltic basin in middle Wenlock (Jaagarahu) times. I—land, II—carbonate shelf, III—deeper basin with argillaceous sediments. 1—stromatoporoids, 2—graptoloids, 3—contour of present-day distribution of middle Wenlock rocks.

Wilson 1975; Kershaw and Riding 1980). Comparatively massive, domical or irregular coenostea and laminar and encrusting forms that were able to stabilize deposits were typical of high-energy environments. In areas protected from wave activity there were cylindrical forms. High domical and bulbous forms also preferred low-energy environments because their base was relatively small and made the colony unstable. In addition to water movement, the shape of a colony also depended on the substrate and on genotypic influence (Kershaw 1981). Water movement directly affected aeration, which may be why the high-energy shoal environment was the most favourable for stromatoporoids, although their oxygen requirements remain unknown.

Bottom type

Soft muddy bottoms were unsuitable for stromatoporoids because they provided no bases to which larvae could attach; they are therefore rare in marls and micritic limestones. In addition, sinking into a deposit would have endangered the colony. Sandy bottoms were not much better as sands accumulate in agitated water and often undergo redeposition. The most unsuitable substrates were terrigenous sands, while skeletal sands, and particularly those that were poorly sorted, were more

favourable. Even more stable were bottoms that consisted of mixed mud and skeletal grains to which stromatoporoid larvae could attach. In the lithified state these are represented by bioclastic wackestones of low-energy facies belts. My observations show that *c.* 10% of bioclasts in a bottom sediment was enough to guarantee the rigidity sufficient for stromatoporoid settlement.

Hard bottoms, represented by lithified sediments, organic buildups, and surfaces of larger skeletal remains were acceptable for different stromatoporoids and particularly for encrusting forms. Stromatoporoids often therefore form compound coenostea, especially in such genera as *Simplexodictyon* or *Lophiostroma*.

Substrate type also influenced colony shape in stromatoporoids. Laminar, low-conical, or small nodular coenostea prevailed on soft, muddy bottoms. On unstable sandy bottoms there were irregularly laminar, low-domical and encrusting forms, while hard bottoms and stable bottoms covered with mixed mud and bioclasts were inhabited by various massive and dendroid forms.

Clastic influx

This factor is often overestimated in the ecology of corals and stromatoporoids, and one dominant opinion suggests that these organisms could not tolerate muddy water and are therefore rare in argillaceous rocks (e.g. Manten 1971). Moore (1964) has shown that Recent corals do not suffer as much from the mud in the water as from fresh-water streams that carry the mud into the sea. In fact in Silurian cratonic basins stromatoporoids often occur in fairly argillaceous rocks (Mori 1968, 1970; Nestor 1976), giving no evidence of direct influence of the intensity of clastic influx as a restricting factor. In cratonic seas the rate of sedimentation was only a few centimetres per century, and provided no real danger of burial in mud for such large organisms as stromatoporoids. Clastic influx becomes a factor in delta areas where rates of sedimentation were very high.

ECOLOGICAL DIFFERENTIATION OF STROMATOPOROID FAUNAS

As discussed above, stromatoporoids were dispersed over the whole subtidal part of the carbonate shelf excluding lagoonal environments of considerably abnormal salinity. Unfortunately, very little is known about the ecological differentiation of stromatoporoid faunas in Silurian seas, and only some preliminary attempts have been made to distinguish lateral stromatoporoid communities (Mori 1970; Nestor 1982).

The most diverse stromatoporoid faunas, comprising up to fifteen species, occurred in the high-energy carbonate shoal belt of cratonic seas, where many typical forms inhabited different niches of this variable environment. Only five or six species occurred abundantly, usually belonging to such widespread genera as *Clathrodictyon*, *Ecclimadictyon*, *Simplexodictyon*, *Stromatopora*, *Parallelostroma*, and *Densastroma*. The same species were often also common in contemporaneous low-energy facies, and particularly in the open shelf facies belt. For example, in the Juuru Stage of Estonia, *E. microvesiculosum* and *C. boreale* occur commonly in various facies. *P. typicum* and *S. bekkeri* are typical of different parts of the Paadla Stage of Estonia and the Hemse Beds of Gotland. In some other cases the reverse was true and specific forms dominated in the shoal environment. For example, in Högklint reefs of Gotland and lower Jaagarahu reefs of Estonia, the main frame builder was *Vikingia tenue*, which has a fine, irregular subvesicular inner structure. Onshore and offshore from the shoal belt the diversity of stromatoporoid faunas fell away remarkably. Semi-lagoonal muddy deposits contained only one to three species belonging to genera with a very irregular, fine skeletal structure (*Araneosustroma*, *Desmostroma*, and peculiar forms conventionally regarded as *Stromatopora s.l.*). In late Silurian times a characteristic lagoonal community was formed consisting of slender cylindrical *Amphipora*-type stromatoporoids (*Paramphipora*, *Clathrodictyella*, *Stellopora*).

In the open shelf environment, five to six species usually existed together. For example, in the Upper Visby Marls of Gotland and the Jaani Beds of Estonia the prevailing species were *Densastroma pexisum*, *Simplexodictyon simplex*, *Stromatopora impexa*, *Clathrodictyon affabile*, and '*Pseudolabechia hesslandi*'. The first two of these were the most widespread stratigraphically and laterally spreading over the whole open carbonate shelf up to relatively argillaceous shelf-margin sediments

(Nestor 1982). The other species extended across the more coastal parts of the open shelf. In extreme conditions in relatively argillaceous sediments of the shelf margin there were representatives of such genera as *Densastroma*, *Actinostromella*, *Pycnodictyon*, and *Pseudolabechia*, which have an extremely fine skeletal lattice. They were accompanied by genera leading an encrusting mode of life (e.g. *Simplexodictyon*).

It is notable that forms with a very fine skeletal structure adapted best to extreme conditions at the margins of stromatoporoid settlement. Stromatoporoids with an irregular and very variable inner structure were typical of variable shallow water conditions, while the more uniform open shelf was characterized by relatively regular forms.

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