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On the ecogenesis of the Paleozoic Stromatoporoids

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ABSTRACT

From all aforesaid we can conclude that during the Ordovician, Silurian and Devonian periods expansion of stromatoporoid habitats took place. It was the most rapid in the Ordovician. Initially stromatoporoids populated shallow well agitated near-shore shoals of skeletal sand. Afterwards they spread almost over the whole carbonate shelf, excluding only tidal flat and hypersaline lagoons. This process is summarized in Fig. 2. The expansion was accompanied by a certain differentiation of the stromatoporoid fauna into ecological communities. The present state of paleoecological studies of stromatoporoids does not allow us to describe this process in greater detail.

Studying Ordovician and Silurian stromatoporoids of the East-European and Siberian platforms and literature sources, three circumstances attracted the author's attention :

1. On three different platforms, those of North-America, East-Europe and Siberia the first appearance of stromatoporoids in the Middle Ordovician is restricted to one and the same type of limestones-bio- and oösparites.

2. In nodular argillaceous biomicrites stromatoporoids are very rare in the Ordovician while in the Silurian they occur frequently.

3. There were no clear evidences of the existence of different contemporaneous ecological stromapotoroid communities in the Ordovician or Early Silurian deposits, while in the Devonian deposits a different facial position of ramose amphiporids and massive stromatoporoids has repeatedly been mentioned (LECOMPTE M., 1970; ELLOY R., 1972, et *al.*).

The author tried to establish whether such phenomena are only apparent or if certain evolution of stromatoporoid habitats through the geological time really took place. The task is a complicated one since the regional investigations on stromatoporoid paleoecology are almost lacking and taxonomic works with rare exceptions do not contain sufficient information on the surrounding rocks. The only possibility is to compile the data from different sources : those on stromatoporoid distribution and those on lithology and facies of the corresponding strata. Naturally, conclusions based on such material are highly disputable and it needs a lot of works to prove the validity of the preliminary theses presented below more firmly.

ENVIRONMENTAL MODEL

In the present paper an attempt is made to locate the habitats of stromatoporoids in the facies pattern of carbonate shelves and to fix the most striking changes which have taken place in the course of time. For this purpose the distribution of stromatoporoids in some best-studied ancient shelf-seas is considered.

An environmental model worked out by E.J. ANDERSON (1971) for stable and transgressing epeiric seas well generalizes the deposition process on shallow broad carbonate shelves, most favourable for stromatoporoids. According to this model (Fig. 1). the wave and current action upon the sea-floor is

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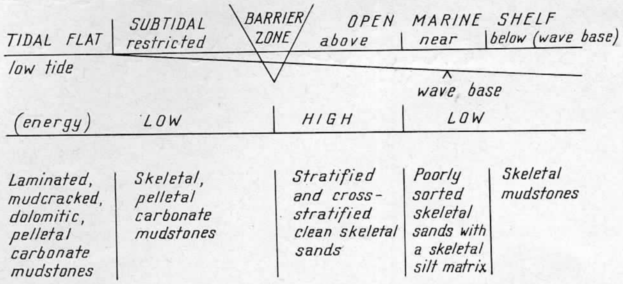

FIG. 1. — Environmental model for stable and transgressing epeiric seas with carbonate-type of sedimentation (after ANDERSON, 1971).

the greatest in the central, high-energy zone, of an extremely flat shelf. Low-energy zones develop both onshore and offshore direction. Five main sedimentary environments are preserved in rocks deposited according to this model. These include (1) tidal flat; (2) restricted subdital; (3) open shelf above wave base (regular wave and current reworking of deposits); (4) open shelf near wave base (occasional wave and current reworking); (5) open shelf below wave base (only organic reworking).

