

SILURIAN BRYOZOANS
WHICH GREW IN THE SHADE

Nils SPJELDNAES *

Abstract

A study is made of bryozoan faunas which grew on the underside of coral and stromatoporoid heads, and in other shade-biotopes from the Silurian of Gotland. An analysis is made of the faunal associations, and the stability of these association in the geological record. Comparison with recent analoges are introduced in order to analyse the physiological and ecologic parameters involved in these rather special biotopes. Some possibilities for using the shade-biotopes as palaeoecological indicators of depth, turbidity and silting conditions are suggested, and it is also noted that the recent shade-bryozoans may be useful as indicators of ecological change, especially pollution.

Résumé

Etude des faunes de bryozoaires croissant sur la partie inférieure des coraux et des stromatopores et dans d'autres biotopes ombragés du Silurien du Gotland. Analyse des associations fauniques et de leur stabilité durant les temps géologiques. Comparaison avec des faunes récentes pour analyser les paramètres physiologiques et écologiques impliqués dans ces biotopes très spéciaux. Possibilité d'employer ces biotopes comme des indicateurs paléoécologiques de profondeur, turbidité et envasement; les bryozoaires "d'ombre" actuels peuvent être utilisés comme indicateurs de changements écologiques, spécialement de pollution.

"Bryozoa 1974" – *Docum. Lab. Géol. Fac. Sci. Lyon* – H.S. 3 (fasc. 2), p. 415-424, 2 fig., 1 pl.

* Zoological Institute, Aarhus University, DK-8000 AARHUS C, Denmark.

INTRODUCTION

It is well known that bryozoans are often found in the shade, under stones, in cavities, and on the inside of convex shells. This is attributed to the photonegativity of the settling larvae in some species (Ryland, 1960), and also possibly to the reaction of the larvae to gravity (Ryland & Stebbin, 1971) which makes them settle on the roof of cavities and under overhanging surfaces.

The purpose of this paper is to analyse this phenomenon both in recent and fossil material in the hope of using it as a palaeoecological indicator.

The results should be regarded as preliminary, and a more detailed quantitative result must await systematic studies of many shade-faunas, most of which - especially the fossil ones - are not well known.

THE RECENT MATERIAL

There are - roughly speaking - three types of shade-biotopes :

- a) caves and crevasses in solid rock or reefs,
- b) spaces below stones, or isolated heads of corals, and
- c) cavities on the inside of larger convex shells, mostly pelecypods, but also brachiopods, gastropodes and others.

Transitions between the groups are met with, but are comparatively rare.

Bryozoans from cavities in coral reefs have been described by R. J. Cuffey (1972), and R. Riedl (1964, 1966) has described the fauna (including bryozoans) and general biology and geometry of sub-marine caves in solid rock. In some of the cases described by R. J. Cuffey (1972) the bryozoans seem to be a dominant element in some of the cavities, especially the smaller ones, but in the larger caves described by R. Riedl (1966), the bryozoans are normally a minor constituent of the fauna.

The biotopes of type b) have been mentioned repeatedly in the literature, but little has been done in the way of quantitative and physiological studies. The cavities of this type are generally much lower than long and wide, and grade into overhanging surfaces which are not in caves, and where the shade is not complete, such as on the underside of *Acropora*-like corals. The fauna in this type is dominated by bryozoans and serpulid worms. Other forms may occur, especially hydroids, and attached foraminifera, but the association of bryozoans and serpulid worms seems to characterize this group.

The type c) cavities, inside shells, are often very small, with a volume of only a few ml. and again the bryozoans are one of the dominating elements in the fauna, often accompanied by serpulid worms. It should be mentioned, that since this study is aimed at the palaeoecology, no mention is made of organisms with no hard parts.

The life condition in the shade-biotypes must be rather special. Because of the low light intensity, photosyntheses must be nil, or very low. All nutrient-supply must therefore come from the outside, and this requires a regular circulation, since the fauna can hardly live from other organisms, swimming into the cavities.

Sedimentation (silting) must be a constant danger to the biotopes where sedimentation is going on. In large caves, and in reefs, where detrital sediments are rare, and turbulence is strong, silting is not critical, but for biotopes of type b) and c) this is a serious problem, which may restrict the effective lifetime of the biotope considerably.

