Environment and quantitative morphology of some Silurian tabulates from Gotland

Jan H. Stel

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An outline is given of reef development in Gotland, Sweden, during the time when the Visby (Llandovery) and Högklint (Wenlock) Beds were deposited together with a sketch of the palaeoecology in the time during which the Hemse and Hamra-Sundre (Ludlow) Beds were formed.

Variation is described in the tabulates *Favosites hisingeri* Edwards & Haime, *F. obliquus* (Sokolov), *F. gothlandicus* Lamarck, *F. forbesi* Edwards & Haime, *Syringolites kunthianus* (Lindström), and *Alveolites suborbicularis* Lamarck.

In order to clarify ecophenotypic variation of corallite size in tabulates, the corallite area and three different corallite diameters were measured. Although the corallite area is more related to the shape of the organism that lived in a corallite, comparison of the several parameters revealed that measuring of a corallite diameter can be applied in such species from which ecophenotypic variation is known. However, the current limitation of variability in corallite diameters within defined morphospecies often is far too narrow, and does not allow for ecophenotypic variation. As a consequence, the number of morphospecies established since Sokolov (1950) is unrealistically large in the *F. forbesi* group as well as in others. Variability in *F. hisingeri* is influenced to a high degree by the environment. The characteristic (genetically controlled?) pattern of larger corallites between smaller ones in *F. forbesi* is hardly influenced by ecological factors. Variation in thickness of the wall, in distance between the tabulae and in intensity of the development of the septal structures is mainly determined by the environment.

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Introduction

MATERIALS AND METHODS

Extensive collections of favositids in which a high degree of variation is seen (*Favosites hisingeri* Edwards & Haime: Lower Visby Beds; *F. forbesi* Edwards & Haime: Högklint and Lower Hamra-Sundre Beds) and favositids with a low variability (*F. gothlandicus* Lamarck: Hemse Beds; *Syringolites kunthianus* Lindström: Högklint Beds) were gathered. As no up to date paleoecological study of the strata, from which these favositids were collected, was available, such a study had to be undertaken first. The results of the palaeoecological studies are described in this paper and in an earlier paper (Stel & de Coo, 1977).

As the area of an individual favositid corallite will reflect to a higher degree the dimensions of the organism living in the corallite than the corallite diameter (which in the literature is considered a reliable characteristic on the species level) both parameters were measured and compared. These parameters were obtained by means of a semi-automatic MOP-AMO2 measuring system, placed at the author's disposal by the firm Ahrin, The Hague, The Netherlands. The MOP-AMO2 system (Fig. 1) is a combination af an electronic planimeter, a transparent measuring plane (with a variable grid) and a pencil. When the periphery of a structure was traced with this pencil, several parameters (area of the corallite, length of the periphery, maximum diameter of the corallite) were obtained at the same time. These parameters are printed on tape by a small automatic rule printer. The parameters shown in Figure 2 were measured for each corallite. When measuring, the periphery of a corallite was defined as the dark line.

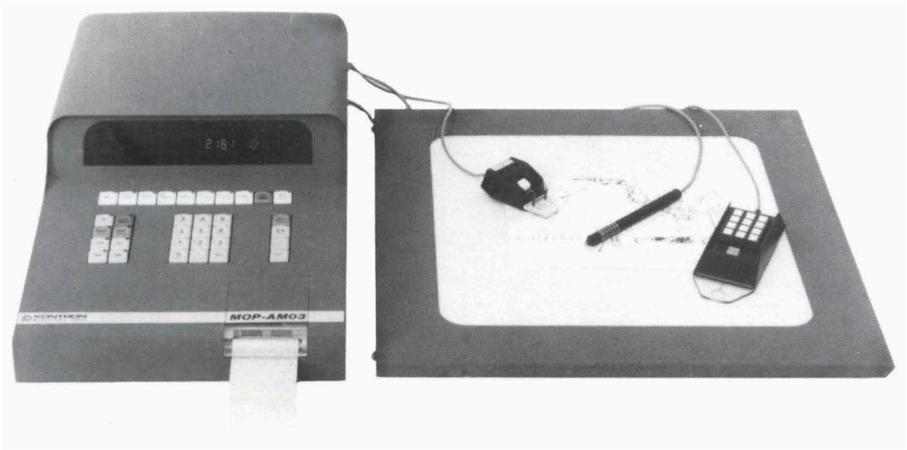

Fig. 1. Semi-automatic MOP-AMO 3, measuring system.

The photographs from which the parameters were measured were prepared as follows:

(1) With a thin dental diamond saw, colony surfaces were cut in squares (20 × 20 × 5 mm). These squares were glued on an aluminium stub. The samples were photographed under a Jeol scanning electron microscope type JSM-35, operated at 25 kV, with an enlargement of ten times. Deviations of the corallite area, caused by the topography of the surface of the colony, were compensated by tilting of the sample. A mosaic of micrographs, with a 50% overlap, was prepared of each square sample. The successive square mosaics are adjacent areas of the colonial surface.

(2) Thin sections were prepared perpendicular to the main growth direction of the corallites. The sections were photographed at a magnification of ten times.

(3) In order to study the morphological variation and reactions during growth, series of transverse peelings were prepared. These peelings were photographically enlarged.

After numbering the individual corallites their parameters were measured. Data were printed on tape by the automatic rule printer, after an automatic correction for the enlargement. Unfortunately standard statistics can not be applied with the MOP-AMO2 (as with the MOP-AMO3).

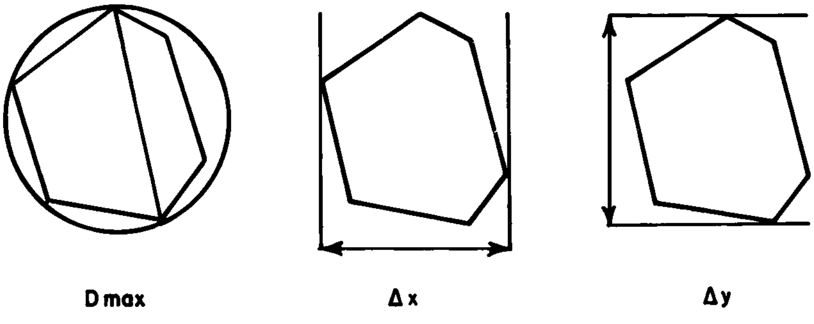

Fig. 2. The three diameters measured for this paper.

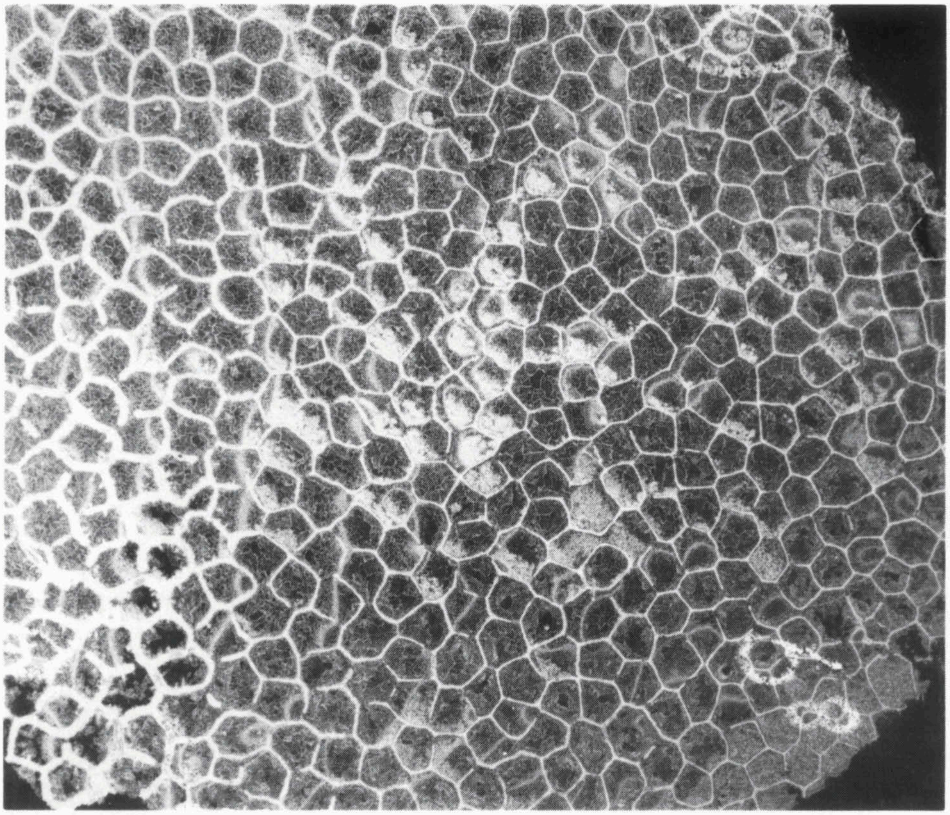

Fig. 3. Measured thin section of *Paleofavosites asper* with solenial growth, erratic boulder, Groningen, The Netherlands, RGM 243 667, × 5.

Statistic procedures were executed by applying standardized WESP-computer programs (van der Weele, 1977) on a CYBER 74-18 at the Rekencentrum of the University of Groningen.

The quantitative approach was tested by measuring a thin section of an erratic boulder of *Paleofavosites asper* d'Orbigny from Groningen (Fig. 3). For a revision of the genus and a detailed description of the type species, with an extensive list of synonyms the reader is referred to the paper by Oekentorp (1976). In his redescription of *P. asper* Oekentorp (1976) summarized the characteristics of this favositid. The type specimen is a paleofavositid with corallites ranging in diameter from 0.8 - 1.5 mm; a diameter of 1.1 mm predominates. Pores frequently

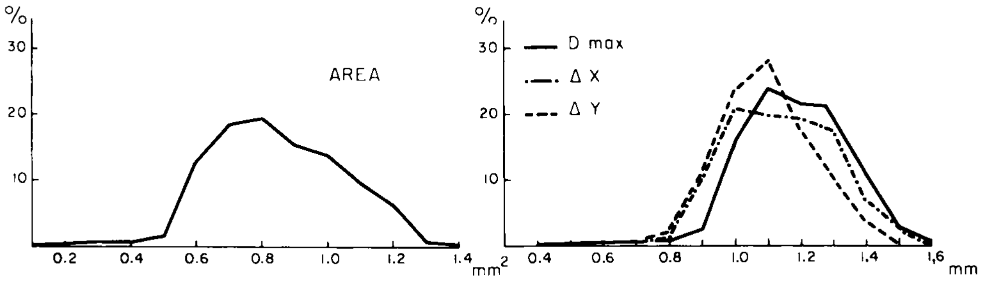

Fig. 4. Frequency distribution in measurings of the thin section of Figure 3.

Table 1. Parameters of corallites in a thin section of *Paleofavosites asper*, RGM 243 667.

Sample RGM 243 667 Erratic boulder; Groningen

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.84	0.20	—0.11	3.18	0.10	1.40	0.83	331
Dmax	1.18	0.16	—0.32	4.31	0.40	1.60	1.18	331
Δx	1.14	0.17	—0.12	3.41	0.40	1.60	1.13	331
Δy	1.09	0.16	—0.61	5.13	0.30	1.50	1.09	331

occur; their diameter is about 0.25 mm. Large spines are found in areas with closely spaced tabulae.

The range of the area and of the diameters of 331 corallites of a specimen of *Paleofavosites asper* measured with the MOP is shown in Figure 4. The employed statistical parameters measured in this transverse section are summarized in Table 1. Corallites are polygonal or somewhat rounded due to solenial growth. Offsets are triangular or quadrangular and arise by lateral increase (Stel, 1979). The range observed in the data from the corallite area measurings is 0.5 - 1.3 mm^2. The data are more or less normally distributed, as is indicated by similar values of the statistic mean and the median (Table 1). The data from the three different corallite diameter measurings are also more or less normally distributed and the graphs are almost the same. This is also indicated by high correlation coefficients. The total range of these data is 0.8 - 1.5 mm and is similar to the range found by Sutton (1966) and Oekentorp (1976). Oekentorp's graph is best compared with the graphs of Δx and Δy which are more or less arbitrary chosen and smaller than the data of the Dmax-graph. Similar relations are seen in Table 1.

Acknowledgements

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The material described is stored in the Rijksmuseum van Geologie en Mineralogie (National Museum of Geology and Mineralogy) in Leiden, The Netherlands, catalogued under numbers RGM 243 667, 243 689, 243 700 - 243 746.

General aspects of the stratigraphy of Gotland

The Silurian of Gotland consists of a succession of limestones and calcareous shales with a thickness of about 500 m. Sedimentation occurred in a shallow epicontinental sea with a maximum water depth of 175 - 200 m (Gray, Laufeld &

Boucot, 1974). Epeirogenetic movements in the basin led to the development of regressive and transgressive sequences.

The Silurian rocks gently dip (0.15 - 0.30°) towards southeast and strike northeast - southwest. Due to this tectonic tilt older deposits are exposed along

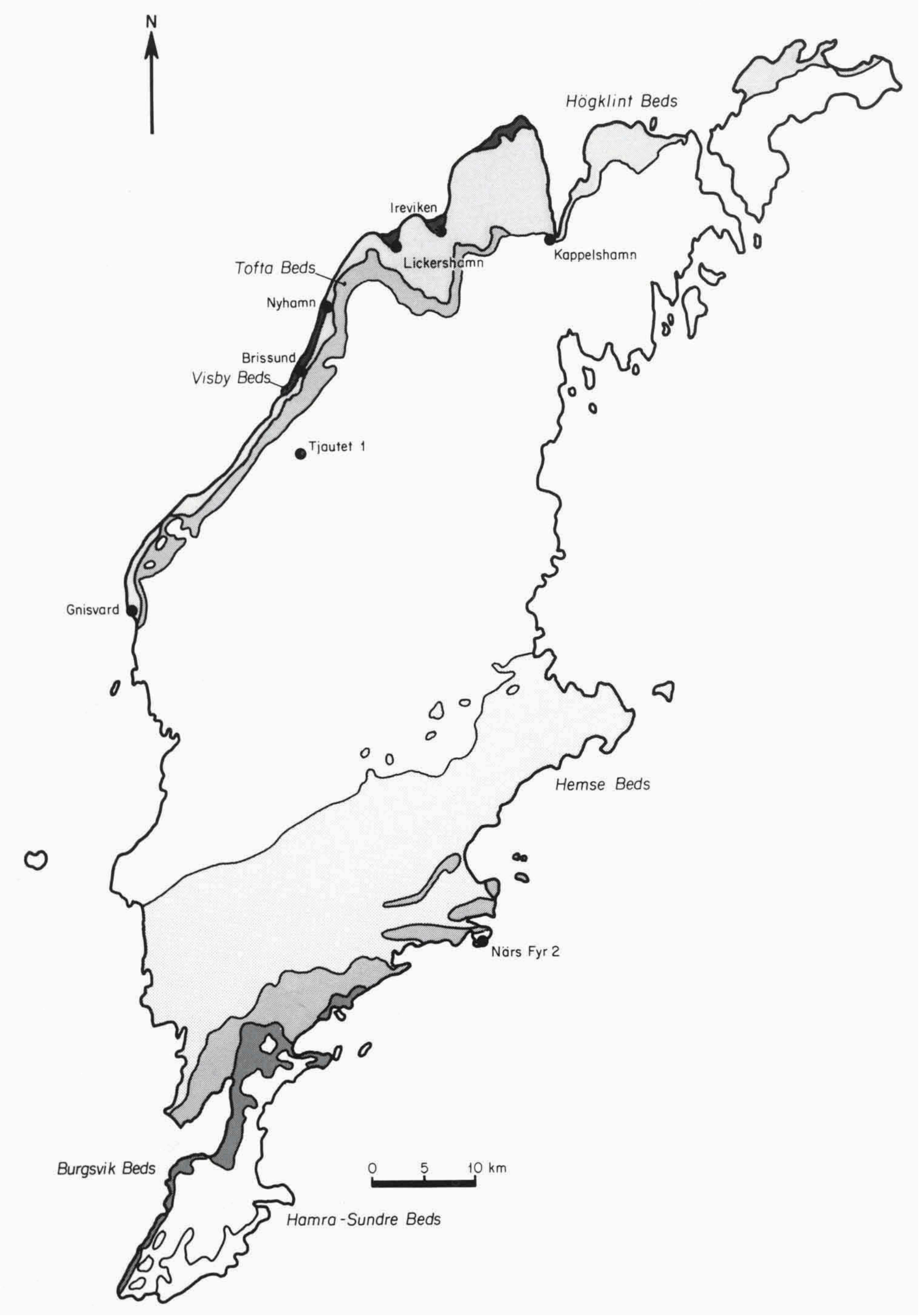


Fig. 5. Geological map of Gotland showing the localities.

the northwest coast of the island (Fig. 5), whereas younger strata crop out towards the southeast.

Various opinions on the stratigraphy of Gotland have been published since the pioneer study of Murchison (1846). For a historical review the reader is referred to Manten (1971). A concise and updated version of Hede's topostratigraphy is given by Laufeld (1974c). An inventory of reference localities in the Silurian of Gotland is also presented by Laufeld (1974a).

In this study a slightly modified version of the Hede stratigraphy (1960) is applied. The author has studied some key exposures of the Gotland sequence in order to place the observations on tabulates in a stratigraphical framework. These exposures are the cliffs along the northwest coast of the island between Nyhamn and Ireviken, and the quarries in the southern part of Gotland. The first give excellent insight in the lowest Silurian exposed on Gotland (Visby, Högklint Beds). The latter present a good opportunity to study part of the uppermost Silurian (Burgsvik, Hamra-Sundre Beds). The middle part of the sequence was not studied in detail.

STRATIGRAPHY OF VISBY AND HÖGKLINT BEDS

Lower Visby Beds — They are the oldest Silurian (Llandovery) deposits which crop out on Gotland. The rocks consist of bedded grey marlstones with intercalated nodules or lenses of grey, dense or fine grained argillaceous limestone. The boundary between the Lower Visby Beds and the underlying strata has not yet sufficiently been defined. The exposed part of the Lower Visby Beds has a thickness of about 10 m. These beds gradually pass into the overlying Upper Visby Beds.