In the fossil record the tidal flat zone is represented by laminated, mudcracked, dolomitic, pelletal carbonate mudstones with intraclasts, vertical burrows and stromatolitic structures. The open shelf above wave vase deposits are stratified and cross-stratified clean sketelal sands (biosparites and biosparrudites). The near wave base deposits are poorly sorted sketelal sands with a skeletal silt matrix (biomicrosparites or calcisiltites). The below wave base deposits are highly burrowed by skeletal mudstones (biomicrites).

The open shelf and restricted subtidal are set apart by a barrier zone. The latter may be represented by :

1) the gradational interface between the zone of wave dissipation and a shoreward lagoon;

2) a physically deposited topographic barrier of mud mounds or sand bard or

3) by a zone of coral patch reefs and associated, interreef deposits.

Several modifications of this model are necessary depending on geological and climatic peculiarities in which the deposition took place.

ORDOVICIAN ENVIRONMENTS

Let us try to fix the position of stromatoporoid habitats on the Ordovician shelves having in view the presented model.

The earliest indisputable stromatoporoids have been found from the Middle Ordovician Chazian Day Point and Crown Point Formations of Lake Champlain area at the western slope of the Appalachian Mountains. The paleoecology of those earliest stromatoporoids was recently studied by U. KAPP (1972). This work as well as the papers by P. OXLEY and M. KAY (1959); M. PITCHER (1964) and others show that Chazian stromatoporoids occur in clean sparry calcarenites which consist mainly of fragments of pelmatozoans. The skeletal sand has been well sorted and winnowed. The cross-bedding, the presence of oncolites and oolites show us that deposition took place in a shallow sea high-energy environment. In the Middle Chazian Crown Point Formation stromatoporoids together with algae, tabulata, bryozoans and sponges form organic mounds (biohermal patch reefs). Frequently erosional channels cut into reefs, suggesting subaerial erosion.

The lateral succession of Chazian facies has not been established yet but it is evident that stromatoporoids occupied the area of skeletal sand shoals and bioherms forming a barrier in the platform margin basin.

In the post-Chazy sequence in many cases the presence of stromatoporoids in the same principal type of facies has been reported. Together with algae, bryozoans and corals they have built similar bioherms in the pelmatozoan calcarenites of the Early Trentonian Carters Limestone in Central Tennessee (ALBERTSTADT L.P., WALKER K.R., ZURAVSKI R.P., 1974). In Central Kentucky stromatoporoids occur in the upper part of the Lexington Limestone (Trentonian), representing a sequence of intercalating biosparites, nodular poorly sorted biomicrites and pelmicrites, i.e. sediments of alternating high-energy and nearshore low-energy environments (see CRESSMAN E.R., 1973). Rocks of Coboconk Formation (upper Black River) in Southern Ontario containing *Stromatocerium* have been considered also as barrier sediments (WINDER C.G., 1960).

On the Siberian platform the author found the earliest stromatoporoids belonging to the Krivoluk Stage (a probable equivalent of the Black River) on the Moiero River. Here they are confined to oosparite and form little bioherms in association with calcareous algae. In the Baltic-Skandinavian area the earliest stromatoporoids have been reported from the Mjøsa Limestone in Norway and from the Saku Limestone in Estonia (the uppermost Middle Ordovician). In the first case they form bioherms and are associated with arenaceous limestone breccias and biopelsparites with *Solenopora* (STØRMER L., 1953; JAANUSSON V., 1973). In the Saku Limestone they are also related to the latter type of rocks. Comparatively late appearance of stromatoporoids in the Baltic region can probably be explained with the fact that underlying Middle Ordovician skeletal mudstones and biomicrites were of deeper water genesis (corresponding more near-shore sediments have not been preserved up to the present day).

One can easily conclude that in the Middle Ordovician stromatoporoids preferred the well-agitated belt of skeletal sand shoals. From that optimum zone they started to colonize the neighbouring shelf areas rather early.