This makes the biotopes especially suitable for opportunistic species, with rapid growth, and short generation time. Some bryozoans are excellently suited for this mode life, since their larvae are photopositive when they are hatched (Ryland, 1960), so that they will move out of the parent cavity. After a few hours they become photonegative, and seek another cavity. It is also interesting to note that serpulids have a similar pattern of larval behaviour (Ryland, 1960), which may explain the bryozoan/serpulid association found in many small shade biotopes.

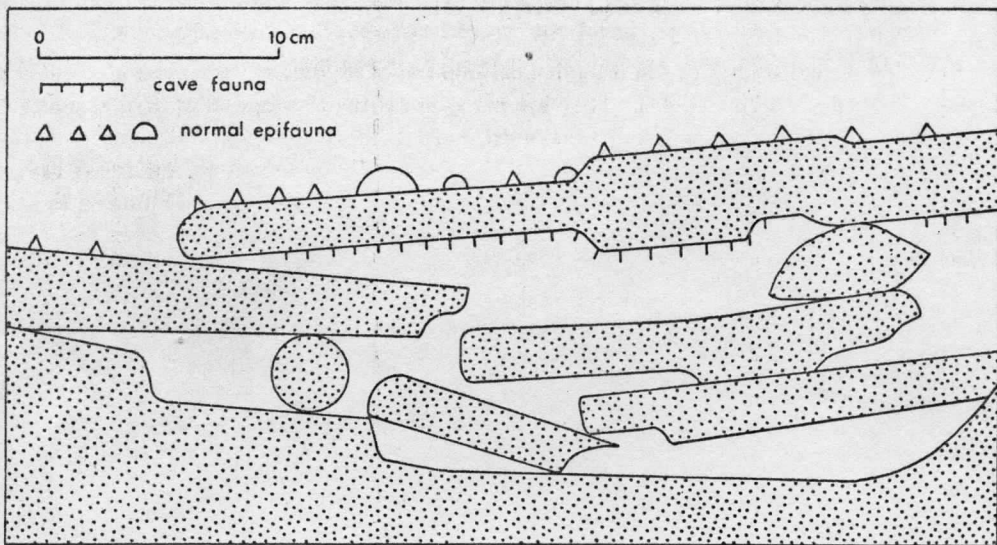


Fig. 1 – Diagrammatic sketch of the occurrence of bryozoan-serpulid shade-faunas. The diagram is taken from a locality at Holy Island, at the NE-coast of England (the material was collected in connection with an excursion led by dr. J.S. Ryland during the IBA-congress in Durham, 1971). The fauna is found on the underside of slabs of carboniferous, dark shale. The locality is in the *Laminaria*-zone normally not exposed at low tide. The shade-fauna is found only on the underside of the highest slabs, the lower ones are sterile, probably due to local anareobic conditions. The shade-fauna is figured on plate 1, fig. 6-7.

Similar larval behavior including sensitivity to gravity is known from acidians (Crisp & Globasky, 1971), and the pattern of light sensitivity is a general feature with many marine invertebrate larvae (Thorson 1964).

R. Riedl (1964) fig. 8, made some calculations on the amount of water exchange necessary in caves to maintain an optimal replenishment of food and oxygen. His figures shows that the water volume in small caves (type b and c) must be completely exchanged every few minutes to maintain this level. This can hardly be a regular feature in most marine environments. The only force (which is also suggested by Riedl) is wave action. Neither deepwater currents nor tidal currents will be able to provide an adequate water circulation.

The data available seems to indicate that the shade communities are all found in the photic zone, and above wave-base. The only material at the authors disposal from deep water is incrusting bryozoans from the inside of shells or *Arctica islandica* and *Mya truncata* from a material described by K. Gripp (1959), from sunken Pleistocene shall beds at about 100 m depth off the Catalonian coast. Because of the peculiar history of this material it is not sure whether they represent real shade communities formed at their present depth, or if the bryozoans are also Pleistocene, and the association was formed in shallower depth than where they are found today.