Martinsson (1962, 1967) found that the Lower and Upper Visby Beds contain different beyrichiid ostracod faunas. However, the macrofauna of these beds does not warrant any subdivision (Spjeldnaes, 1959; Mori, 1968; Basset & Cocks, 1974; Klaamann, 1977). The rugose coral *Palaeocyclus porpita,* which is considered as characteristic of the Lower Visby Beds (Hede, 1940), was often seen by the present author in the uppermost part of the Upper Visby Beds. In the uppermost part of the Lower Visby Beds two bentonites occur (Laufeld & Jeppsson, 1976).

Upper Visby Beds — They consist of stratified grey marlstones with embedded irregular nodules, thin lenses and thin beds of grey, fine-grained, argillaceous limestone. The thickness of the Upper Visby Beds varies from 10 to 15 m. This variation in thickness is probably due to differential compaction by overlying Högklint reef limestone bodies. The thickness and number of limestone nodules, lenses and beds increases upwards from 2 to 15 cm, whereas the marl layers become thinner. In the upper part of the Upper Visby Beds small knoll, lens, or inverted cone shaped bioherms occur (Manten, 1971). They are mainly built up by tabulates and heliolitids, although some stromatoporoids and rugosa are also present. The grey biohermal limestone is argillaceous. Three bentonite beds are found in the Upper Visby Beds (Laufeld & Jeppsson, 1976). The uppermost bentonite (Fig. 6) occurs just below the boundary with the Högklint Beds, as defined by Laufeld (1974c).

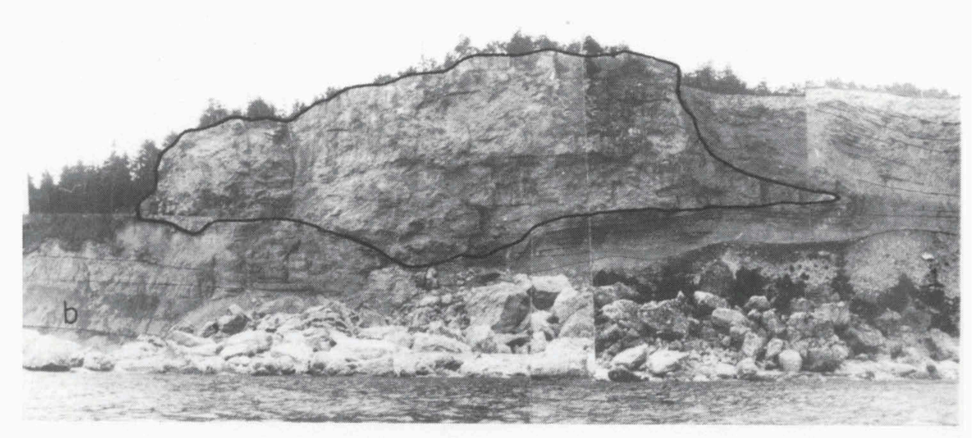


Fig. 6. View of Ireviken 3, Lower Visby-Högklint Beds. Two bentonite beds (b) are seen in the outcrop.

Högklint Beds — They consist of a variety of sediments. The maximum thickness is about 35 m. Around Visby, Laufeld (1974c) subdivides the Högklint Beds into four units, whereas in the southwestern area this is not possible because only few bioherms are found.

Högklint-a is about 15 m thick and consists of biohermal limestone with its lateral equivalents: grey crinoidal limestone (talus) and, at a greater distance, thin bedded grey argillaceous limestone with grey marlstone intercalations (mixed clastic carbonates).

Högklint-b is about 14 - 15 m thick and consists of bedded grey, often conglomeratic limestones, with intercalations of thin bedded brown argillaceous limestones.

Högklint-c is composed of bedded grey limestone, which is 4 - 5 m thick and locally rich in stromatoporoids.

Högklint-d, (the '*Pterygotus* and *Palaeophonus nuncius* Beds') is only present from Visby to Ireviken. It consists of 0.5 m grey-to-black marlstone and grey-red or speckled bituminous limestone with trilobites and eurypterid remains.

According to Hedström (1910) and Hede (1940) the Högklint Beds are discordantly overlain by the Tofta Beds, a limestone with a basal conglomerate and rich in algae. These strata would thin out towards northeast.

Hadding (1956) demonstrated that in core samples from northern Gotland (Smöjen, Storungs 1, Kappelshamn) a continuous sequence occurs from the Upper Visby Beds towards the overlying Lower Slite Beds. Even in sediments with algal lumps, indicating shallowest water depth in the succession, no sedimentary break is found. Therefore Hadding concluded that these sediments were deposited at a somewhat greater depth than synchronous sediments in the Visby area. In the latter an oncolitic/biostromal facies (Hede's Tofta Beds) developed while in the northern and eastern part of Gotland a biohermal limestone was deposited, similar to the strata underlying the 'Tofta Beds'. Such a difference in water depth already existed during early Visby times, as is demonstrated by Manten (1971). The present author includes, just as Hadding (1956) and Manten (1971), Hede's

'Tofta Beds' as a local facies in the uppermost Högklint Beds. Sediments of this facies indicate a shallow-marine-current environment (a mud-flat?), in which algal lumps and some sponge-biostromes occur.

REEFS IN THE VISBY AND HÖGKLINT BEDS

Terminology — The term *reef* in this paper is used, as defined by Heckel (1974), for a carbonate build up giving evidence of potential wave resistence or of turbulent water implying wave resistance and evidence of some degree of control over surrounding environments. A *biostrome* is, according to Heckel (1974), a bed of skeletal remains indicating no topographic relief.

Lower Visby Beds

During the time when the Lower Visby Beds were formed the depositional area of the sediments now exposed at the northwest coast of Gotland was situated in the deeper, more central part of an epicontinental sea. This situation corresponds with the maximum extension of the transgression in late Llandoverian - early Wenlockian times. This transgression coincided with an intensive volcanic activity in the Caledonians and Variscians (Barrandian area). Offshore conditions are indicated by the lithology which consists of limy muds and by the composition of faunas of both macrofossils (Hurst, 1975) and microfossils (Laufeld, 1974c; Gray, Laufeld & Boucot, 1974).

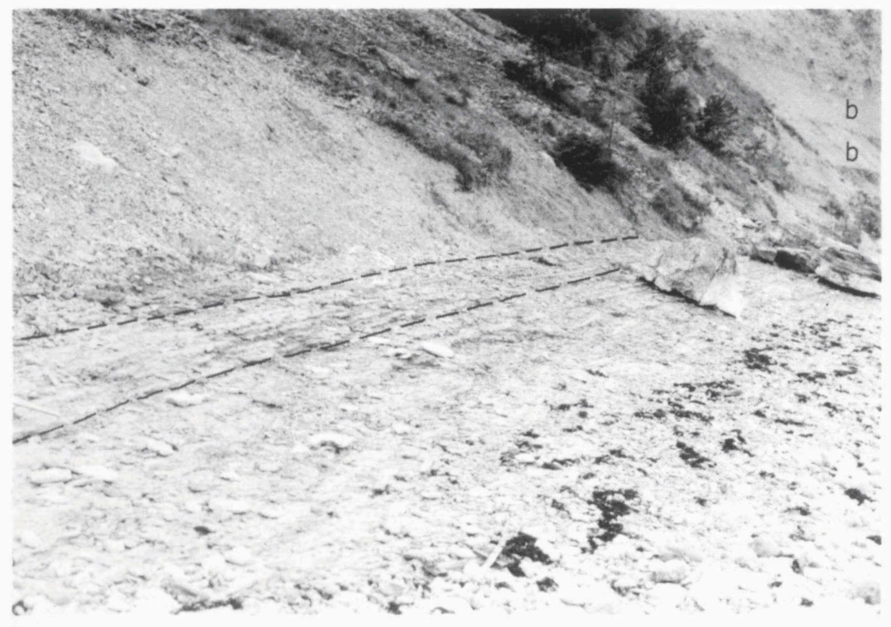


Fig. 7. View of the northwestern part of the *Catenipora-Favosites* biostrome at Ireviken 3. The outline of this biostrome is indicated by dashed lines. Two bentonite beds (b) are seen on the right.

The low-diversity brachiopod fauna is predominated by strophomenids *(Eoplectodonta transversalis* (Wahlenberg)) which are considered as characteristic of low energy environments. The fauna is comparable to the offshore *Stricklandia* benthic assemblage that Ziegler (1965) established for similar Llandoverian deposits in Wales and the Welsh borderland. These brachiopod data are corroborated by the occurrence of tiny ramose ectoprocts *(Clonopora gotlandica* Brood) and tabulates having high mud-tolerance such as halysitids.

Slow constant influx of terrigenous mud is probable. The bentonite beds prove that part of the mud is airborne volcanic matter. It is not clear how much of the lime content is detritic. It must at least have been partly derived from aragonitic fossils such as bivalves and cephalopods which are often found as badly preserved impressions. Diagenesis included concentration of calcareous matter in porous strata, resulting in the characteristic nodules and lenses of limestone now found in the Visby marls.

Small *Catenipora* biostromes are sometimes present in the upper Lower Visby Beds (Fig. 7). During heavy storms in the autumn of 1974 such a biostrome, normally covered by beach gravel, was swept clean at Ireviken 3. This biostrome has been studied in detail, because it is rich in *Favosites hisingeri* Edwards & Haime (Fig 8).

In the pioneering stage of this biostrome a sediment baffling community is found, which consists for about ninety percent of *Catenipora* colonies, forming a diachronous layer. *Catenipora maxima* Klaamann is, like most halysitids, adapted for colonizing muddy substrates. The corallite chains form large lacunae resulting in a load of the substrate as small as possible and preventing the colony from sinking into the mud. Moreover removal of mud from the surface of the chains was not difficult as the mud could be dumped into the lacunae which acted as sediment traps. Consequently, high mud tolerance of halysitids is explained by the morphology of the colony. Within the basal *Catenipora* bed, clusters of *Ketophyllum* are frequently found in life position together with small colonies of *Favosites hisingeri* Edwards & Haime and *Densastroma pexisum* (Yavorsky). Higher on, the *Ketophyllum* colonies are replaced by bushes of dendroid rugose corals. The press-button shaped rugose *Palaeocyclus porpita* (L.) frequently occurs. The morphology of this coral also suggests an adaption to muddy substrates. Just as in the pioneer community some brachiopods such as *Rhynchotreta cuneata* (Dalman) are found in this association together with some ostracods *(Craspedobolbina unculifera* Martinsson).

In the intermediate stage (the upper part of the biostrome) huge colonies of *F. hisingeri,* sometimes covering areas of about one square metre, are found in between but mostly on top of *Catenipora* layers. Small (maximum diameter of about 20 cm) discoidal or mushroom shaped colonies of alveolitids *(Subalveolites eichwaldi* Sokolov), heliolitids *(Heliolites* sp.) and stromatoporoids *(Densastroma pexisum* (Yavorsky)) regularly occur. In this *Catenipora-Favosites* association small brachiopods *(Rhynchotreta cuneata* (Dalman); *Atrypa reticularis* (L.)) and ostracods are more frequently found. This might have been caused by an increased mud sedimentation rate as is indicated by the occurrence of marly intercalations in the topmost part of the biostrome. In this stage of the biostrome, solitary rugose corals are rare (compound rugose corals do not occur).

In the overlying sequence of marls and marly limestones (bioclastic mudstones to bioclastic wackestones, with many crinoid ossicles and ostracod shells) larger coenostea of *Densastroma pexisum* (Yavorsky) are sporadically found. A

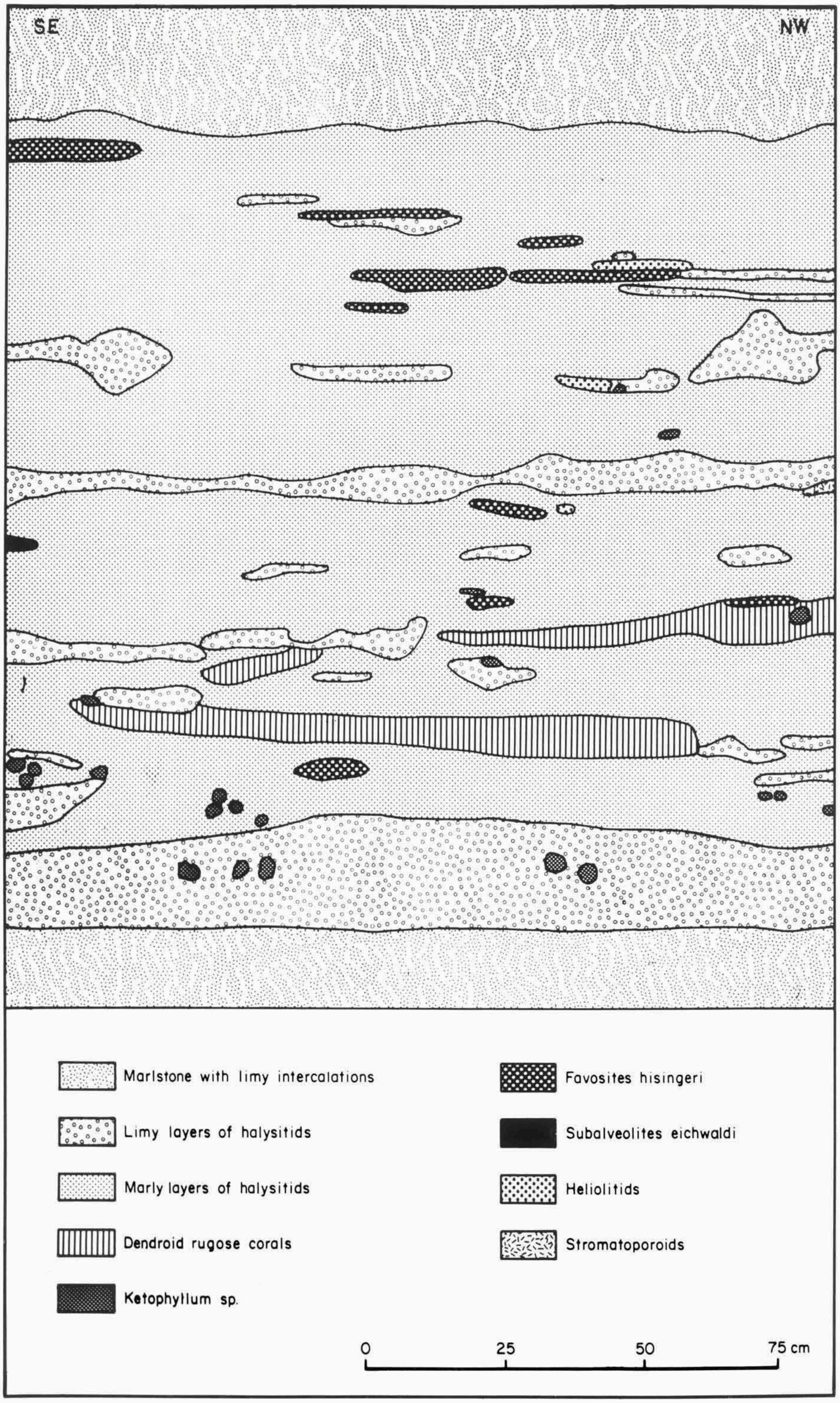


Fig. 8. Schematical section of the *Catenipora-Favosites* biostrome at Ireviken 3.

rich ichnofauna was found. Borings occurred in almost every stromatoporoid, heliolitid or tabulate colony. Endobionts *(Chaetosalpinx huismani* Stel) are frequently noticed in colonies of *Heliolites* (Fig. 9) and sometimes in those of *Favosites hisingeri*. Burrows sometimes occur in the surrounding beds. The fossils in this biostrome indicate low diversity and as most specimens were found in life position, the biostrome certainly developed below wave base. Moreover, a depth below the photic zone is plausible as fossil algae are not observed.

Low diversity in this biostrome may also be influenced by the occurrence of volcanic-ash falls, a dozen of which are demonstrated (Laufeld & Jeppson, 1976) by silicified beds and bentonites in the Visby and Högklint Beds. However, the occurrence of more less-extensive ash-falls in the area is plausible.

Upper Visby Beds

In the time when the Upper Visby Beds were deposited, the sedimentation pattern gradually changed as is indicated by the increasing number of limestone beds, with upwards increasing thickness. Early during deposition of the Upper Visby Beds wave action may periodically (storms?) have influenced the seafloor by washing out the marl, leaving behind a carbonate skeletal gravel. This substratum was colonized by a tabulate assemblage similar to the one described before and having mud tolerance comparable to the communities described before. Mud deposition continued during the development of this pioneer community as is indicated by the marly matrix of the reefs. Manten (1971) estimated that the marly matrix of the carbonate build ups constitutes about 40 - 50% of their total volume.

On account of this marl content Manten (1971) subdivided the reefs exposed at the northwest coast of Gotland in 'Upper Visby' and 'Hoburgen' reef

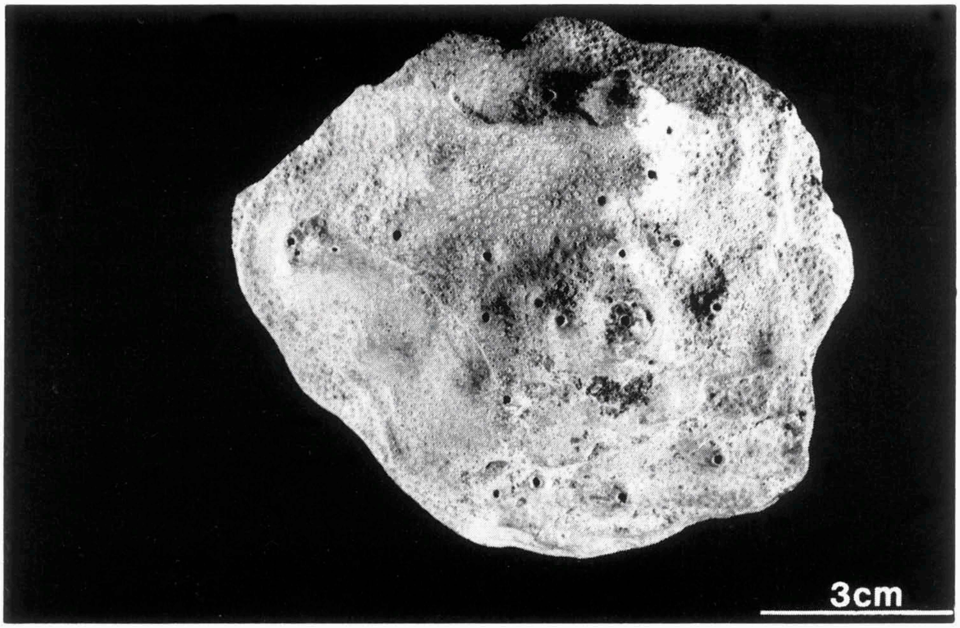


Fig. 9. *Heliolites* colony with *Chaetosalpinx* trace fossils. The heliolitid apparently formed small hills around the apertures of the tubes. Lower Visby Beds, Ireviken 3, RGM 243 722.

types. The shapes most frequently found in the Upper Visby reefs is a knoll (in the lowest part of the reefbearing strata), an inverted cone (in the middle part) and a lens near the basis of the overlying Högklint Beds.