At the beginning of the Blackriveran, stromatoporoids spread into the near-shore quiet-water environment. It is proved by the fact that the cylindrical stromatoporoid *Cryptophragmus antiquatus* has been found in the Gull River Formation of Southern Ontario and Pamelia Formation of New York, represented by cryptocrystalline or fine-grained magnesian limestones (intramicrite, micrite, dolomicrite), probably of tidal flat-lagoonal origin (WINDER C.G., 1960; TEXTORIS D.A., 1968). Also, representatives of the genus *Stromatocerium* occur in the Blackriveran thick-bedded bioturbed bio- and pelmicrites together with dalmanellid brachiopods, ramose ectoprocts, rugose and tabulate corals, epifaunal snails, girvanellid oncolites and calcareous algae (the Chaumont Formation in New York, Murfreesboro and Ridley Limestones of Central Texas). K.R. WALKER, L.F. LAPORTE (1970) and E.J. ANDERSON (1971) treat this community as a restricted subtidal one. However, rather diverse biota suggests that the hydrochemical regime was near to normal. Probably a real topographic barrier was lacking on the very flat Blackriveran shelf and the wave dissipation was gradual, leaving a wide transitional belt between the wave-acted and wave-protected parts of subtidal.

The offshore expansion of stromatoporoids began, perhaps, somewhat later.

As it has already been mentioned, seaward from the high-energy belt of skeletal sand follows a belt of badly sorted skeletal sand mixed with carbonate mud (see also JAANUSSON V., 1973). These sediments are represented in the fossil record by nodular biomicrites with thin interbedded mudstones deposited near and below wave base. Scattered settlements of stromatoporoids appear in this facies belt probably as early as in the Trentonian time. The author has collected stromatoporoids from the mentioned type of rocks from the Mangaseya Stage on the Siberian Platform where they formed isolated patchy settlements. The species *Stromatocerium pustulosum* in the Cannon and Calheys Formations of Central Tennessee (see BASSLER R.S., 1932) and in the Millersburg Member of the Lexington Limestone in Central Kentucky (see CRESSMAN E.R., 1973) probably also habitated a similar environment. However, as the author's experience has shown, stromatoporoids remain untipical of this facies belt up to the end of the Ordovician.

The Cincinnatian Series of the western shelf of the Appalachians (Cincinnati Arch) is generally represented by alternating thin beds of calcareous shales and several limestones varying from biosparrudites to clayey micrites (WEISS M.P., NORMAN C.E., 1960). Stromatoporoids are extremely rare in the rocks of the Eden and Maysville Groups that are of deeper water genesis. In the Richmond Group, intercalations of calcarenitic rocks are more frequent. According to W.T. FOX (1962) its upper part, the Whitewater Formation, represents the deposits of a shoal area and the submerged mud flats. R.G. BROWNE (1964) has mentioned that stromatoporoids of the Richmond Group are mostly associated with certain coral horizons. Apparently in the Richmondian time in the type area the conditions of above, near and below wave base open shelfs altered, with the second one prevailing. On the Siberian Platform during the Late Ordovician Dolbor age the conditions seem to have been very similar to those in the Richmondian. Stromatoporoids were apparently restricted to above and near wave base conditions.

The same conclusion is confirmed by distribution of stromatoporoids in the Upper Ordovician of East Baltic. For example, stromatoporoids are very abundant in biohermal and sparitic pelmatozoan limestones of the Porkuni Stage while in the underlying Pirgu Stage, in nodular argillaceous biomicrites of the outer shelf origin, they are extremely rare.

A generalized scheme of stromatoporoid distribution on Ordovician shelves has been given in Fig. 2a.

SILURIAN ENVIRONMENTS

The Silurian stromatoporoids have been studied most thoroughly in the regions bordering the East-European Platform. Especially suitable for paleoecological conclusions are the Baltic and the Podolian sedimentary basins which in the Silurian represented typical pericontinental seas with the carbonate type of sedimentation, very favourable for stromatoporoids. H. NESTOR and R. EINASTO (1976) have compiled a sedimentary model for the Baltic Silurian Basin which in principle well coincides with E.J. ANDERSON's generalized model. Five macrofacies have been distinguished :

1) primary dolostones,
2) sparites,
3) biomicrites,
4) mudstones,
5) shales; corresponding to (1) lagoonal, (2) shoaly, (3) open shelf, (4) transitional, (5) basinal environments (Fig. 2b).