In any case, the figures shown by R. Riedl (1964) indicate that water circulation was extremely critical in the small shade communities. Only a short period of quiet water would lower the oxygen level dangerously, and most of the food supply would also be cut off. Very few animals can survive under such conditions, and the explanation for the bryozoan/serpulid association in the shade communities as well as in fouling situations, may indicate that they were able to inhabit this niche because they could survive short term drops in oxygen level.

Very few actual studies of the oxygen consumption of bryozoans have been made (Margum & Schopf 1967, Ryland 1970, p. 47-49). They are made under the assumption of normal oxygen level, and indicate that the bryozoans studied may have difficulties obtaining a normal oxygen supply from this water without special coelomic circulation. No studies have been made on the lower oxygen level for bryozoans, but observations of bryozoans in fouling situations, and in polluted waters, indicate that many bryozoans, and serpulids may be able to survive even rather drastic conditions in this respect.

The shade communities may therefore have also some wider ecological importance, since several of the species which occur "in the shade" are among those rapidly expanding today, either by human transplantation (Powell 1970) or by pollution (Dudley 1973). They form a hidden reservoir of potentially pollution-resistant forms, which may spread explosively out of their present hidden niches when, and if, the ecological conditions change in a direction (low oxygen level, general pollution) which favours them.

THE FOSSIL MATERIAL

In the palaeontological literature there are numerous - mostly casual - references to bryozoans (and other organisms) growing on the inside of shells, under coral heads and in other shade-biotopes. A review of both the literature and the author's material indicate that the modern shade-biotopes were established already in the Middle Ordovician, and have continued remarkably unchanged up to the present day.

Two examples are given, from the material collected by the author in the Silurian of Gotland, to illustrate the ecology and composition of some characteristic shade-biotopes.

In the Visby Marl (uppermost Llandovery to basal Wenlock) there are numerous patch-reefs, and isolated heads of corals and stromatoporoids are common, especially in the upper part. A detailed account of the geology and stratigraphy is given by J.E. Hede (in : Lundqvist, Hede & Sundius, 1940), and by A. A. Manten (1971). Up to date reviews of the stratigraphy of Gotland in general, are found in J.E. Hede (1960), A. Martinsson (1967) and M. G. Bassett & L. R. M. Cocks (1974).

Shade-faunas including bryozoans are common on the underside of stromatopoid and coral heads of different size. There is a gradual transition from small individual heads through large, repeatedly regenerated ones to the real patch-reefs. Ecologically these individual heads may (as suggested i. a. by St. Jean (1971) be regarded as minireefs. The larger reef masses are often badly recrystalli-

zed, and there are few cavities preserved, where the lining can be observed. This type of shade-biotope is therefore hardly known in the Silurian of Gotland, but this may rather be the result of preservation than real absence.

Most of the material - and the best preserved - from the shade-biotopes in the Visby Marl is found loose, in the scree off the coastal cliffs. Care was there taken to collect material in situ, to make sure that the bryozoans really grew under the colonies, and not on the upper surface of overturned ones. A check on the orientation of the coral and stromatoporoid heads in the Visby marls, in a number of localities showed - as expected - that most heads were in growing position (84 - 98 %).

It was somewhat surprising that so many were either oriented at high angles or completely overturned. Considering the fine-grained marly sediment, which seemingly indicate very quiet water, one would not expect many overturned specimens. Some of the overturned heads are more than one half meter in cross section, and must have been rather heavy, even before diagenesis. The samples with the highest percentage of overturned heads are found just below the larger patch reefs, and on the flat close to their base, and not at the reef flanks, where they could have been explained by sliding down from the reefs.

The distribution of the shade-fauna (on the undisturbed heads) shows a slight correlation with the percentage of overturned heads. In samples with very few overturned specimens, there are normally few (0 - 7 %) colonies with cave-fauna on the underside, and the fauna is sparse. In some of the cases close to the base of patch-reefs, the incidence of shade-faunas may be close to 100 %.

The significance of these correlations is not too well established, partly because it is hard to determine the presence, and composition of the cave-fauna in some of the specimens collected in situ, because of the clay cover usually found on the underside, and partly because the samples are rather small ($n = 50 - 100$). This is further complicated by suspected differences both in rate of overturning and incidence of cave-fauna between the different groups of host-colonies.