When the Upper Visby Beds were formed the shoaling of the depositional area reached a critical stage during which the seafloor came within the wave-base range. This event is recorded in the fauna and in the reefshape. According to Manten (1971) the dominant reefbuilders of the Upper Visby reefs are tabulates, such as halysitids, favositids and heliolitids. These forms have, as noted above, a high mud tolerance. Stromatoporoid sponges which have a lower mud tolerance (Lecompte, 1970), are mostly absent or rare. The knoll-shaped tabulate build ups could be considered as the first large scale reef growth in the area. In these reefs a sediment baffling pioneer community was able to develop under rather adverse conditions. However, local shifts in mud influx destroyed the pioneer assemblages because the tabulates were not able to get rid of the mud anymore. This process may have caused the knoll-shaped outline of the reefs in the lowermost Upper Visby Beds. Similar knoll-shaped reefs are sometimes seen between the Högklint patch reefs (Fig. 10). Due to the persistent shallowing of the basin, the environment became more favourable to reef growth leading to the development of the inverted cone shaped reefs. Pioneer communities in these reefs could cope with the mud sedimentation. However, mud influx remained high and the reef building fauna had to grow in an upwards direction. This is indicated by the dimensions (see Manten, 1971) and inverted cone shape of these carbonate build ups.

Late during the deposition of the Upper Visby Beds, however, conditions rapidly became favourable to extensive reef growth and patch reefs (the socalled lens-shaped Upper Visby reefs of Manten, 1971) developed. In these reefs a palaeoecological succession (Copper, 1974) is seen from the sediment-baffling

Fig. 10. Reef knoll in mixed clastic carbonates NW of Snipklint, Högklint Beds.

pioneer stage (= quiet water stage of Lowenstam, 1957) to the mature stage (= rough water or wave resistent stage of Lowenstam, 1957).

Högklint Beds

Reef growth continued and culminated in the early period of deposition of the Högklint Beds when huge algal-sponge reefs were formed (maximum thickness: 20 m, length: several hundred metres; Hadding, 1950). These reefs are beautifully exposed at the present northwest coast of Gotland and in some cliffs of *Littorina* age (Snäckgärdsbaden, Brissund) and of *Ancyclus* age (Galgberget) in the same region.

During 'Upper Visby' times reef growth started, as is demonstrated by Manten (1971) in the area S of Visby. In early 'Högklint' times patch reefs are found in the whole area between Gnisvard and Hallshuk.

Due to the increasing niche differentiation in the reef ecosystem, maximal diversity is reached in the Högklint reefs. These do not have a marly matrix. Stromatoporoid sponges and algae (Hadding, 1950; Rutten, 1958) are the most conspicuous frame builders; tabulates are subordinate. The shape of the stromatoporoid coenostea, found in this environment, is highly variable. Moreover, as a rule these colonies are larger than similar shaped forms from the mixed clastic carbonates, which are found in between the reefs. In the latter conical, bell or dome shaped coenostea predominate. Mori (1969) found that a characteristic stromatoporoid fauna, dominated by *Actinodictyon tenue* Nestor, lived in the reef core and talus. The fauna of the mixed clastic carbonates in between the reefs is predominated by *Densastroma pexisum* (Yavorsky), *Clathrodictyon simplex* (Nestor) and *Pseudolabechia hesslandi* Mori.

Niche differentiation is also indicated by the tabulate fauna. The speciation is striking in this Wenlockian reefzone. Klaamann (1964) showed that the optimum for Silurian favositids occurred during Wenlock times. In a later (1977) paper he noted the similarity between the Wenlockian tabulate fauna of Estonia and Gotland. New forms like *Favosites desolatus, F. oculiporoides* Sokolov, *F. forbesi* Edwards & Haime, *F. hisingeri,* and *Pachypora lamellicornis* (Lindström) are found together with older forms like *Paleofavosites asper* (d'Orbigny) with solenial growth and *Syringolites kunthianus* (Lindström). Although I agree that a more diverse favositid fauna was developed I have severe doubts about the high number of new species supposedly present in the *Favosites forbesi* group. In my opinion, niche differentiation resulted in various ecotypes.

The brachiopod fauna (Hurst, 1975) of the Högklint Beds indicates that several level-bottom communities occurred, including the ones being indicative of nearshore to offshore clastic settings in similar deposits in Wales and the Welsh borderland. *Dicoelosia verneuiliana* (Beecher), which is considered to be indicative of quiet water offshore communities, occurs in both the reef facies and the mixed clastic carbonates of the Högklint Beds. Consequently, *D. verneuiliana* (Beecher) probably had a wider tolerance than most *Dicoelosia* species.

The rise of the huge patch reefs in the Högklint Beds caused the development of several environments: reef, reef talus and mixed clastic carbonates between the reefs. In the uppermost part of the patch reefs, cross bedding is sometimes seen (e.g. at Brissund). Small marly intercalations, which probably were pools in the reefs, often occur. When the lateral parts of the patchreefs, which are rich in crinoids, are exposed in the cliff section the reefs apparently are separated in smaller bodies due to marly intercalations (e.g. at Lusklint).

The structure of the talus halo around a patch reef is well exposed in the first (Lusklint) and third reef of the cliff coast between Nyhamn and Stenkyrkehuk. The patch reefs mentioned above developed on top of marly sediments (the Visby Beds). These heavy reefs sunk into the muddy bottom and load structures formed. The results of this synsedimentary process were fixed by lithification. They are well exposed in both the submarine platform and the cliff coast. In the coastal profile downbending of the marl and marly limestone layers under, and a raised rim of the same beds near the reefs is seen (Fig. 12). In the recent foreshore erosional platform, reef distribution is indicated by shallow circular - ellipsoidal depression structures, the so-called Philip-structures (Fig. 13). The distribution (Fig. 11) of the Högklint reefs near Kappelshamn was described by Hadding (1956). The Högklint reefzone is at least 10 km wide. It may have run more or less parallel to the coast.

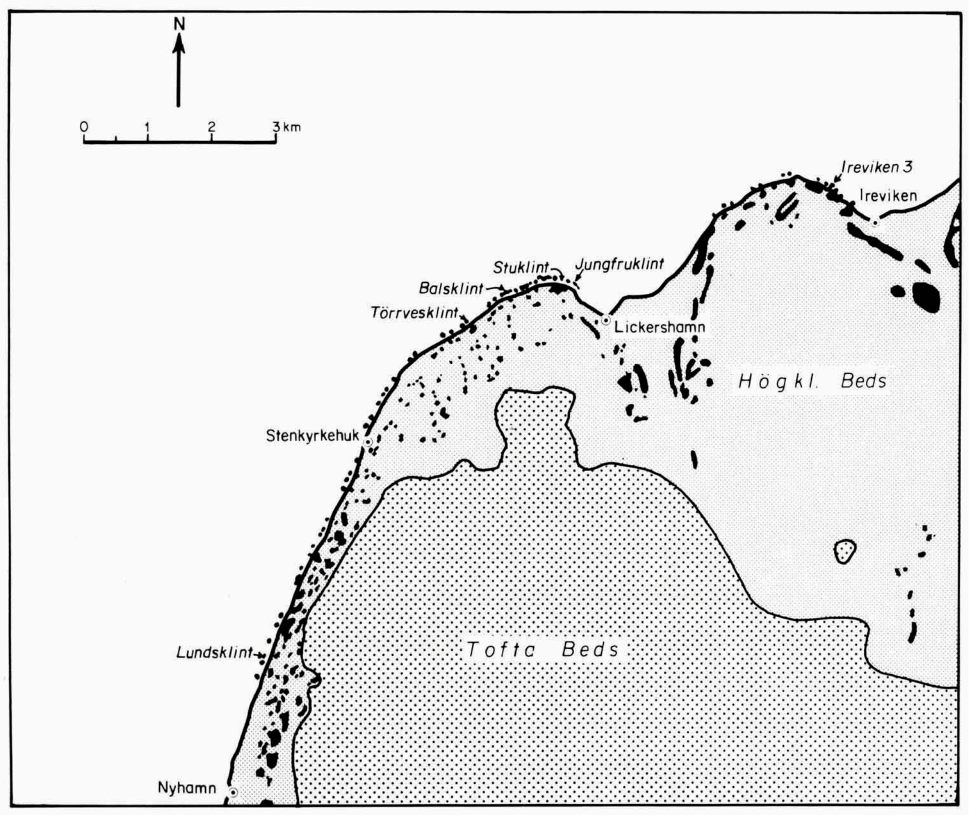


Fig. 11. Northwest coast of Gotland between Nyhamn and Ireviken, black: reefs of Högklint age; black dots: offshore concentric and semicircular depression structures (from Eriksson & Laufeld, 1978, p. 11 - 12).

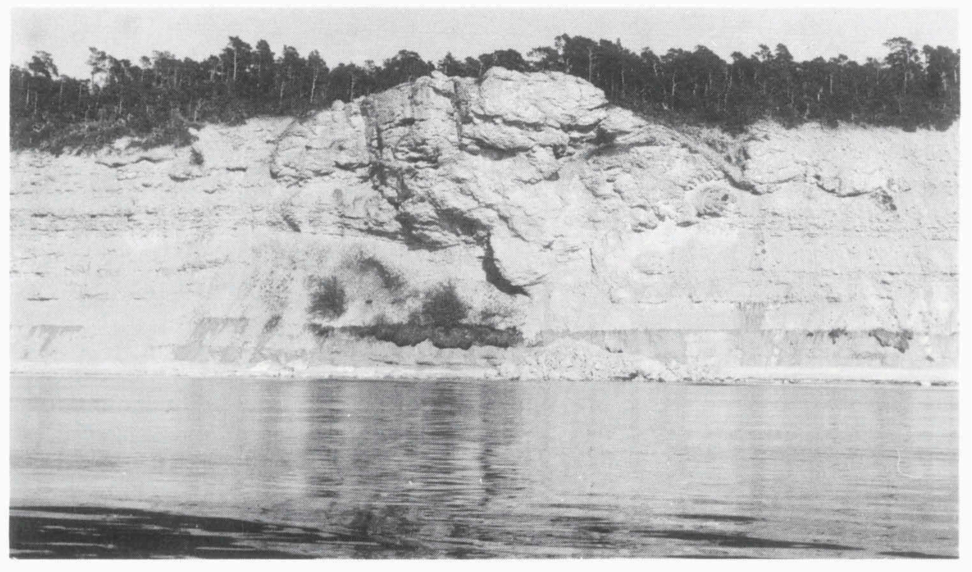


Fig. 12. Photograph of the cliff 360 m NNE of Lundsklint. Note the sagging of the reef as indicated by the two bentonite beds in the lower part of the section. A slump (?) is seen in the SSW part of the reef.

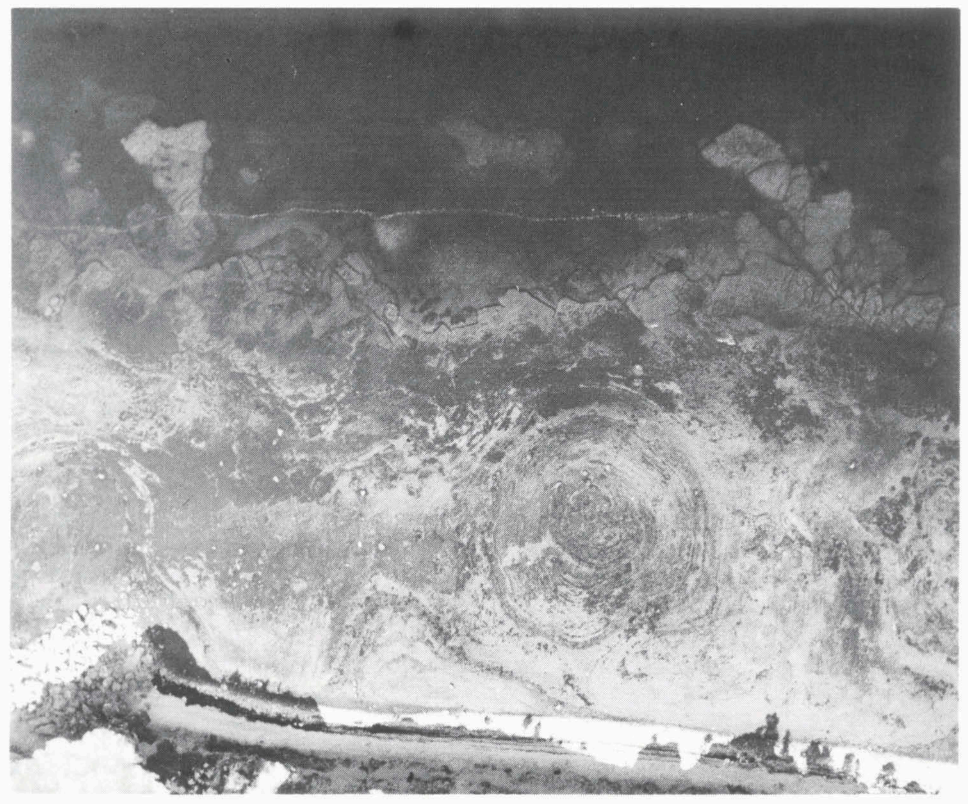


Fig. 13. Circular and semicircular depression structures between Predikstolan and Balsklint. Joints are seen in the wave-cut platform. Approximate scale 1 : 15 000. Aerial photograph by Arne Philip (1973-08-17, 12:10), photo courtesy of Dr S. Laufeld, Stockholm, Sweden.

STRATIGRAPHY OF SOME LUDLOVIAN DEPOSITS ON GOTLAND

Hemse Beds

The lithology of the Hemse Beds suggests a complicated pattern of facies types. In the north, the Hemse Beds are composed of a limestone sequence which Hede (1960) subdivided into five units.

The basal Hemse-a consists of thinly bedded, fine grained, grey limestone with some biostromes, rich in stromatoporoids. The unit, only a few metres thick, is rich in crinoids and locally characterized by the bivalve *'Megalomus' gotlandicus* Lindström.

Hemse-b is a thinly bedded, grey, argillaceous limestone interbedded with thin layers of blue-grey marlstone. This unit is rich in brachiopods and ostracods; it is 1 - 1.5 m thick (Manten, 1971).

Hemse-c, about 15 m thick, is built up by thin bedded, grey or brown, dense or fine grained more or less argillaceous limestone.

Hemse-d is about 25 m thick and is composed of bedded, grey or red limestones, mainly biostromal or crinoidal in character.

The topmost Hemse-e, Hede's (1960) Millklint Limestone, is composed of thin-bedded, fine-grained grey limestone. The unit above is about 6 m thick.

To the south and south-west the above described limestone facies is replaced by a more or less synchronous marlstone facies, the 'Hemse Marl'. Although faunal differences are known (Hede, 1927; Martinsson, 1962; Hurst, 1975; Laufeld, 1974c) no subdivision of this marl is made. The Hemse Marl is overlain by a silty, dolomitic limestone, extremely rich in *Dayia navicula* (Sowerby), the uppermost deposit of the Hemse Beds.

The Hemse Beds, about 100 m thick, were laid down on a shallow epicontinental shelf (Laufeld, 1974b). The lithology and palaeobiology of these sediments suggest that early during deposition of the Hemse Beds the western part of this shelf was deeper than the eastern part. In the former graptolitic shales occur, while in the latter shallow water, sometimes biohermal, limestones are found. The biohermal limestone is part of an ENE - WSW running zone of bioherms (Manten, 1971). Epeirogenetic movements late during deposition of the Hemse Beds caused shoaling of the area and according to Manten (1971), a new east - west direction of the depth contours. However, Laufeld (1974b) demonstrated that during that time the direction of the shore line was about N57°E. Local deviations of this direction are found in the western (NE - SW), central (ENE - WSW) and easternmost part (NE - SW) of Gotland.

Hamra-Sundre Beds

They have been grouped as one stratigraphical unit by Martinsson (1967), Mori (1970) and Manten (1971), since the lithological subdivision of Hede (1960) is not warranted by the fauna. The basal part of the Hamra-Sundre Beds consists of an argillaceous, mostly indistinctly stratified grey to light-brown algal limestone. Stel & de Coo (1977) found that the oncolitic grainstone and poriferan boundstone of this facies were deposited in a shallow marine current environment. On the Hoburgen Peninsula, this algal limestone is overlain by a grey to brownish grey, stratified, argillaceous limestone intercalated with grey marlstone. In the upper and main part of the Hamra-Sundre Beds three distinct facies are found: in the southwestern part of the Hoburgen Peninsula a biohermal limestone (1), surrounded by bedded, mainly crinoidal, limestone (2), and in the northeastern part an argillaceous limestone, intercalated with marlstone and some fetid limestone with lenses of stromatoporoidal limestone (3).

Correlation of these sediments with similar beds in the Burgen-Närsholm area is problematic. This correlation problem was investigated by scuba diving (Mr J. van Dijk and Miss G. Klein Nulend) off the exposure Närs Fyr 2. This exposure was chosen because of the following considerations:

(1) In the topostratigraphy of Hede (1960) the boundary between the Burgsvik Beds and the overlying Hamra-Sundre Beds is fixed just below the oncolitic boundstone.

(2) Stel & de Coo (1977) demonstrated a characteristic lithological sequence in the uppermost Burgsvik and lowermost Hamra-Sundre Beds. The transgressive sequence starts with a fine grained quartz sandstone followed by a variable unit composed of alternating calcareous quartz sandstone and bioclastic quartz sandstone (with *Pteronitella* valves), an oolite passing in a pisolite and an oncolite with small biostromes.

(3) The characteristic sequence was easily traced to Innerholmen, as already mentioned by Munthe (1910), and to Ronehamn 1 (Laufeld, 1974a).