In the Baltic Silurian Basin stromatoporoids are uncommon to the argillaceous dolomitic and micritic (often slightly bituminous or greatly bioturbed) deposits which accumulated in the near-shore calm-water (« lagoonal ») environment, corresponding to the tidal flat and partly to the restricted subtidal in ANDERSON's model.

As in the Ordovician, in the Silurian stromatoporoids were also the most typical of the high-energy « shoaly » facies belt. They formed bioherms on different stratigraphic levels (see A.A. MANTEN, 1971). Interreef sediments were usually pelmatozoan sands. Reef and interreef sediments apparently formed a topographic barrier. In some cases organic banks (e.g. the Early Llandoverian *Borealis* bank in the Juuru Stage, the Late Llandoverian *Pentamerus* banks in the Adavere Stage) also served as a barrier. Stromatoporoids are common to such brachiopod banks with a rather specialized, poorly diversified fauna. The off-shore slope of the barrier was probably represented by well-sorted, sometimes cross-bedded biosparite and intrabiosparite, often containing rounded fragments of stromatoporoid coenosteums.

Seaward from the shoaly belt there was situated a wide belt of open shelf. In the fossil record its deposits are represented by rhythmically intercalated thin beds of unsorted biomicrites and mudstones. The nodular structure of rock is typical of this facies belt. The distribution of stramotaporoids in the formations, considered as typical open shelf deposits (e.g. the Llandoverian Varbola and Rumba Formations in Estonia, the Wenlockian Upper Visby and Sõrve Formations on Gotland and in Estonia respectively) suggests that unlike the Ordovician, when only patchy settlements of stromatoporoids were situated on the open shelf, confined to its shallower, near wave base part, in the Silurian stromatoporoids occupied the whole open shelf rather uniformly.

Basinward interbedding biomicrites and mudstones of the open shelf grade into thick monotonous series of mudstones, considered as deposits of the basin slope (NESTOR H., EINASTO R., 1976). Ostracodes, trilobites, brachiopods, gastropods associate with the last type of rocks. Algae, stromatoporoids and corals with rare exceptions of tiny solitary corals and halysitids are entirely lacking. Mudstones with sparse benthic fauna are followed by graptolite bearing basinal shales.

From this review of the facies relations of the Paleobaltic epeiric basin it follows that in the Silurian stromatoporoids spread over the entire carbonate shelf up to its outer edge. Permanently unoccupied remained only the near-shore tidal flat — lagoonal belt with the abnormal hydrochemical regime (Fig. 2a).

No striking change in stromatoporoid habitats took place during the Silurian period. But there are some evidences that in this period differenciation of the stromatoporoid fauna into ecological communities began. The author has studied numerous stromatoporoid specimens from different facies of the Early Llandoverian Juuru Stage and has concluded that there were similar stromaporoid communities in different types of sediments. Only bioherms of the Hilliste Member have a richer stromatoporoid fauna (NESTOR H., 1964), but even this may be explained with the age of this member, situated in the uppermost part of the Juuru Stage. K. MORI (1970) has shown that already in the Wenlockian and Ludlowian on Gotland, there existed two different assemblages of stromatoporoids, one characteristic of massive reef limestones (i.e. deposits of a shoaly facies belt) and another characteristic of the marls and the marly limestones (i.e. deposits of the outer shelf).