The bryozoan faunas found in the shade-biotopes are decidedly different from those found around, and on the exposed side of the same colonies. Only in one case (in situ) was the "exposed" fauna found directly overgrowing the shade-fauna on an overturned specimen.

The shade-fauna consist mostly of species which are restricted to this environment, and partly of species which do occur outside, but in much smaller numbers. Some of the latter occur with different zoarial shape in the caves and outside. The fauna includes both cryptostomes, cyclostomes, cystiporates, trepostomes and ctenostomes, and up to 11 species has been found under a single specimen, less than 12 cm in diameter. A number of the species are new ones, and there are some unsolved taxonomic problems involved in the species which do occur both inside and outside the caves.

In most of the caves in the Visby Marl, the bryozoans do not show much overgrowth of one colony over another, and small incrusting zoaria dominate, indicating a short lifespan for the fauna. The coral and stromatoporoid heads often show repeated regenerations (text-fig. 2) suggesting that they were almost completely suffocated by clay, and thereafter regenerated. Shade faunas are sometimes found in the "pockets" formed between the old and new parts of the colony but they are generally more sparse than at the base of the colony.

Only a few cases (less than 1 % of all heads studied) the shade-fauna showed repeated overgrowth, indicating a prolonged lifetime of the fauna. In these cases some of the bryozoans (trepostomes and fistuliporids) showed mamillate or even branching colonies, and there are also some new types not occurring in the ordinary caves, such as articulated bases for ptilodichthyid and cellariform bryozoans.

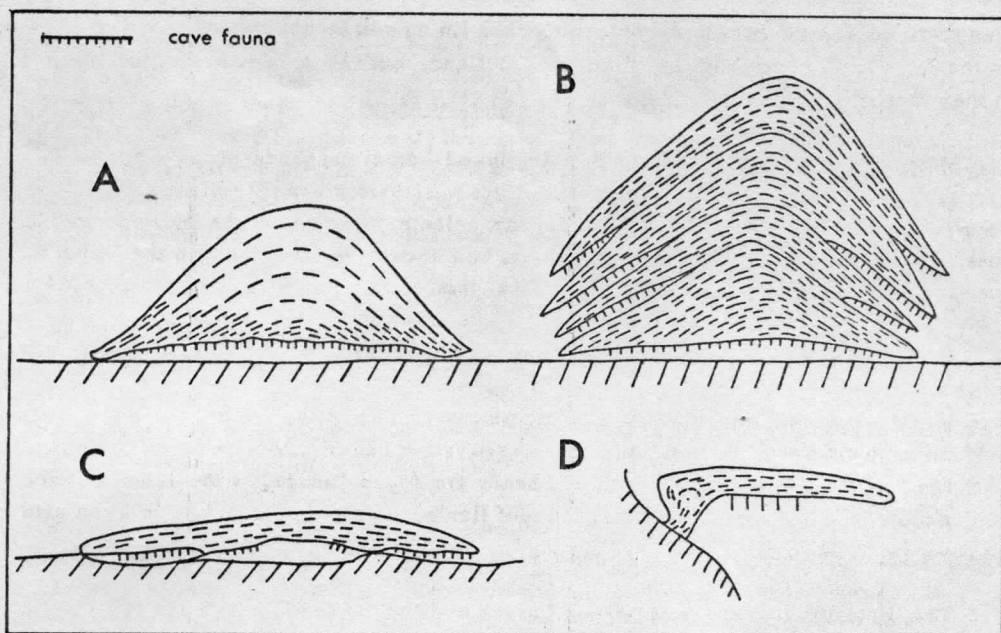


Fig. 2 — Diagrammatic sections through coral and stromatoporoid heads from the Silurian of Gotland. A. is the normal, hatshaped colony, B. represent the multiple regeneration with lateral "pockets" of sediment. C. is the disc-like colonies, and D. represent the *Acropora*-like situation, which is normally found on the fringe of patch-reefs, and growing on larger colonies. The diameter of the colonies shown ranges from less than 10 cm, to more than 1 m.

Analysis of the supposed daily growth-lines (the author's unpublished information) in corals and stromatoporoids from the Visby Marl indicate that the times between the regenerations were from considerably less than one, to two-three years. This agrees with the type of shade-faunas found in shortlived recent caves. This indicate that the bryozoan growth therefore seems to have been about as fast in the Silurian as it is now, (this has some interest, as most of the bryozoans belong to extinct suborders, the biology of which are unknown from recent analogues).