(4) Trask's parameters of the sandstone in the clastic dikes on the southeastern shore of Närsholm (Larsson, 1975) correspond with those found by Stel & de Coo (1977) on the Hoburgen Peninsula.

(5) Correlation of Stel & de Coo's sections Burgen 6 and 7 with Uddvide 1, 2 and Rovalds 3 was not possible because of pronounced lithological differences.

Although the diving project was impeded by stormy weather and no section could be measured, the complete sequence, as defined above, was observed below the grey reef limestone now exposed in small rauks. Moreover, large (up to 20 cm in length) fragments of the basal Hamra-Sundre oncolite were collected on the beach together with smaller fragments from the Upper Burgsvik oolite. These observations and the overall development of the Upper Burgsvik and Hamra-Sundre Beds (see Manten, 1971; Stel & de Coo, 1977) together with the lithology of the sediments in the Burgen exposures seem to warrant an attribution of the Burgen-Närsholm reefs to the Hamra-Sundre Beds. The oncolites in Burgen 6 and 7 are considered as an oncolitic bank in the Hamra-Sundre Beds. During deposition of the Hamra-Sundre Beds the transgression, which started in late 'Burgsvik' times, continued and a new roughly SSW - NNE running reef zone developed. In this reef zone, stromatoporoids are the dominating reef builders. Cracks occurred as a result of the instability of the underlying sandstone beds.

Morphology and systematics

MORPHOLOGY

Although the current interpretation of tabulates as corals has been widely accepted since this attribution was postulated by Edwards & Haime (1849), data about sclerosponges discovered by Kirkpatrick (1911) suggest an attribution of tabulates or groups of tabulates (e.g. favositids) to the sponges (Hartman & Goreau, 1975; Flügel, 1976; Stel & de Coo, 1977). As a consequence of the coral interpretation, the descriptive terminology usually applied to recent corals has also been applied to tabulates (Hill & Stumm, 1956; Sokolov, 1962; Schouppé & Oekentorp, 1974). In the present paper this terminology is also used but only in a purely descriptive sense.

The form of the skeleton of tabulate colonies varies widely and depends on the shape and arrangement of the corallites. A colony may be a laminar expansion, a domed, a spherical, a hemispherical, a nodular, or an irregular body. It may also be slenderly or coarsely branching with either cylindrical or flat branches. Cylindrical corallites are found in syringoporines and auloporines; polygonal corallites occur in favositids. Skeletons of the latter are classified (Oliver, 1968) in four morphological types.

(1) Massive: lenticular, hemispherical, or irregular in shape.
(2) Laminar: thin sheets or layers, frequently encrusting.
(3) Ramose: more or less cylindrical branches.
(4) Foliose: flat laminar branches.

Corallites in the above mentioned colonies may be:

(1) Cerioid; if the corallite walls are closely pressed together and in contact on all sides. The polygonal form is caused by mutual pressure (Thompson, 1917).
(2) Meandroid; if the walls separate strings of more or less confluent corallites.

As a result of optimal space utilization corallites in favositids are mostly hexagonal in transverse section. Their diameter ranges from less than 1 mm to about 5 mm. In this paper the wall is defined as the lateral skeletal deposit of the organism living in a single corallite. The skeletal formations between adjacent corallites, which mostly are described as the corallite 'wall', actually consist of two walls as defined above. Therefore this 'wall' is labelled as the double-wall. A complex terminology of double-wall structures and microstructures has been developed by various authors. For a detailed review the reader is referred to the papers of Schouppé & Oekentorp (1974) and Stel (1978b).

As opinions about the primary calcitic (Sokolov, 1962; Stel, 1978b) or aragonitic (Sorauf, 1971; Schouppé & Oekentorp, 1974) nature of the tabulate skeleton are controversional, the author considers for the moment systematics mainly based on this feature (Dubatolov, 1959) as questionable.

Pores, circular or oval ellipsoidal shaped connections between neighbouring corallites, are a characteristic feature of many tabulates, such as Favositidae (as defined by Sokolov, 1962). In favositids two types of pores are present:

(1) Corner pores, which show a characteristic undulation of the wall (Oekentorp & Schouppé, 1969). They are typical of paleofavositids. In such paleofavositids with small (< 1 mm) corallites, corner pores are arranged in funnel-shaped parts of the corallite and so-called 'solenia' develop (Stel & Oekentorp, 1976).
(2) Mural pores, not causing the wall to undulate. These are typical of favositids.

The only type of skeletal transverse elements are tabulae; horizontal or saucer shaped floors. Sorauf (1974) demonstrated that the formation of tabulae occurred through centripetal growth, as in scleractinian corals (Sorauf, 1974) and sclerosponges (Kirkpatrick, 1911).

Radially arranged longitudinal elements in the corallites are the septa, the spines and the squamulae. Continuous septa, which would be homologous to the septa in scleractinian and rugose corals are found in some Lower Palaeozoic tabulates like theciids. In middle and late Palaeozoic times spines and/or squamulae predominate. As the occurrence of spines and/or squamulae is controlled to a high degree by ecological conditions (see Swann, 1947; Philips, 1960; Oekentorp, 1975) the author considers this feature as taxonomically unimportant.

SYSTEMATICS

Classification of the tabulates is handicapped to a high degree by the absence of directly comparable living organisms. The biological significance of morphologic structures in tabulates is not clearly defined and as a consequence the taxonomic hierarchy of features is unsettled. Skeletal structures are mostly interpreted by indirect means. This provides the motive for many controversial views and frequently results in a more or less artificial classification. Current systematics of tabulates is again influenced to a high degree by the interpretation of the latter as corals. In the early period systematics of favositids was based on general morphologic features such as colony form, size of the corallites, presence or absence of septal spines, etc. As a consequence only few species were distinguished by authors such as: Goldfuss (1826), Edwards & Haime (1850), Hall (1852), Nicholson (1879), Lindström (1896) and Počta (1902).

Tripp (1933), studying extensive collections of favositids from Gotland, introduced his 'form-complexes' in order to demonstrate interactions between morphologic characters. Tripp explained his three basic colony forms (cylinder, plate and sphere) by 'growth impulses' (Wachstumsimpulse) which are more or less based on the regular increase that was described by Beecher (1881) from colonies of *Michelinia convexa* d'Orbigny. If these 'growth impulses' were directed in one, two, or three dimensions, the three colony forms would be the result. Tripp distinguished three important 'form complexes' *(Favosites asper, F. gotlandica* and *F. hisingeri)* in the Silurian of Gotland. However, each 'form complex' was subdivided in some 'form ranks' which in turn were divided in 'groups'. Although Tripp correctly supposed that a wide range of colony morphotypes would be present within a species, his division of the favositid fauna in 'form complexes' is influenced to a high degree by his admittance of descriptive rather than phyletic taxonomy.

Since Sokolov (1950 - 1955) published his studies on tabulates from the Baltic area his quantitative approach has become generally applied. In this approach, subdivision of the Tabulata in groups (suborders and families) is mainly based on colony form. However, recent studies of Grauss (1977), Morton (1974) and Wijsman-Best (1974) demonstrated a close relationship between several ecological factors and skeletal morphogenesis in recent massive corals. Grauss & MacIntyre (1976) demonstrated that light adapted growth in *Montastrea annularis* is reflected in three depth-related colony morphotypes: a hemisphere (depth 1 m), a column (depth 20 m), and a plate at a depth of 30 m.

Differentiation at the genus level is mainly based on a combination of such morphologic characteristics as arrangement of pores, the development of septal formations, etc. Species differentiation is mainly based on such quantitative features as diameter of the corallite, thickness of the wall, pore-diameter, etc. and qualitative characteristics as microstructure of the wall, degree of septal formations, etc. As a consequence of this quantitative approach a considerable number of new 'species' and 'genera' has recently been described and identified (Klaamann, 1962; Stasinska, 1967; Stel, 1975; Nowinsky, 1976).

After studying erratic favositids (Stel, 1975), I found that the range of quantitative and qualitative features, currently applied to identify favositids, often is too narrow to allow for ecophenotypic responses of the colony. To elucidate this problem some selected samples of favositids from the Silurian of Gotland were studied in detail.

Morphology of *Favosites hisingeri* Edwards & Haime, 1851

In 1936 Jones established the new name *Angopora,* for a genus previously (1930) described under the preoccupied name *Laminopora.* He assigned to this genus all tabulates, resembling *Favosites* but with discontinuous lamellar septa. The type species *Angopora hisingeri* was obtained from the Upper Visby Beds at Högklint, south of Visby (Gotland). When discussing the affinities of Edwards & Haime's (1851) *Favosites hisingeri,* Jones (1936) concluded that more than one favositid species could be characterized by the rather vague descriptions of these authors. He therefore redefined *F. hisingeri,* and chose the specimen figured by Edwards & Haime (1855, pl. 61, fig. 1) as the lectotype. Similar specimens with lamellar septa only, and lacking the septal spines observed in *F. hisingeri* Edwards & Haime, were labelled as *Angopora hisingeri* Jones. However, he does not definitively reject the possibility that these species could be synonyms.

Stasinska (1967) invokes a difference in septal microstructure between *Thecia* Edwards & Haime, *Angopora* Jones and her new genus *Kiaerites.* The latter genera were assigned to a new family, the Angoporidae.

Oekentorp (1970) stressed the difference of the dark line in the septa and wall of *Thecia* and *Angopora.* In theciids these dark lines are in contact suggesting that both septum and wall were formed simultaneously, whereas this was not observed in *A. hisingeri.* Oekentorp grouped *Angopora,* together with several other tabulates like *Kiaerites* Stasinska, in the Angoporinae Stasinska, which he considers as a subfamily of the Theciidae Edwards & Haime.

Klaamann (1970), in studying the variability and taxonomic position of *A. hisingeri,* noticed a high degree of variation in the morphology of the wall and the septal formations. As periodically increased development of the septal formations and the accompanied increased wall thickness did not simultaneously develop all over de colony, Klaamann suggested that this feature would be genetically controlled. Klaamann presumes that *Angopora* might be related to *Mesofavosites* Sokolov; he united *Angopora* and *Kiaerites* in the Angoporinae Stasinska, which he considers as a subfamily of the Favositidae Dana, sensu Sokolov, 1962.

An extensive collection of *F. hisingeri* colonies was taken from the biostrome temporarily exposed at Ireviken 3 (Figs. 6 - 8) and from the beach between Nyhamn and Ireviken. Early during deposition of the Visby Beds this biostrome was situated below wave base as is indicated by the life position of the tabulates and heliolitids. The biostrome developed under high stress conditions. This is suggested by the low diversity of the fauna; moreover, a depth below the photic zone is indicated by the lack of algae.

Favosites hisingeri Edwards & Haime, 1851

1851 *Favosites hisingeri* sp. nov. — Edwards & Haime, p. 240, pl. 17, fig. 2.
1855 *Favosites hisingeri* Edwards & Haime — Edwards & Haime, p. 25, pl. 61, fig. 1
1930 *Laminopora hisingeri* sp. nov. — Jones, p. 35.
1933 *Favosites hisingeri* Edwards & Haime — Tripp, p. 109, pl. 13.
1936 *Favosites hisingeri* Edwards & Haime — Jones, p. 17 - 18.
1936 *Angopora hisingeri* sp. nov. — Jones, p. 18 - 19, pl. 2, figs. 4 - 7, pl. 3, figs. 1 - 2.
1937 *Favosites hisingeri* var. *regularis* var. nov. — Ruhkin, p. 31, pl. 3, figs. 1 - 5.
1951b *Favosites hisingeri* Edwards & Haime — Sokolov, p. 94 - 98, pl. 37, figs. 4 - 5.
1952a *Favosites multicarinatus* sp. nov. — Sokolov, p. 41 - 43, pl. 15, figs. 1 - 2.
1952a *Favosites hisingeri* var. *regularis* Ruhkin — Sokolov, p. 54 - 55, pl. 21, figs. 1 - 3.
1962a *Favosites effusus* sp. nov. — Klaamann, p. 42 - 44, pl. 12, figs. 1 - 5.
1962a *Favosites vicinalis* sp. nov. — Klaamann, p. 44 - 46, pl. 10, figs. 3 - 4.
1964 *Favosites hisingeri* Edwards & Haime — Klaamann, p. 65.
1964 *Favosites multicarinatus* Sokolov — Klaamann, p. 73 - 74.
1967 *Angopora hisingeri* (Jones) — Stasinska, p. 61 - 62, pl. 10, figs. 1 - 3.
1970 *Angopora hisingeri* (Jones) — Klaamann, p. 62 - 68, pls. 1 - 4.
1971 *Angopora hisingeri* (Jones) — Klaamann, p. 356 - 358, pl. 1, figs. 1 - 3.
1971 *Angopora parva* sp. nov. — Klaamann, p. 358 - 359, pl. 1, figs. 4 - 5.
1975 *Favosites multicarinatus* Sokolov — Stel, p. 77 - 78, pls. 39 - 40.

Diagnosis of Edwards & Haime (1851, p. 240) — Polypier à surface subgibbeuse; calices peu inégaux, séparés par des murailles un peu épaisses, en général assez régulièrement polygonaux, larges à peu près d'un millimètre et demi; 12 cloisons subégales, médiocrement épaisses, arrivant presque jusqu'à l'axe des polypiérites, formées par des poutrelles bien développées et légèrement arquées; planchers minces, assez serrés, horizontaux ou un peu flexueux.

Description of Angopora hisingeri Jones (1936, p. 18 - 19) — The corallum is typically discoid, of irregular shape, and attains a large size but usually no great thickness, though hemispherical and pyriform colonies are also found. The underside is flat and is covered by a stout, concentrically wrinkled epitheca; whilst the distal surface, as a rule, is unevenly developed, rising into knobs and ridges. The coral is built up of superimposed layers, which correspond to the strong annulations on the basal epitheca and thus suggest pauses in growth,

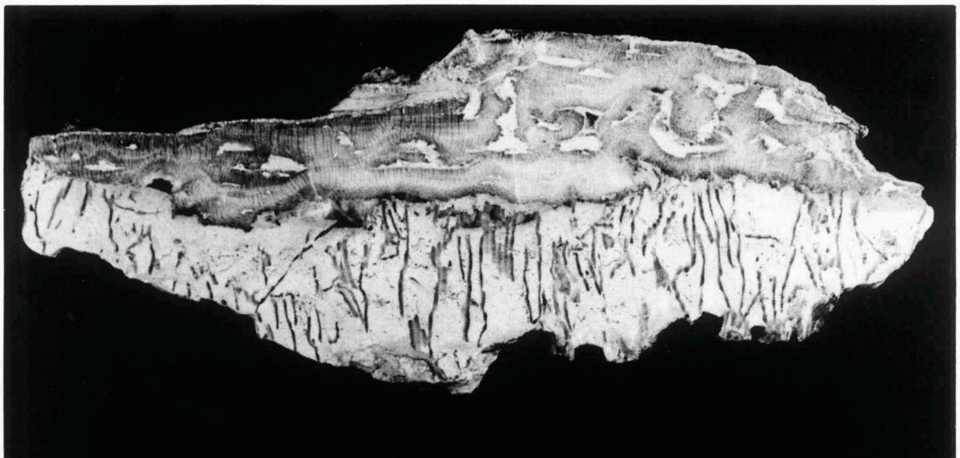


Fig. 14. Overgrowth of halysitid by a foliaceous colony of *Favosites hisingeri*, Lower Visby Beds, Ireviken 3, RGM 243 731.

followed by the formation of a new layer of coral, which overlaps irregularly the layer previously formed. The corallites, which are of fairly uniform size, have generally six sides and attain a diameter of about 1 mm; the walls are moderately thick. The septa — about 12 in number — are very short lamellar septa, which, however, do not necessarily persist through the entire length of the corallite and, in fact, appear to be entirely absent in places. The axial edges of the lamellae break up into long spines which reach inwards halfway, or more than halfway, towards the axes of the corallites, and which usually curve distally. The mural pores are small, rather widely spaced, and are found usually in two rows which are generally placed near the angles. The tabulae are complete and numerous, seven to nine in a space of 3 mm.

Description — The form of the colonies is highly variable and ranges from an expanding succession (max. area 1 m^2; max. thickness 25 cm) of thin sheets to thick massive colonies. The morphology of the colonies found in the biostrome at Ireviken 3 is influenced to a high degree by ecological factors. Colonies were never observed in the pioneering stage of the biostrome, during which a sediment baffling community occurred. Larvae could, just as in all tabulates, only settle upon a hard substratum. *Favosites hisingeri* is frequently overgrowing halysitid colonies in thin (some millimetres to about 2 cm) sheets. It appears that the halysitids were competitively overgrown (Fig. 14). This is suggested by the continuation of growth in not overgrown parts of the halysitid. This shows that the latter was not killed by abiotic factors, like an increased sedimentation rate or a volcanic-ash fall, prior to the settlement of the *F. hisingeri* larvae. Moreover competitive overgrowth is also indicated by ridges of *Catenipora* corallites in the peripheral parts of this favositid (Fig. 15). Topographical differences in the substratum caused only small growth irregularities in the colony which look like small hills (Fig. 16). The basis of the colony is covered by an epitheca with beautifully preserved growth bands (Fig. 17). Mushroom shaped colonies (Fig.