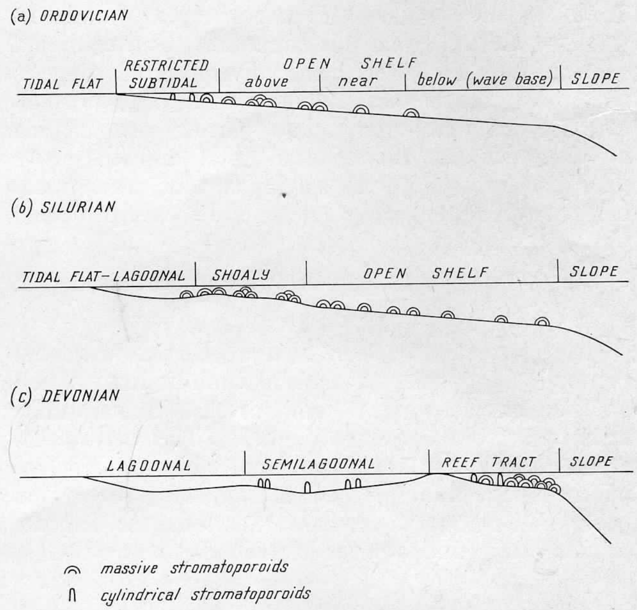

FIG. 2. — Distribution of stromatoporoid habitats on continental shelves. For the model of the Ordovician (*a*) has been taken mainly the western Appalachian shelf sea; of the Silurian (*b*) -- the Baltic pericontinental sea; of the Devonian (*c*) -- the western Ural and the western Canadian shelf-seas. The migration of stromatoporoid habitats towards the outer shelf is striking.

DEVONIAN ENVIRONMENTS

The Devonian sedimentation differed remarkably from the Ordovician and Silurian ones as the continents of the Northern hemisphere were uplifted due to the Caledonian orogenesis and produced a large amount of clastics, deposited on continental lowlands as Old Red Magnafacies and in marginal sea basins as Rhenish Magnafacies (ERBEN H.R., 1964). Only the areas of the so-called Bohemian or Hercynian development (Barrandian Basin, Western Urals, etc.). show in the Early Devonian the facies pattern in many respects comparable with the Ordovician and Silurian carbonate facies succession. The distribution of stromatoporoids in such areas was similar to that in the Silurian. When compared with the Ordovician and Silurian deposition, the most conspicuous peculiarity of the Devonian epeiric carbonate sedimentation is that in many cases there developed shelf-edge reef-tracts resembling recent barrier reefs. The high-energy hydrodynamic zone was in such cases situated near the outer margin of the shelf. The open shelf was reduced or wholly lacking. On the wide back-reef part of the shelf lagoonal or semilagoonal environments prevailed.

Such conditions, recently studied by V.P. SHUISKI (1970), were typical of a sea which spreads over the Western Urals during the Early and Middle Devonian. In the Gedinnian, along the eastern margin of the East-European platform a sand bar was formed, consisting mostly of pelmatozoan debris. In the Eifelian it developed into a barrier reef consisting of :

1) a windward slope,

2) a reef-plateau with an outer subtidal zone of algae-stromatoporoid-coral thickets and an inner-accumulative terrace from bioclastic material,

3) supratidal islands,

4) a leeward beach. Massive stromatoporoids have been considered as inhabitants of the windward part of the reef-plateau, including the zone of surf.

Ramose stromatoporoids were more common in the median and leeward part of the reef-plateau. The barrier reef separated the Zilair depression filled with deep-water cherty clayey deposits from the inner-shelf lagoon where dolomitic or lime muds with sparse biota of ostracods and a few species of amphiporids deposited.