The bryozoans in the shade-faunas are normally associated with serpulid worms, and attached brachiopods (*Liljevallia*, which seems to be restricted to this habitat). Echinoderm holdfasts, structures interpreted as agglutinating foraminifera, and some problematica are also found.

The attached brachiopods may occur without bryozoans, but the association of bryozoans and serpulid worms seems to be obligatory, such as in most recent (and other fossil) shade-faunas. The serpulid worms are either spiral (two or three species of *Spirorbis*) and more stright conical forms (some of these may also be small comulitids). Some of these association are strikingly similar in appearance to the recent ones (compare plate 1, fig. 1-2 and 6-7).

The "Visby" type of shade-biotope, characterized by faunas on the underside of hat-shaped to hemisphaerical heads in a marly matrix, is found also in a number of other areas and stratigraphic levels. In Gotland it is found at the base of reefs at Hørsne Kanal (in the Klinteberg beds) and at Ös-

tergarn (in the Hemse Beds), as well as in a number of other localities, from which only a few specimens are available, and the spatial and stratigraphical relationship therefore is not well established. The same type is also found in the Wenlock Limestone at Wenlock Edge, England, and in some of the mid-continent Silurian reef and interreef-facies in U. S. A.

A slightly different type of shade-biotope is found in the upper part of the Burgsvik Formation (high Ludlov) on Southern Gotland. In the oolite facies, there are a number of small, flat patch-reefs. The localities studied for this paper are found 2,5 and 3,5 km's N of Hoburgen, on the W-ern coast of Gotland.

The reefs grade laterally into a rather pure oolite, which sometimes contains large oncholithes (cf. Munthe 1921). The structure of the oncholithes is rather complex, involving both algae and corals, and sometimes also bryozoans. The core is often formed by bryozoans or other fossils. In both cases studied the reef started directly from the underlying Burgsvik Sandstone, and in one case its position was clearly related to large-scale, sedimentary structures in it. Just below the reef-lens there was also a thin bed at the top of the sandstone where the fossils were preserved complete (mostly crinoids, asteroids, trilobites and brachiopods).

The structure of the reefs is rather loose, with most of the framework consisting of crust-like stromatopoids, partly forming a mud-filled framework, and partly as fringing small Acropora-like colonies.

The shade-fauna is found both in the reef-mass itself, which is not recrystallised, and on the shaded side of the Acropora-like colonies. The fauna differ in species composition from that of the Visby-type, and multiple overgrowths are common. In the reef fringe there are also a number of shade-biotopes formed by large isolated shells of the pelecypod Pteronitella retroflexa with rich bryozoan and serpulid faunas, similar to those on the underside of the stromatopoids.

This type - the Burgsvik-type - is less common than the Visby-type in Gotland, partly because of the more restricted distribution of the oolites. It has been found in connection with "mini-reefs" (complex individual stromatopoids) in the Wenlockian Bara Oolite.

PALAEOECOLOGICAL INTERPRETATIONS

The palaeoecological interpretation of the Burgsvik type is stright forward. Both the analogy with recent associations, and the presence in an oolite environment strongly suggest deposition in a littoral or slightly sub-littoral environment, with agitated, highly oxygenated water. This would explain both the frequency, and the stability (long life) of the shade-biotopes. The reefs are often resting on a thin shell bed of Pteronitella retroflexa, and Lingulas (sometimes in live position) are found in the top beds of the underlying sandstone. This is in excellent agreement with the interpretation of the Lingula community as indicating shallow-water (Ziegler, Cocks and Bambach, 1968).

The interpretation of the environment of the Visby Marl is much more difficult. The fine-grained marl, which surrounds most of the shade-biotopes, suggests quiet and deep water. The brachiopod association are interpreted (Bassett & Cocks 1974, and Bretsky 1969) as deep water ones. If the somewhat extreme suggestions of Hancock, Hurst & Fürsich (1974) are accepted, the depth may have reached 1500 m. This depth is probably in any case excessive in the Baltic Basin in the Silurian, but it is difficult to explain the presence, and distribution of the shade-biotope. The turbulence necessary to sustain the cave faunas is much higher than what is indicated by the surrounding sedi -

ments. Even if the bryozoans grew very fast, and were able to sustain very low oxygen levels, the silting rate must have been too high, and the ventilation of the cave too low to make shade-biotopes similar to the recent ones realistic. Since, however, the associations in the shade-biotopes are so similar to the recent ones, it is reasonable to suggest that they originated under comparable conditions.