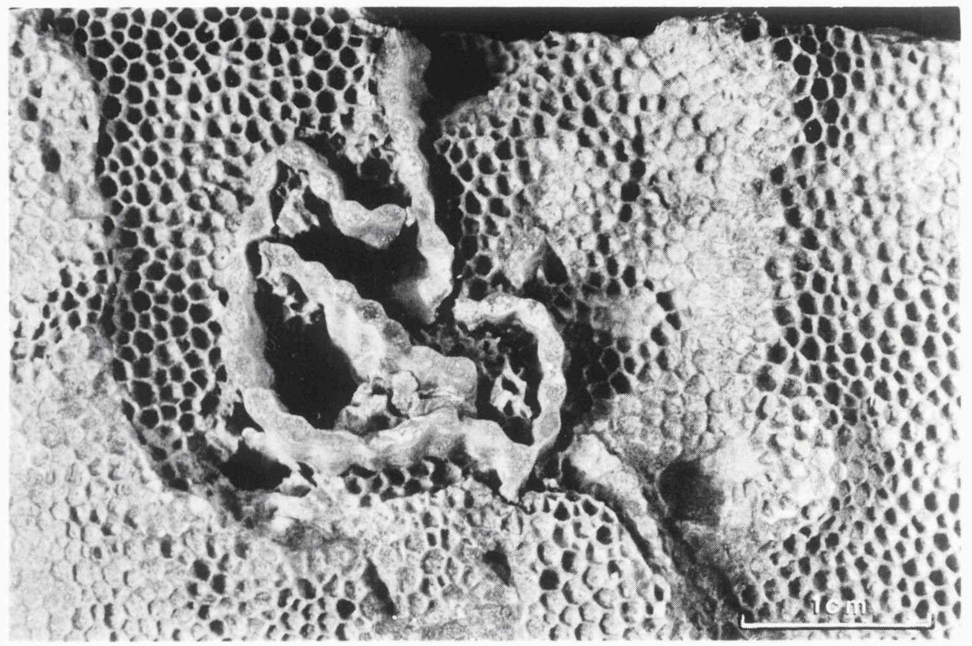


Fig. 15. Competitive overgrowth of a *Catenipora* colony and a colony of *Favosites hisingeri*, Lower Visby Beds, Ireviken 3, RGM 243 739.

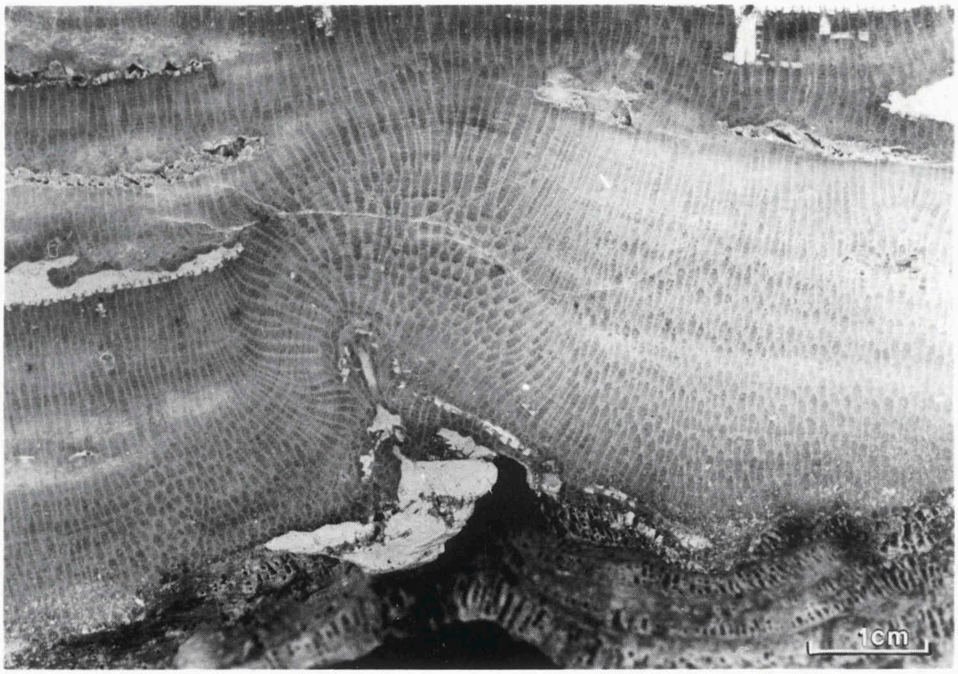


Fig. 16. Small hill in a *Favosites hisingeri* colony caused by the substratum, Lower Visby Beds, Ireviken 3, RGM 243 733.

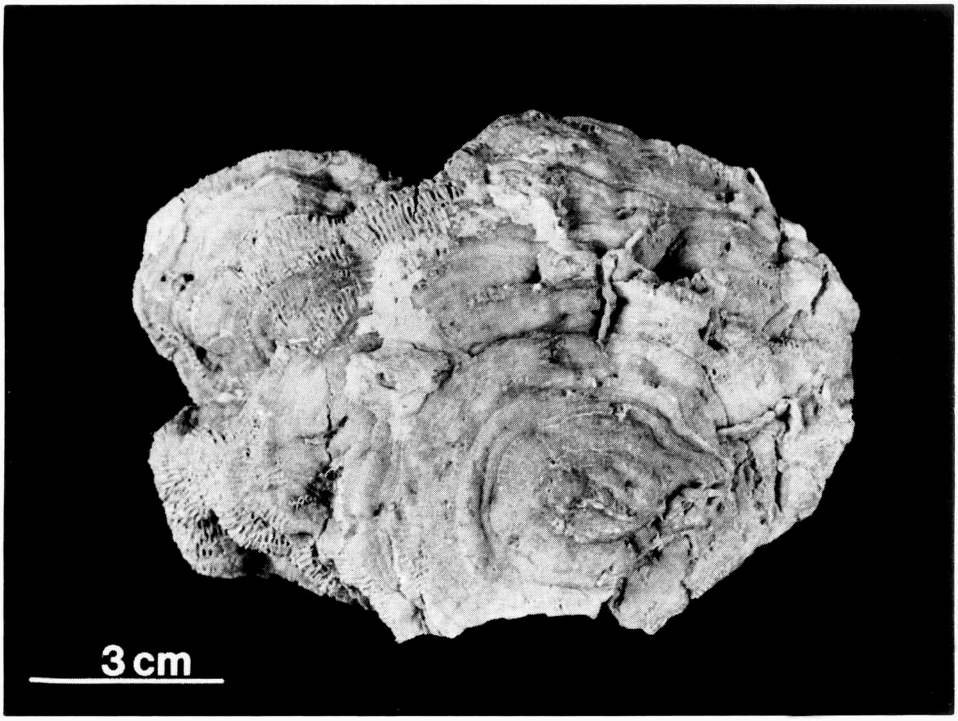


Fig. 17. Growth bands at the underside of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 726.

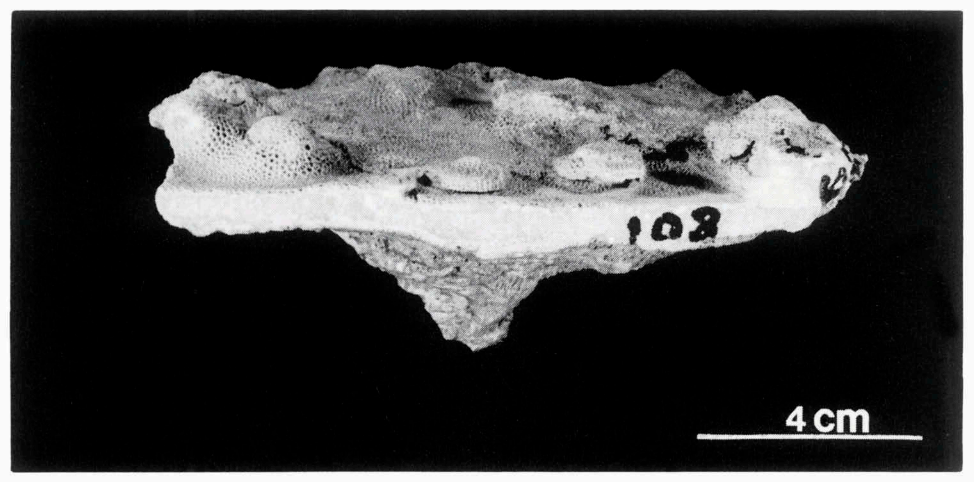


Fig. 18. Mushroom shaped colony of *Favosites hisingeri,* Lower Visby Beds, Ireviken 3, RGM 243 727.

18) or parts of larger colonies are also frequently observed. At the underside of these colonies epibionts occur like stromatoporoids and bryozoans. The colony surface shows many irregularities (Fig. 23) like small hills, knobs (diameters up to 3 cm; height up to 2.5 cm) and raised platforms (Fig. 24). Small cracks frequently occur in colonies which consist of a succession of thin sheets. They are probably caused by fractioning during early compaction.

A fragment (13 × 16 × 4 cm) of a foliaceous colony, found at Ireviken 3, was sectioned into eleven slices in order to obtain detailed information about growth irregularities, regularly observed in similar colonies. The colony has encrusted the substratum, a *Catenipora* colony. In the lowest part of these slices lightbrown growth bands are seen, suggesting that maximum growth occurred in the area of slices 1 - 3 (Figs. 19a - b). In the lateral parts (slices 5 - 8) the colony slowly expanded over the substratum. In slice 1 a small hill developed as a reaction on local dying of and covering with sediment of a part of the colony. As shown by differences of the distance between the tabulae, growth in the left part of slice 1 was less fast than growth in the right part, probably because of topographical differences in the substratum. In the middle (Fig. 19a) a knob (diameter 7 mm; height 15 mm) arose. In the peripheral parts of the colony growth was slow as is indicated by closely spaced tabulae. Growth probably was also influenced to a high degree by the environment as is suggested by the increasing number of mud-coverings.

Four main crises in the life history of the organism, secreting this skeleton, can be deduced from the morphology of the colony. During the first crisis (I) almost the entire surface of the colony was covered by mud (Fig. 19). It is noteworthy that the thickest mud-covering occurred in the central part of the colony as is indicated by the fact that even the elevated knob (diameter 22 mm; height 15 mm) of slice 1 was covered by the sediment, while in peripheral parts (slices 7 - 10; Fig. 19d - f) the covering was less extensive. From the latter area the colony grew across the older now mud-covered parts (slices 1, 5, 8; Fig. 19a, c, e). Growth in the new central area (slices 9, 10; Fig. 19f) was, just as before this crisis, influenced by environmental parameters: mud intercalations, indicating

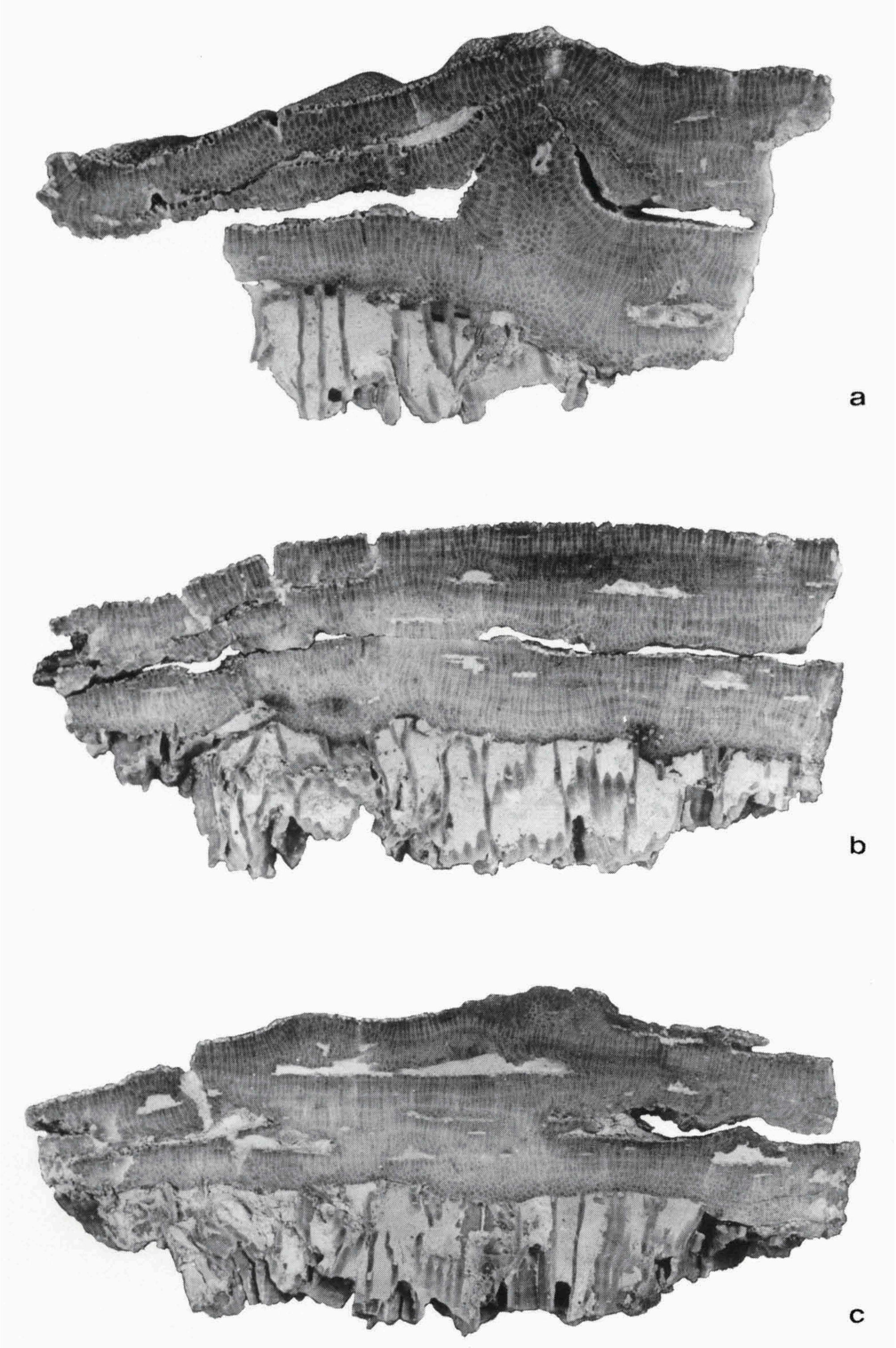
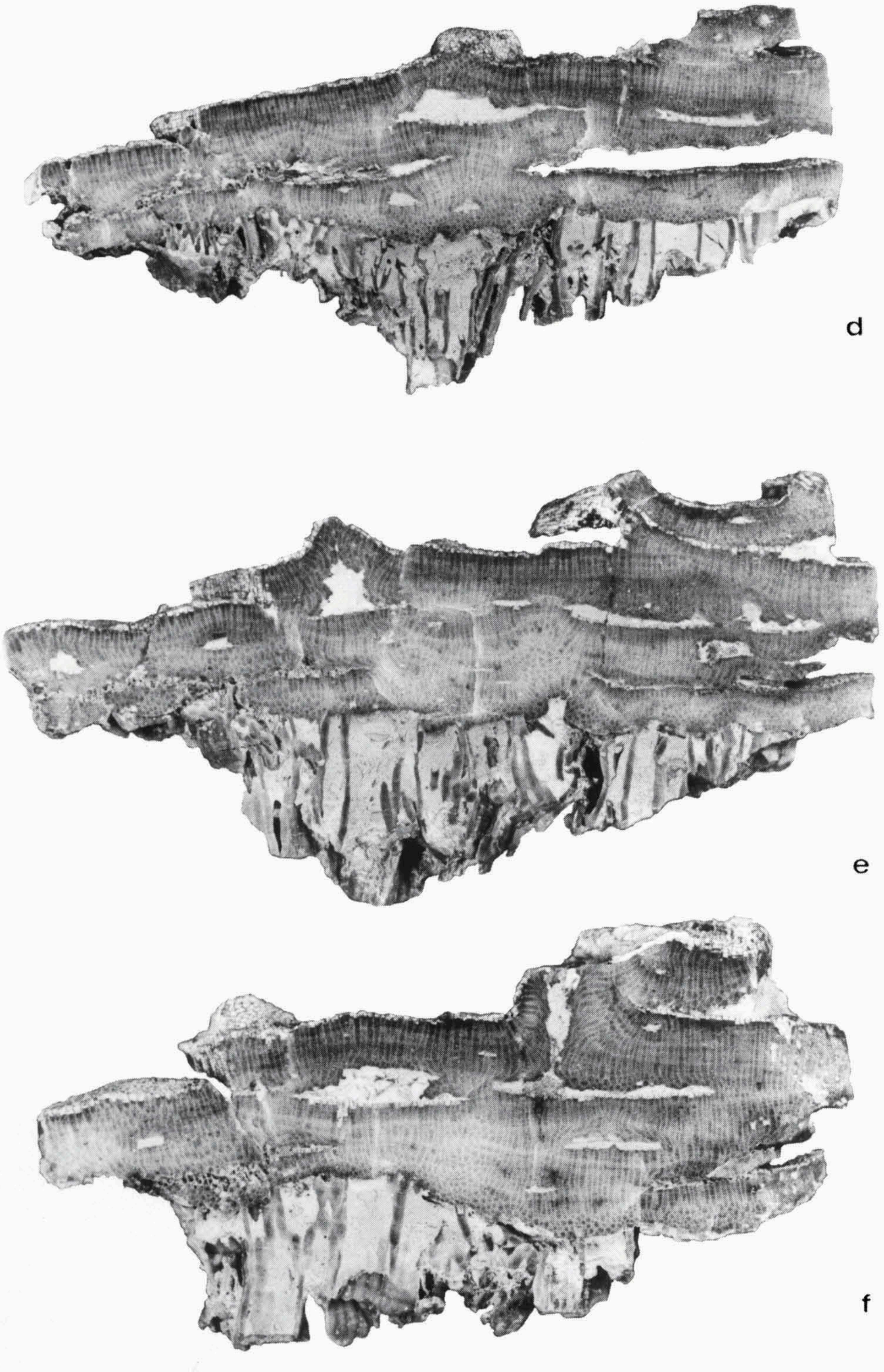


Fig. 19. Selected examples from a series of eleven longitudinal sections of a *Favosites hisingeri* colony (see explanation in the text), Lower Visby Beds, Ireviken 3, RGM 243 734, approximately natural size.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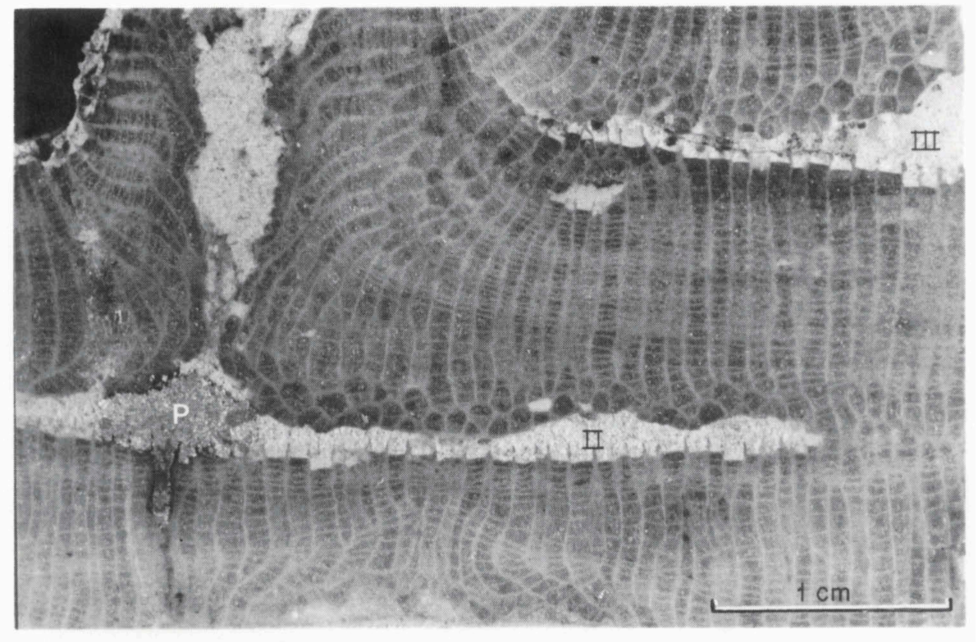

Fig. 20. Peculiar sediment covers leading to growth irregularities in a *Favosites hinsingeri* colony. In the sediment cover pyrite cubes (P) occur. Traces of two (II, III) of the four main crises in the life history of the colony are seen. Lower Visby Beds, Ireviken 3, RGM 243 734.