Rather similar lateral facies progression has been considered typical of the Western Canada Internal Shelf during the Middle and Late Devonian. Here the site of the shelf edge was also of the highest carbonate production and formed a barrier to water circulation shelfward (BASSETT H.G., STOUT J.G., 1967). The optimal conditions for the sessil benthos (corals, stromatoporoids, calcareous algae) developed along the platform margin and periodically reef tracts were formed (Keg River, Swan Hills, Leduc Formations). On the carbonate platform slope dark biomicritic open-marine limestones are accumulated, composed mainly of skeletal debris of crinoids, brachiopods and solitary corals, grading seaward into the basinal shale facies. Shoreward from the barrier semirestricted, restricted, evaporite-carbonate, evaporite and terrigenous clastic facies belts have been distinguished. Amphiporids together with ostracods, gastropods and calcisphaeres occur in semirestricted lime mudstones but are wholly lacking in all other lagoonal facies listed.

The depositional models mentioned above cannot be applied directly to Devonian geosyncline areas with well-differentiated vertical tectonical movements.

But in spite of different lateral facies relations the bathymetric and hydrodynamic characteristics of geosynclinal carbonate facies were evidently the same as in platform and platform margin carbonates. M. LECOMPTE (1970) has distinguished the following bathymetric zones in which the Ardennian Devonian rocks have been formed :

1) deep-water zone, represented by black goniatite shales;

2) calm-water zone where mudstones with carbonate nodules and thin interbeds accumulated;

3) quiet-water zone with clayey limestones containing tabulata, colonial rugosae and rare laminar stromatoporoids, initiating reef building;

4) subturbulente zone, represented by pure limestones with laminar stromatoporoids, ramose tabulata, solitary corals and brachiopods;

5) turbulente zone, consisting of pure limestones with a lot of reef building organisms (massive stromatoporoids prevailing);

6) sublagoonal zone (intertidal), represented by clayey micritic limestone with ostracodes, *Girvanella*, rare gastropods and amphiporids;

7) lagoonal zone with dolomicritic and evaporitic deposits.

As this brief review shows, no principal changes in stromatoporoid habitats took place in the Devonian in comparison with the Silurian period. Only ecological differentiation of stromatoporoid fauna seems to have been more distinct in the Devonian and some specialized taxonomic stocks evolved that were adapted to the living conditions deviating from the normal-sea ones, (Amphiporids in the sublagoonal environment).

MIGRATION OF THE REEF-BUILDING CENTRE

A most remarkable phenomenon in the Devonian is the shifting of the optimum reef-building zone from the near-shore site of the continental shelf to its outer margin. Some early shelf-edge reef-tracts are known already from the Ordivician, e.g., the bryozoan Holston Reef from the Middle Ordovician of East Tennessee (WALKER K.R., 1974). The Late Ordovician Buda Reefs in Central Sweden, consisting mostly of stromatactis-type structures seem to occupy a similar position. Stromatoporoids are lacking in those Ordovician reefs while in the same regions they are common in the contemporaneous inner shelf patch reefs of the same age (Carters Reefs in Central Tennessee, Niiby Reefs in North-West Estonia).

The best-known Silurian reefs, those of the Great Lakes area in North America and Gotland Island, as well as Estonian and Podolian ones are of patch-reef type, forming wide inner-shelf belts or having been scattered over the whole shelf area (LOWENSTAM H.A., 1950; MANTEN A.A., 1971). Stromatoporoids became the main reef builders of Silurian build-ups in case they reached out into the agitated environment (TESTORIS D.A., CARROZZI A.N., 1964).

In the Devonian, stromatoporoids became common builders of the first complicated barrier-reefs situated along the shelf margin (e.g. Eifelian Reefs of the Urals, Late Devonian Reefs of Western Canada and Western Australia, etc.).

One of the possible explanations for the migration of the reef-building centre to the shelf edge is the increase in atmospheric oxygen content connected with rapid evolution of terrestrial vegetation in the Devonian period. This influenced supplying of ocean currents with oxygen and nutrients and created favourable living conditions for reef-building organisms on the shelf margin.

As to the Ordovician and the Silurian, the main producers of oxygen for sea water were evidently algae, living in the shallower, onshore site of shelf which was then better supplied with oxygen than the deeper offshore site, and offered better conditions for reef-building animal organisms, including stromatoporoids.

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