This may explained in two ways. The sedimentary environment may have changed periodically from one with agitated water, and no or very little net sedimentation (silting), and periods with ample clay sedimentation, and much lower turbidity. At present we have no safe way of estimating the relative length of these periods. The hard-bottom epifauna of the turbulent periods, and in the fauna of soft sediments of the silting periods may have been mixed by subsequent biotubation.

Another possible explanation is that the bottom of the marl areas was partly covered by sedimenttrapping plants (algae operating much in the same way as the present eel-grass). This may explain why the shade-biotopes is more common on topographically high areas (where the reefs later formed, resulting in a reversal of the relief due to differential compaction under the reef, Spjeldnaes 1959). Here the turbulence may have been high, and still a vegetation protected soft bottom community may have existed close by, and in only slightly deeper water.

A combination of these two explanation may give some ideas for direction of solving the problems of the palaeoecological interpretation of the Visby Marl, where much work remains to be done.

CONCLUSIONS

The study of the bryozoan shade-biotopes are only in the very beginning, and the following conclusions are therefore highly tentative, and only intended to suggest directions of further research.

1) The bryozoan shade-faunas, accompanied by serpulids seems to be an old association, occurring under similar ecological conditions at least since the Middle Ordovician.

2) The Bryozoan shade-faunas seems to occur only in turbulent water (above wave-base), in the photic zone.

3) Preliminary results indicate that the growth-rate of the Silurian trepostomes, cryptostomes and cystiporates were roughly similar to those of recent cheilostomes.

4) The bryozoan shade-biotopes may be of considerable importance in palaeoecological studies as an indicator of shallow, turbulent nonsilting conditions in the photic zone. Their presence or absence may also be an useful indicator in the study of recent ecological conditions.

REFERENCES

- BASSETT M.G. and COCKS L.R.M. (1974) - A review of Silurian brachiopods from Gotland. Fossils and Strata, Oslo, vol. 3, 56 p., 11 pl., Universitetsforlaget.
- BRETSKY P.W. jr. (1969) - Evolution of paleozoic benthic invertebrate communities. Palaeogeography, Palaeoclimatology, Palaeoecology, Amsterdam, vol. 6, p. 45-59.
- CRISP D.J. and GLOBASKY A.F.A.A. (1971) - Responses of the larvae of Diplosoma listerianum to light and gravity. p. 443-465. in : Crisp, D.J. Fourth European Marine Biology Symposium. Cambridge University Press (Cambridge).
- CUFFEY R.J. (1972) - The Roles of Bryozoans in Modern Coral Reefs. Geol. Rundschau, Stuttgart, vol. 61, fasc. 2, p. 542-550.
- DUDLEY J.E. (1973) - Observations on the reproduction, early larval development and colony astogeny of Conopeum tenuissimum (Canu). Chesapeake Science, vol. 14, n° 4, p. 270-278, 6 fig.
- GRIPP K. (1959) - Ecologie de quelques madréporaires de la Méditerranée. Vie et Milieu, vol. 9, p. 379-411.
- HANCOCK N.J., HURST J.M. and FÜRSICH F.T. (1974) - The Depth inhabited by Silurian brachiopod communities. Journ. Geol. Soc., London, vol. 130, p. 151-156.
- LUNDQVIST G., HEDE J.E. and SUNDIUS N. (1940) - Beskrivning till kartbladen Visby och Lumme-lunda. Sveriges Geol. Unders., Stockholm, ser. Aa, vol. 183, 167 p.
- MANGUM C.P. and SCHOPF T.J.M. (1967) - Is an ectoproct possible ? Nature, London, n° 213, p. 264-267.
- MANTEN A.A. (1971) - Silurian Reefs of Gotland. Elsevier, édit., Amsterdam, 539 p.
- MARTINSSON A. (1967) - The succession and ostracode faunas in the Silurian of Gotland. Geol. Fören. Förh., Stockholm, vol. 89, p. 350-386.
- MUNTHE H. (1921) - Beskrivning till kartbladet Burgsvik jämte Hoburgen och Ytterholmen. Sveriges Geol. Unders., Stockholm, Ser. Aa, vol. 152, 172 p.
- POWELL N.A. (1970) - Schizoporella unicornis - An Alien Bryozoan introduced into the Strait of Georgia. Journ. Fisheries Res. Board Canada, Ottawa, vol. 27, n° 10, p. 1847-1853.
- RIEDL R. (1964) - Die Erscheinung der Wasserbewegung und ihre Wirkung auf sedentier im mediterranen Felslittoral. Helgol. Wiss. Meeresunters, Hamburg, vol. 10, p. 155-186.
- RIEDL R. (1966) - Biologie der Meereshöhlen. Verlag Paul Parey, Berlin and Hamburg, 636 p.
- RYLAND J.S. (1960) - Experiments on the influence of light on the behaviour of polyzoan larvae. Journ. Exp. Biol., London, vol. 37, n° 4, p. 783-800.