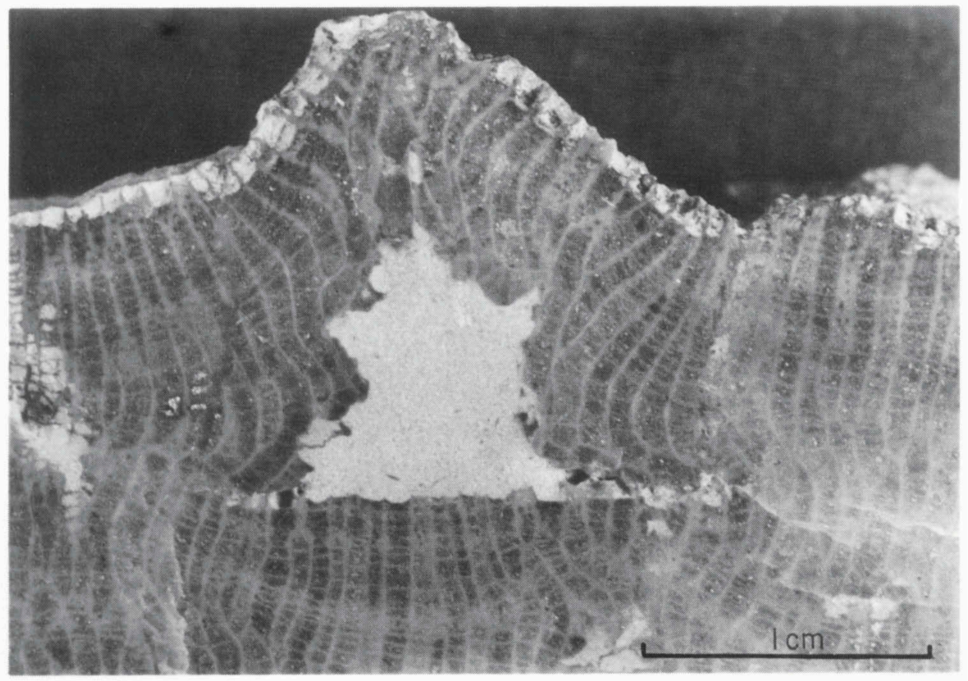

Fig. 21. Mud intercalation in a *Favosites hisingeri* colony. Erosion of this favositid is indicated by the presence of tabulae at the mud/favositid interface. Lower Visby Beds, Ireviken 3, RGM 243 734.

local dying and subsequent overgrowth of the mud-covered area from adjacent intact parts of the colony occur just as pronounced differences in tabulae distance, suggesting local variation in the growth rate. The second crisis (II) is again indicated by mud covers of extensive areas of the colony surface. A more or less coherent cover is seen in the peripheral part (slice 1, Fig. 19a) whereas in the central part this crisis is indicated by a horizon of smaller mud intercalations. The latter are mostly situated in the shallow sheltered areas, while the more elevated parts of the colony were not covered with mud (slice 7; Fig. 19d), although densely spaced tabulae are now seen in the corallites. These mud-covered areas were in turn laterally overgrown from intact parts of the colony. Some peculiar growth irregularities (slices 8, 9; Fig. 20) are observed in this stage. During the third crisis (III) the colony almost completely died and was covered again with mud. After this crisis the last expansion across the mud-covered area occurred.

It is noteworthy that below some sediment covered areas or marly intercalations an eroded part of the surface of the colony is exposed (Fig. 21). This is demonstrated by the occurrence of tabulae in the uppermost part of the corallites. Even in places where such growth interruptions are not covered with mud (slice 1; Fig. 19a), tabulae are sometimes also observed in the uppermost part of the corallites and erosion is suggested. As a majority of the colonies are found in life position it is unlikely that the development of these eroded surfaces was influenced by heavy storms. The occurrence of gentle currents is suggested by the main growth directions of the colonies. The high correlation between the occurrence of zones with closely spaced tabulae prior to the mud coverings suggests that environmental parameters influenced both local and large scale dying of the colony.

The *F. hisingeri* colonies apparently developed under such severe stress conditions that small shifts of the equilibrium between environment and growth would cause predomination of either growth or sedimentation.

During growth of an encrustive colony two stages are distinguished (Fig 22). In the first stage, reptant growth occurs more or less parallel to the topography of the substrate. Rather rapid growth is seen and new offsets are frequently formed. In the second stage, growth occurred at right angles to the substrate and few offsets develop. In mushroom-shaped colonies this distinction can also be made in the 'cap' while in the 'stem', as a matter of fact, oblique or vertical

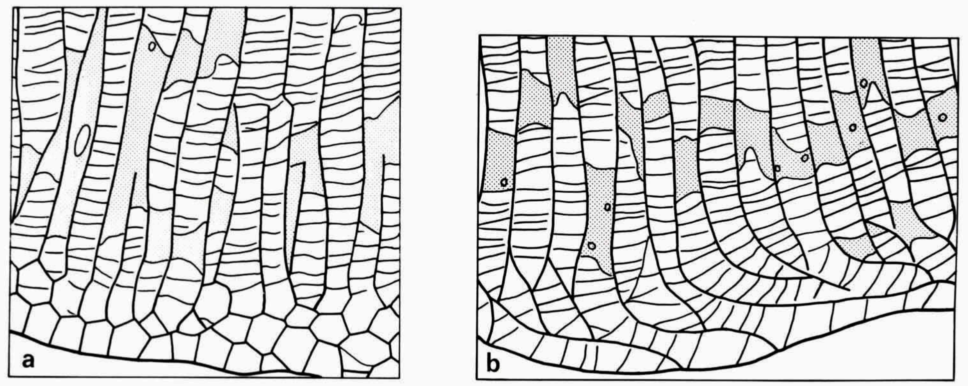

Fig. 22. Diagrammatic representation of longitudinal sections of *Favosites hisingeri*. Longitudinal section a is perpendicular to longitudinal section b, × 5.

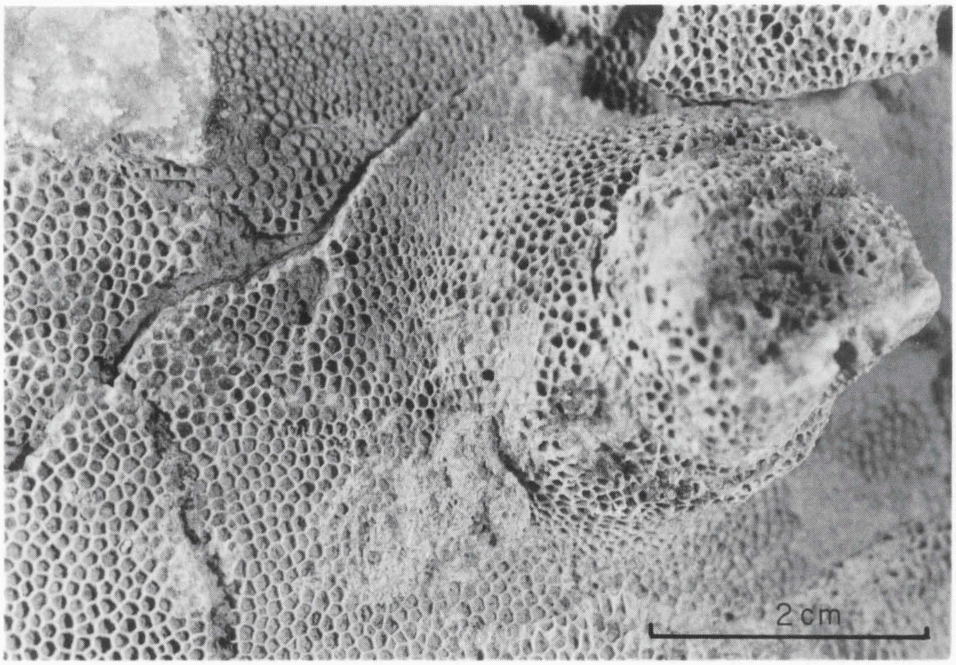

Fig. 23. Variation in corallite size near a knob at the surface of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 725.

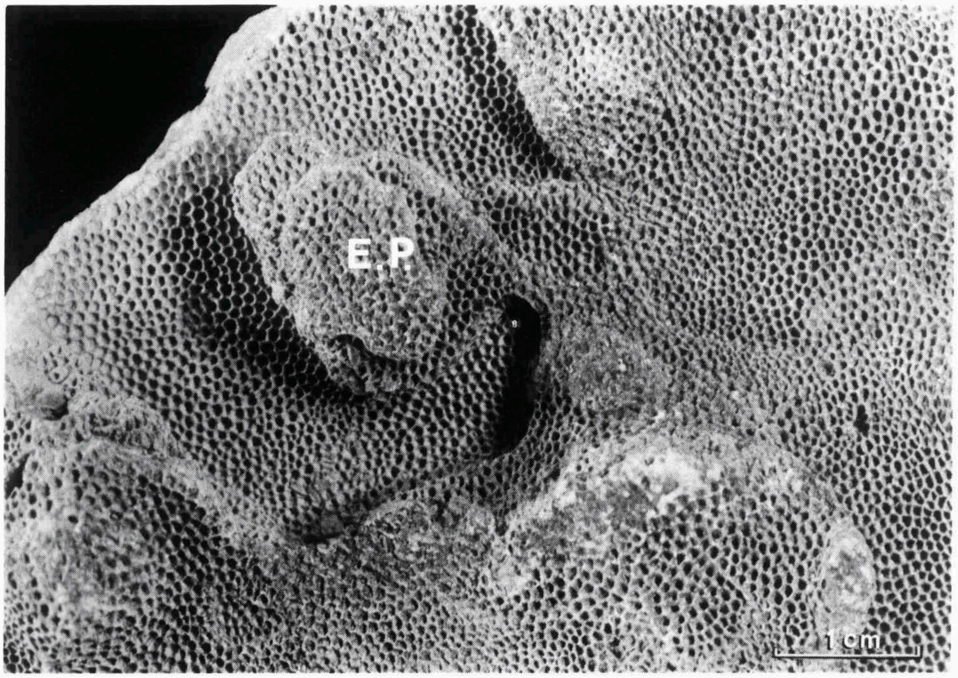

Fig. 24. Variation in corallite size near an elevated platform (E.P.) at the surface of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 727.

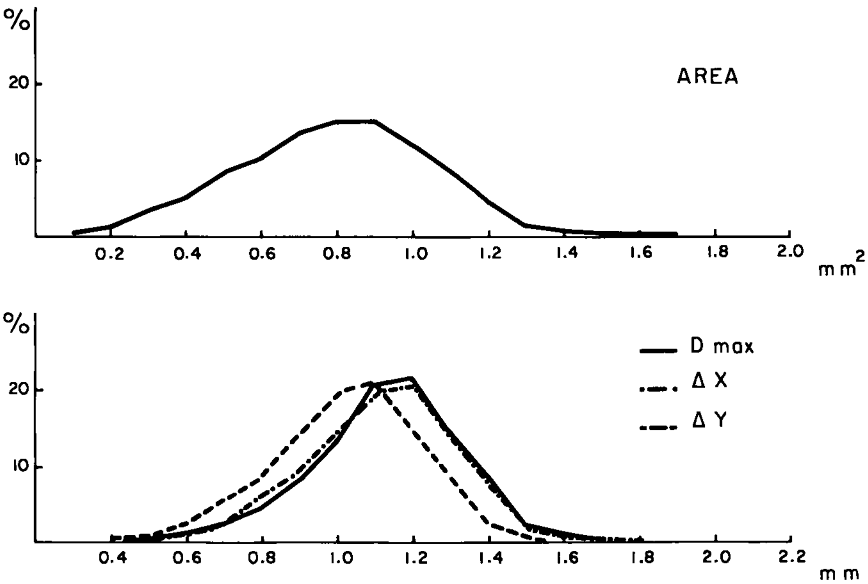

Fig. 25. Frequency distribution in 2843 measurings on scan micrographs of samples of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 700.

orientated growth is observed. The mode of increase was studied by means of closely spaced serial sections and lateral increase was found in *F. hisingeri.*

The variability in corallite size is striking. Smaller corallites are mostly found near hills and knobs on the surface (Fig. 23). In colonies, with a surface consisting of elevated platforms (Fig. 23), small corallites are also observed in more sheltered areas (Fig. 24). In colonies with large flat surfaces such a striking differentiation is rarely seen.

The graphs shown in Figure 25 were constructed from the data of 2843 measurings of samples from the surface of a *F. hisingeri* colony (RGM 243 700). The data are normally distributed. The statistic parameters of the characters are summarized in Table 2. The range of the corallite areas is 0.1 - 1.7 mm^2; most frequent is the range between 0.2 and 1.3 mm^2. The ranges of the corallite diameters vary to some extend as a result of different measuring methods. The graph of Δy and Dmax are mostly identical and the range is 0.6 - 1.5 mm. The graph of Δx slightly differs from the other two; the values vary between 0.6 - 1.4 mm. The values of the corallite diameters are also normally distributed. The variation of Δx and Δy in a fixed group of the corallite area is shown in Figure

Table 2. Parameters of corallites in scan micrographs of surface samples of a *Favosites hisingeri* colony, RGM 243 700.

Sample RGM 243 700 Lower Visby biostrome, Ireviken 3

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.79	0.26	0.01	2.93	0.10	2.00	0.80	2843
Dmax	1.14	0.20	—0.23	3.27	0.50	1.90	1.15	2843
Δx	1.11	0.21	—0.31	3.12	0.40	1.80	1.12	2843
Δy	1.03	0.20	—0.24	3.06	0.40	1.70	1.04	2843

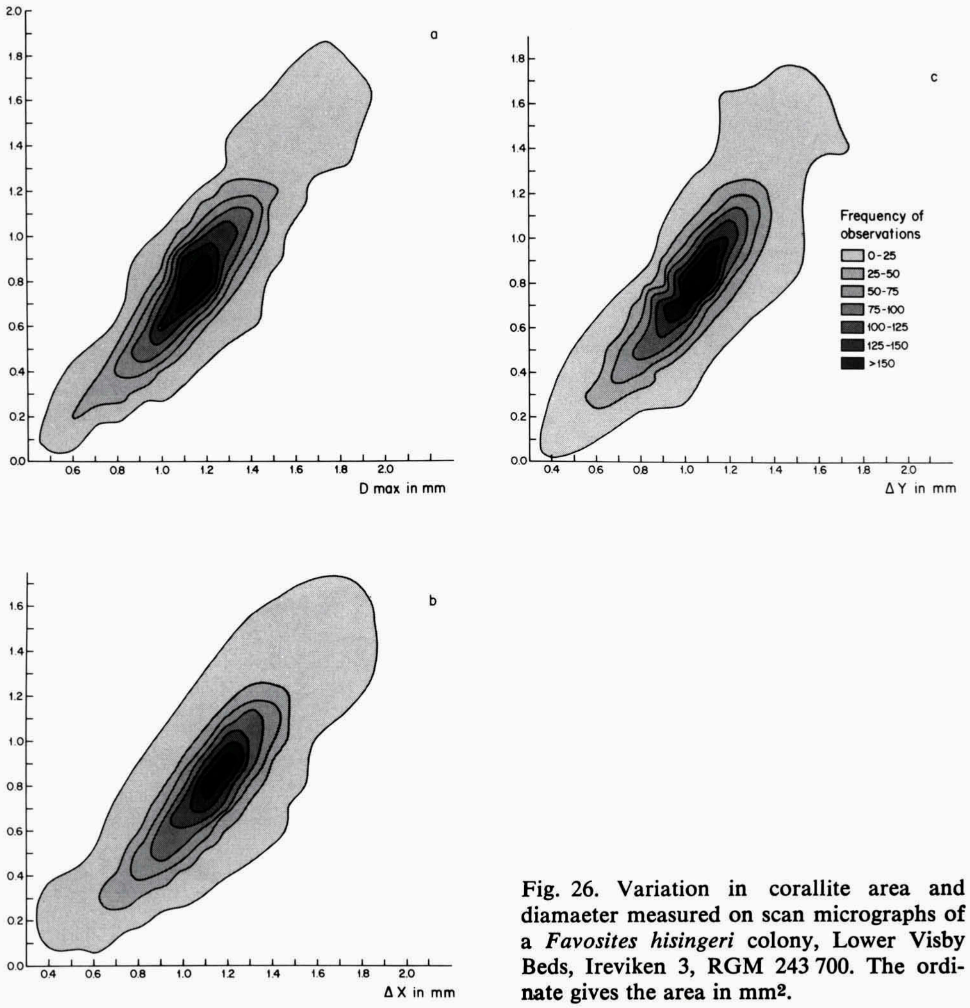

Fig. 26. Variation in corallite area and diamaeter measured on scan micrographs of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 700. The ordinate gives the area in mm².

26. From this figure can be learned that the range of the diameter measurings is extensive, even in such fixed groups. Several thin sections and peelings of transverse sections were also measured. The statistic parameters of the features are listed in Table 3.