- RYLAND J. S. (1970) - Bryozoans. Hutchinson University Press, London, 175 p. , 21 fig.
- RYLAND J. S. and STEBBING A. R. D. (1970) - Settlement and orientated growth in epiphytic and epizoic bryozoans, p. 105-124, in : Crisp, D. J. Fourth European Marine Biology Symposium. Cambridge University Press (Cambridge).
- SPJELDNAES N. (1959) - Silurian bentonites from Gotland, Sweden, Geol. Foren. Forhandl. , Stockholm, vol. 81, p. 582-587.
- St. JEAN J. jr. (1971) - Paleobiologic considerations of Reef Stromatoporoids. Proc. North. Americ. Paleont. Convention, Chicago, part J, p. 1389-1429.
- THORSON G. (1964) - Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia, Copenhagen, vol. 1, p. 167-208.
- ZIEGLER A. M. , COCKS L. R. M. and BAMBACH R. K. (1968) - The composition and structure of Lower Silurian marine communities. Lethaia, Oslo, vol. 1, p. 1-27.

PLATE 1

- Fig. 1-2 - 1 - Epifauna from the underside of a favositid coral colony from the Visby Marl (Uppermost Llandovery-Basal Wenlock) at Kneippbyn, S. of Visby, Gotland. The fauna consist of a number of bryozoans, serpulid worms, and the attached brachiopod *Liljevallia*.
- 2 - Is an enlargement of the central part of fig. 1, in order to show the variety of bryozoans, and the small serpulids. Coll. nr. 4332.
- Fig. 3 - Epifauna from the underside of a small stromatoporoid colony from the Visby Marl (Uppermost Llandovery-Basal Wenlock) at Ireviken, NNE of Visby, Gotland. The fauna consists mainly of serpulid worms with some few bryozoans. Coll. nr. 4314 F.
- Fig. 4 - Epifauna (bryozoans, and serpulid worms) from the underside of a crust-like stromatoporoid colony from the Burgsvik oolite (Upper Ludlov) at Kettelviken, N. of Hoburgen, Gotland. The large bryozoan colonies are multilayered, and indicate a long life-time for the biotope. Coll. nr. 5013 D.
- Fig. 5 - Epifauna from the underside of a small favositid coloni from the Visby Marl (Uppermost Llandovery-Basal Wenlock) at Kneippbyn, S. of Visby, Gotland. The fauna consist of several bryozoan species, Cornulites-like tubes, and large specimens of *Liljevallia*. Coll. nr. 4325 A.
- Fig. 6-7 - 6 - Epifauna from the underside of a slab of Carboniferous shale at the exposed, NE-ern coast of Holy Island, N. England. The locality is just below the normal low water mark, in the Laminaria zone. The shale slabs are stacked in small depressions on the bottom, and the epifauna is strikingly different on the upper and lower side. They are also bored into by pholadid pelecypods and often completely penetrated. The situation is illustrated in text fig. 1.
- 7 - Is an enlagment of the left side of fig. 6 to show details of the serpulid tubes and bryozoan colonies. Coll. nr. 4402.