In order to investigate differences in corallite diameter within a colony three samples from selected areas (Fig. 27) were measured. The graphs of the data are shown in Figure 28; the statistical parameters in Table 4. Although visual differences between these three samples seem small, the actual differences between the values of the parameters are large. The mean corallite area in the first sample is 0.7 mm², in the second 1.0 mm² and in the third 0.6 mm². The average mean of the corallite diameter respectively is 1.04, 1.24 and 0.94 mm.

Student's t distribution (Table 5) of the samples indicates the inequivalency of the three samples. However, because the three samples are derived from the same colony this does not indicate that three different species are present. Therefore the author holds the opinion that application of statistical methods to samples of unknown phenotypic variability will easily lead to the description of new morphospecies which are ecotypes of classical species.

Table 3. Parameters of corallites in thin sections of four *Favosites hisingeri* colonies, RGM 243 701 - 243 704.

Sample RGM 243 701-I, II Lower Visby biostrome, Ireviken 3

		$\bar{x}$	S	Sk	K	min.	max.	G	N
I :	Area	0.68	0.25	−0.42	2.32	0.10	1.20	0.72	372
	Dmax	1.03	0.21	−0.84	3.35	0.40	1.40	1.07	372
	Δx	0.99	0.21	−0.81	3.55	0.30	1.40	1.02	372
	Δy	0.98	0.20	−0.80	3.18	0.30	1.30	1.01	372
II :	Area	0.69	0.26	−0.33	2.37	0.10	1.20	0.72	393
	Dmax	1.05	0.21	−0.79	4.36	0.50	1.50	1.08	393
	Δx	1.00	0.21	−0.52	2.94	0.40	1.50	1.03	393
	Δy	0.99	0.20	−0.65	3.02	0.40	1.40	1.01	393
I + II :	Area	0.68	0.26	−0.37	2.36	0.10	1.20	0.72	765
	Dmax	1.04	0.21	−0.81	3.89	0.40	1.50	1.07	765
	Δx	0.99	0.21	−0.67	3.26	0.30	1.50	1.03	765
	Δy	0.98	0.20	−0.73	3.12	0.30	1.40	1.01	765

Sample RGM 243 702-I, II Lower Visby biostrome, Ireviken 3

		$\bar{x}$	S	Sk	K	min.	max.	G	N
I :	Area	0.93	0.37	−0.08	2.32	0.10	1.80	0.96	463
	Dmax	1.23	0.26	−0.19	3.23	0.40	2.00	1.26	463
	Δx	1.16	0.27	−0.29	2.81	0.30	1.90	1.19	463
	Δy	1.16	0.27	−0.23	3.18	0.40	2.00	1.19	463
II :	Area	0.94	0.27	−0.44	2.91	0.20	1.50	0.97	216
	Dmax	1.23	0.18	−0.52	3.50	0.60	1.60	1.24	216
	Δx	1.15	0.19	−0.60	3.74	0.40	1.50	1.17	216
	Δy	1.20	0.20	−0.47	3.52	0.60	1.70	1.21	216
I + II :	Area	0.93	0.34	−0.16	2.53	0.10	1.80	0.96	679
	Dmax	1.23	0.24	−0.23	3.51	0.40	2.00	1.25	679
	Δx	1.16	0.25	−0.33	3.12	0.30	1.90	1.18	679
	Δy	1.17	0.25	−0.32	3.43	0.40	2.00	1.20	679

Sample RGM 243 703 Upper Visby/Högklint Beds, Nyhamn 7

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	1.00	0.29	−0.19	2.75	0.20	1.80	1.00	425
Dmax	1.27	0.20	−0.15	3.83	0.70	2.00	1.28	425
Δx	1.20	0.19	−0.41	4.09	0.40	1.70	1.22	425
Δy	1.18	0.22	−0.23	2.91	0.60	1.80	1.19	425

Sample RGM 243 704 Högklint reef, Nyhamn 7

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.79	0.23	−0.19	4.17	0.10	1.70	0.80	259
Dmax	1.13	0.19	−0.36	6.16	0.20	2.00	1.13	259
Δx	1.06	0.18	−0.42	4.52	0.40	1.70	1.06	259
Δy	1.07	0.20	−0.11	5.08	0.40	2.00	1.08	259

The range of the corallite area, from the data of thin sections and peelings, is 0.1 - 1.8 mm^2; the range of the corallite diameters is 0.3 - 2.1 mm, but a diameter of 0.5 - 1.5 mm predominates. Although the individual samples sometimes deviate to a high degree from the value obtained by measuring at the colony surface, the sum of these data (Table 3) confirms the variation observed in the scan samples.

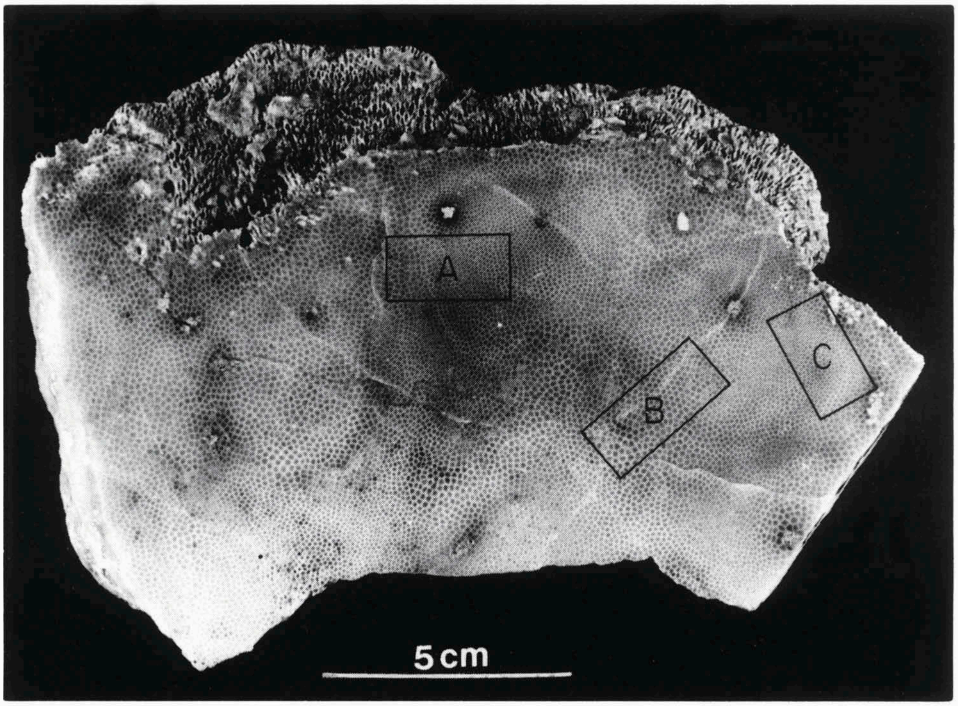

Fig. 27. Selected areas (A, B and C) of a measured peel of a *Favosites hisingeri* colony. Upper Visby Beds, Ireviken 3, RGM 243 705.

Table 4. Parameters of corallites in three selected areas of an acetate peel of a *Favosites hisingeri* colony, RGM 243 705.

Sample RGM 243 705-A Upper Visby biostrome, Ireviken 3

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.72	0.18	1.04	3.78	0.40	1.30	0.67	617
Dmax	1.09	0.16	0.80	3.50	0.70	1.70	1.07	617
Δx	1.02	0.16	0.80	3.84	0.60	1.70	1.00	617
Δy	1.00	0.14	0.77	3.77	0.70	1.50	0.98	617

Sample RGM 243 705-B

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	1.04	0.17	0.08	3.07	0.60	1.50	1.04	276
Dmax	1.27	0.12	0.10	3.13	0.90	1.60	1.27	276
Δx	1.23	0.14	0.18	2.98	0.90	1.60	1.22	276
Δy	1.21	0.13	0.14	2.49	0.90	1.60	1.21	276

Sample RGM 243 705-C

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.59	0.16	0.54	4.29	0.20	1.30	0.57	429
Dmax	0.98	0.15	0.18	3.54	0.50	1.50	0.98	429
Δx	0.94	0.15	0.24	3.68	0.50	1.50	0.93	429
Δy	0.89	0.14	0.26	4.17	0.50	1.50	0.89	429

Table 5. Student's t test values, for an infinite number of degrees of freedom, samples RGM 243 705 A, B, C.

	Sample	Sample	t-test		Sample	Sample	t-test
Area	2	1	15.264	Δx	1	2	—17.507
	1	3	11.835		1	3	7.602
	2	3	18.251		2	3	23.779
Dmax	2	1	13.843	Δy	2	1	21.110
	3	1	—10.679		3	1	—11.870
	2	3	19.167		3	2	—28.030

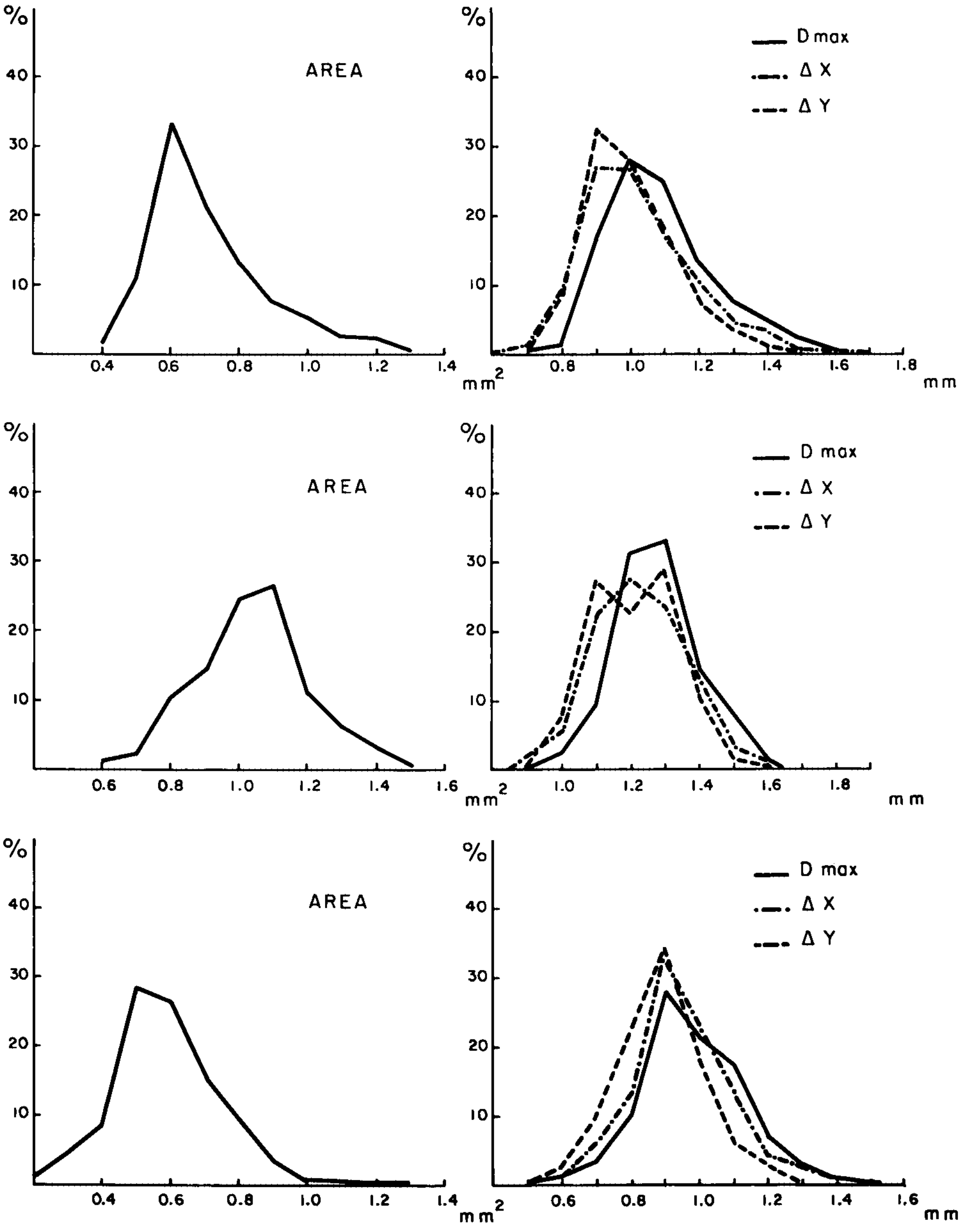

Fig. 28. Frequency distribution in measurings of the three selected areas shown in Figure 27. Upper Visby Beds, Ireviken 3, RGM 243 705.

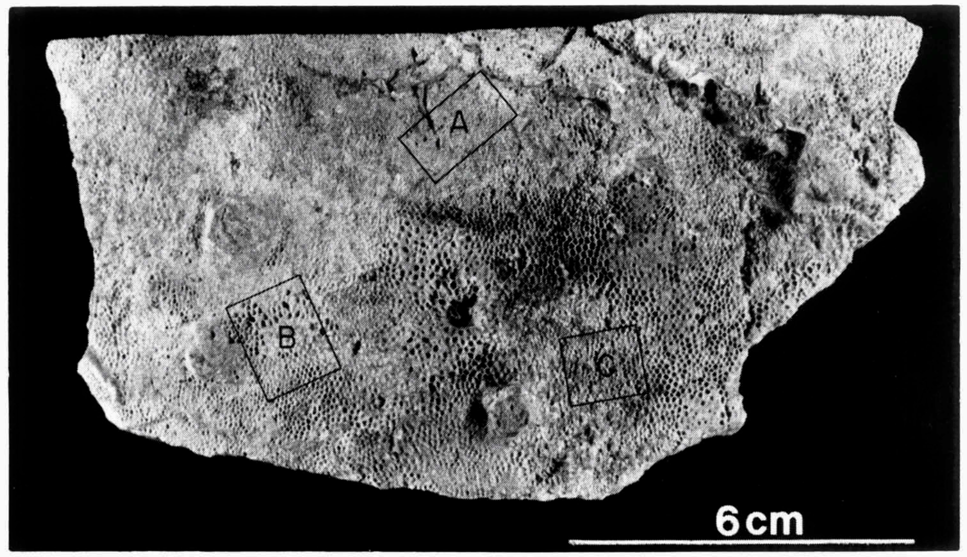

Fig. 29. Selected areas (A, B and C) of the measured surface of a *Favosites hisingeri* colony, Visby Beds, Nyhamn 8, RGM 243 706.

Table 6. Parameters of corallites in three selected areas of the surface of a *Favosites hisingeri* colony, RGM 243 706.

Sample RGM 243 706 - surface A Visby Beds, Nyhamn 8

	x̄	S	Sk	K	min.	max.	G	N
Area	0.42	0.14	1.33	5.78	0.20	1.10	0.39	249
Dmax	0.82	0.14	0.83	4.54	0.50	1.40	0.80	249
Δx	0.77	0.13	0.77	5.12	0.40	1.40	0.76	249
Δy	0.75	0.16	0.78	4.64	0.40	1.50	0.74	249

Sample RGM 243 706 - surface B

	x̄	S	Sk	K	min.	max.	G	N
Area	0.82	0.25	0.65	3.16	0.20	1.70	0.79	339
Dmax	1.16	0.18	0.41	3.40	0.50	1.80	1.14	339
Δx	1.10	0.19	0.44	3.40	0.50	1.80	1.09	339
Δy	1.09	0.19	0.44	2.87	0.60	1.60	1.07	339

Sample RGM 243 706 - surface C

	x̄	S	Sk	K	min.	max.	G	N
Area	0.95	0.21	0.29	2.89	0.40	1.60	0.94	358
Dmax	1.23	0.14	0.17	3.13	0.90	1.70	1.23	358
Δx	1.16	0.14	0.04	2.72	0.80	1.50	1.16	358
Δy	1.20	0.17	0.31	3.49	0.80	1.90	1.20	358

Sample RGM 243 706 - surface A-C

	x̄	S	Sk	K	min.	max.	G	N
Area	0.77	0.30	0.16	2.38	0.20	1.70	0.77	946
Dmax	1.10	0.23	—0.17	2.53	0.50	1.80	1.12	946
Δx	1.04	0.22	—0.09	2.53	0.40	1.80	1.05	946
Δy	1.04	0.25	—0.11	2.56	0.40	1.90	1.06	946

Table 7. Parameters of corallites in three selected astogenic sequences of a *Favosites hisingeri* colony, RGM 243 706.

Sample RGM 243 706 Visby Beds, Nyhamn 8

	$\bar{x}$	S	Sk	K	min.	max.	G	N
3: Area	0.36	0.14	1.04	4.85	0.20	1.00	0.35	746
Dmax	0.76	0.14	0.44	3.30	0.50	1.30	0.76	746
Δx	0.72	0.14	0.44	2.89	0.40	1.20	0.71	746
Δy	0.72	0.16	0.64	3.46	0.40	1.30	0.70	746
2: Area	0.61	0.17	0.67	4.09	0.20	1.40	0.59	399
Dmax	1.00	0.17	0.77	4.24	0.60	1.70	0.98	399
Δx	0.97	0.19	0.45	3.14	0.60	1.60	0.96	399
Δy	0.91	0.13	0.59	4.93	0.60	1.60	0.91	399
1: Area	071	0.21	0.83	3.40	0.40	1.60	0.66	298
Dmax	1.06	0.16	0.52	3.06	0.70	1.60	1.04	298
Δx	1.02	0.19	0.50	2.85	0.70	1.60	1.00	298
Δy	1.02	0.16	0.55	2.82	0.70	1.50	1.00	298
3: Area	0.48	0.22	1.52	4.91	0.20	1.30	0.41	293
Dmax	0.86	0.19	1.08	3.67	0.60	1.50	0.81	293
Δx	0.81	0.20	1.11	3.71	0.50	1.40	0.74	293
Δy	0.85	0.18	1.10	3.85	0.60	1.50	0.81	293
2: Area	0.61	0.20	0.77	3.37	0.10	1.20	0.59	388
Dmax	1.00	0.16	0.38	3.03	0.60	1.50	0.99	388
Δx	0.96	0.17	0.41	3.00	0.60	1.50	0.94	388
Δy	0.93	0.16	0.49	3.53	0.50	1.50	0.92	388
1: Area	0.66	0.29	1.14	4.02	0.20	1.70	0.59	299
Dmax	1.03	0.23	0.78	3.43	0.60	1.80	0.99	299
Δx	0.97	0.23	0.90	3.74	0.60	1.80	0.94	299
Δy	0.97	0.22	0.43	2.77	0.66	1.60	0.95	299
3: Area	0.41	0.20	1.80	6.53	0.20	1.40	0.35	459
Dmax	0.81	0.18	1.27	4.60	0.50	1.50	0.77	459
Δx	0.78	0.18	1.27	5.04	0.50	1.50	0.73	459
Δy	0.76	0.17	1.17	4.41	0.50	1.40	0.72	459
2: Area	0.69	0.31	1.30	4.33	0.10	1.80	0.60	360
Dmax	1.05	0.24	1.08	4.52	0.50	2.10	1.00	360
Δx	0.97	0.24	0.78	3.40	0.40	1.70	0.93	360
Δy	1.02	0.22	0.97	4.14	0.50	2.00	0.98	360
1: Area	0.69	0.22	1.43	5.91	0.40	1.60	0.66	258
Dmax	1.06	0.18	0.91	4.09	0.80	1.70	1.04	258
Δx	0.99	0.22	0.93	3.84	0.60	1.80	0.95	258
Δy	1.04	0.16	0.84	3.84	0.70	1.60	1.02	258

A fragment of a colony, with a rather flat surface (Fig. 29) in which only some small knobs (diameter 15 mm; height 10 mm) occur, was cut into four slices in order to study the astogenic differentiation during growth. Before cutting the colony, the areas to be measured were selected. The data of these series of measurings, which were obtained from peelings, are shown in Figure 30. Apart from these measurements some selected areas at the colony surface were also measured (Fig. 29). Because of optical limitations only the first (Fig 29a) of the three selected areas could be taken on top of the succession shown in Figure 30a. The statistic parameters of this astogenic sequence are given in Tables 6 and 7.

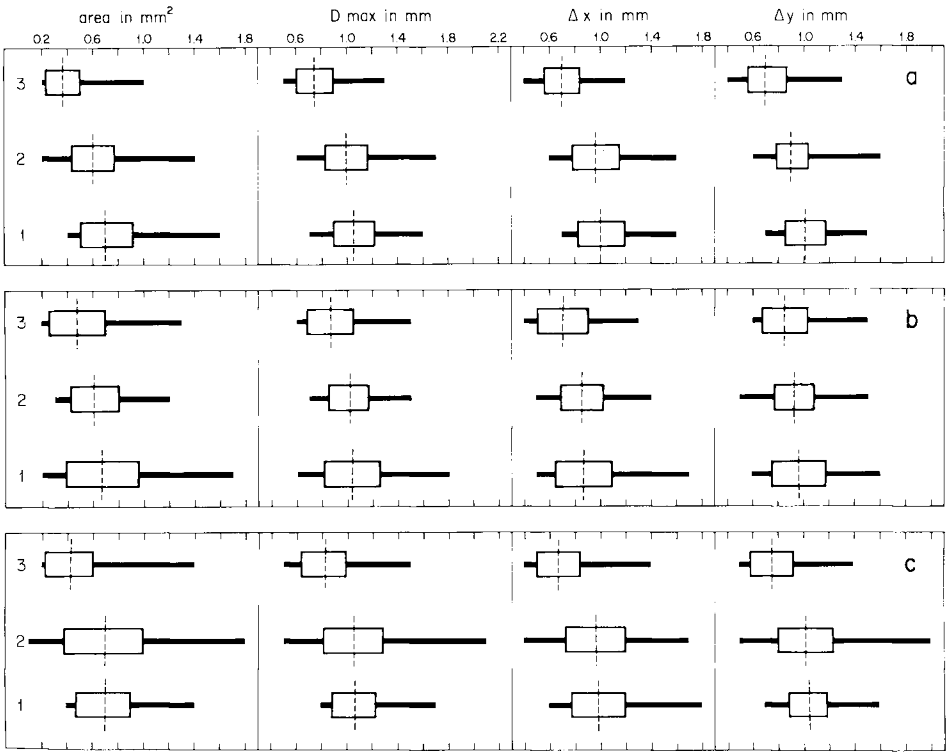

Fig. 30. Variation of parameters in three astogenic sequences (see Fig. 29) of a *Favosites hisingeri* colony, Visby Beds, Nyhamn 8, RGM 243 706.

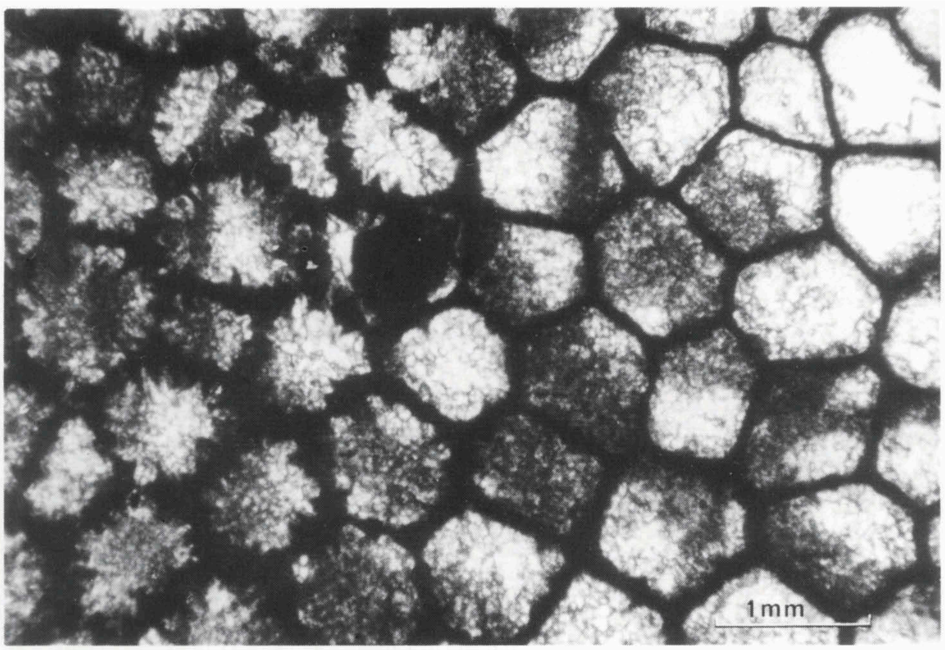

Fig. 31. Variation in wall thickness within one thin section of a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 728.

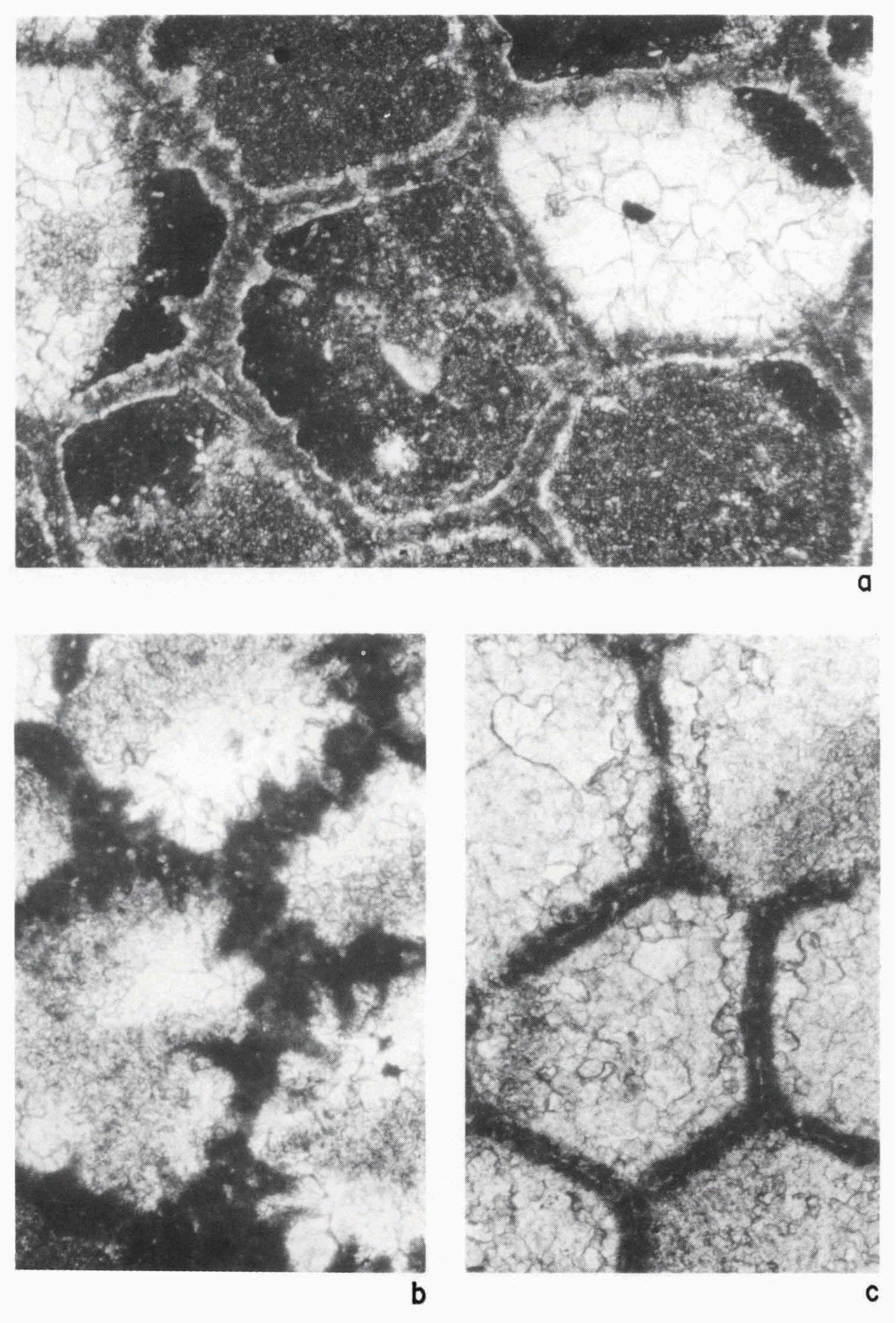

Fig. 32. Aspects of the dark line in *Favosites hisingeri* colonies, × 45.
a. Dark line as usually seen, Upper Visby Beds, Nyhamn 7, RGM 243 703.
b. Dark line as a row of white spots, Lower Visby Beds, Ireviken 3, RGM 243 702.
c. Dark line as a white line, Lower Visby Beds, Ireviken 3, RGM 243 701.

Just as is seen in the series of longitudinal slices described above, this sequence of transverse slices also indicates that the morphology of the colony surface changes rapidly. Such rapid morphological changes, like the development of a new knob, apparently could cause degeneration of some corallites, as is suggested by diminishing corallite areas and diameters (Fig. 30a).

Careful examination of longitudinal sections revealed that the parameters of sample 2 and 3 from the first astogenic sequence (Fig. 30a) indeed are derived from the same corallites. A comparable situation is suggested by the parameters of the corallite area from the third succession (Fig. 30c), which is also situated near a knob. Such a situation is not seen in the second series, in which the corallites, on the contrary, are not situated near knobs. The measurings of the samples from the surface of the colony again indicate a high degree of variability; the mean corallite area of the smaller corallites is less than half of the same parameter from larger corallites. On the other hand, this high degree of variation is less pronounced in the corallite diameters.

The thickness of the double-wall varies to a high degree. In the same thin section (Fig. 31) thin double-walls (0.08 - 0.16 mm) without septal spines and thick double-walls (0.20 - 0.40 mm) with septal spines are observed. The dark line (Fig. 32), a typical feature in most favositids, is developed in various ways. At low magnification the dark line is not at all seen in the double-wall of some, mostly small, corallites whereas in larger corallites the structure is either indicated by a row of white spots (Fig. 32b - c) or is fully developed (Fig. 32a). However, at higher magnifications a dark line is also observed between the walls of small corallites (Figs. 33, 34).

With Klaamann (1970), the present author supposes that the more conspicuous rows of white spots and the white lines are caused by recrystallization.

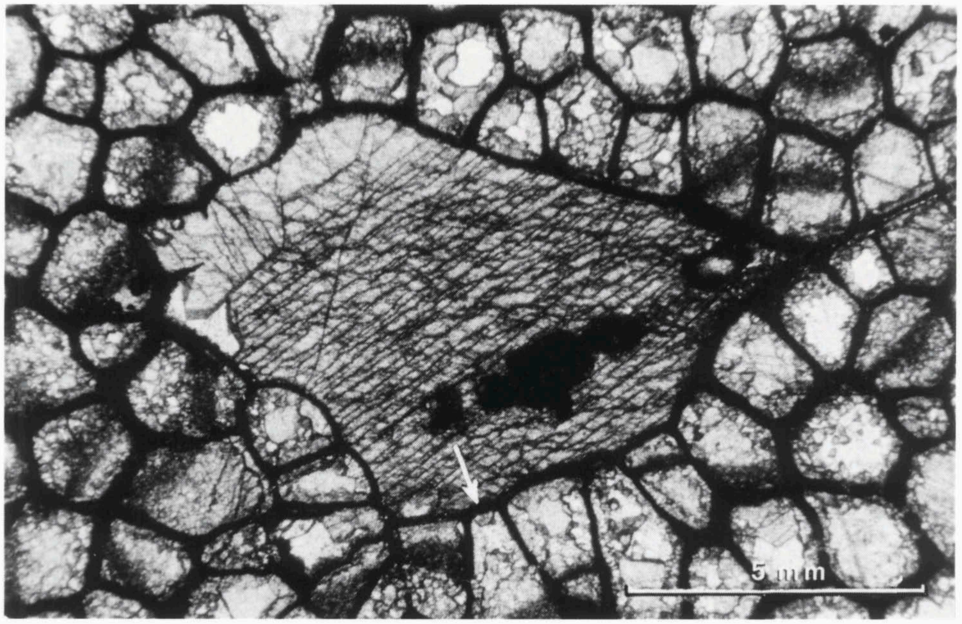

Fig. 33. Enclosure in a *Favosites hisingeri* colony. Dark line is not seen. Lower Visby Beds, Ireviken 3, RGM 243 702.

A possible interpretation of such white spots as traces of endobionts, as suggested by Klaamann (1970, 1971), is unlikely, because:

(1) A continuous sequence is found from a normal dark line towards a row of white spots, a stippled white line, and a continuous white line.

(2) Embedding reactions, as described by Stel (1976), could only be observed in those parts of the colony, where thick walls with septal spines are found. In these parts of the colony, presumed embedding could be confused with the development of white spots, caused by recrystallization, in such places where wall thickenings occur due to growth of septal spines.

(3) In double-walls without septal spines such presumed reactions are lacking.

Many enclosures are observed in *F. hisingeri* colonies. The structure of the double-wall of adjacent corallites indicates that most enclosures formed obstacles during growth of the colony. A dark line is seen between the walls of adjacent corallites, whereas this structure is not observed in the wall contiguous to the obstacle (Fig. 34). Similar reactions are observed around marly intercalations, even in such as depicted in Figures 19 - 21.

A striking difference is observed between the way in which a favositid or a heliolitid overgrew such a mud-covering (Fig. 35). In *F. hisingeri,* young corallites, from the adjacent intact parts of the colony, slowly envelop the mud covered area in such a way, that the growth direction of these corallites is fixed by the topography of the substratum. As a consequence the organism secreting these corallites also grew, at least partly, parallel to this surface. However, in heliolitids (from the same locality) such an orientation mostly is not observed. The horizontal arrangement of the dissepiments in the tubules and the tabulae in the corallite (Fig. 35a) suggests that the skeleton was deposited by a tissue overflowing the mud covered area. This difference is easily explained if a thick tissue

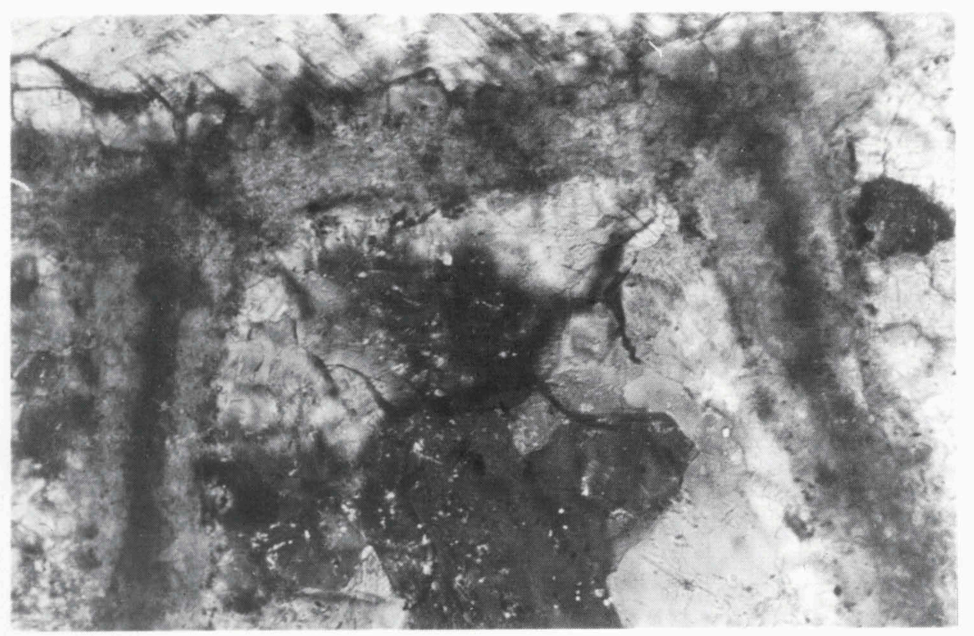

Fig. 34. Detail of Figure 33 (see arrow). A distinct dark line is seen in the corallite double-wall at higher magnification. At the outside of the corallite wall around the enclosure no dark line is observed. Lower Visby Beds, Ireviken 3, RGM 243 702, × 130.

layer is postulated on top of the skeleton of the heliolitid, a situation suggested by Hill & Stumm (1956) and Sokolov (1962).

In his diagnosis of *Angopora hisingeri,* Jones (1936) only mentioned the occurrence of mural pores. Klaamann (1970) noticed that both mural pores and 'corner pores' are found; an arrangement also observed in '*Mesofavosites*' Sokolov. The occurrence of pores near the corner of a corallite is indeed frequently seen in transverse sections. Countings of some hundreds of pores (Fig. 36) in transverse sections demonstrate that about 30 - 50% of the pores occur near the corner. However, in longitudinal sections the characteristic undulation

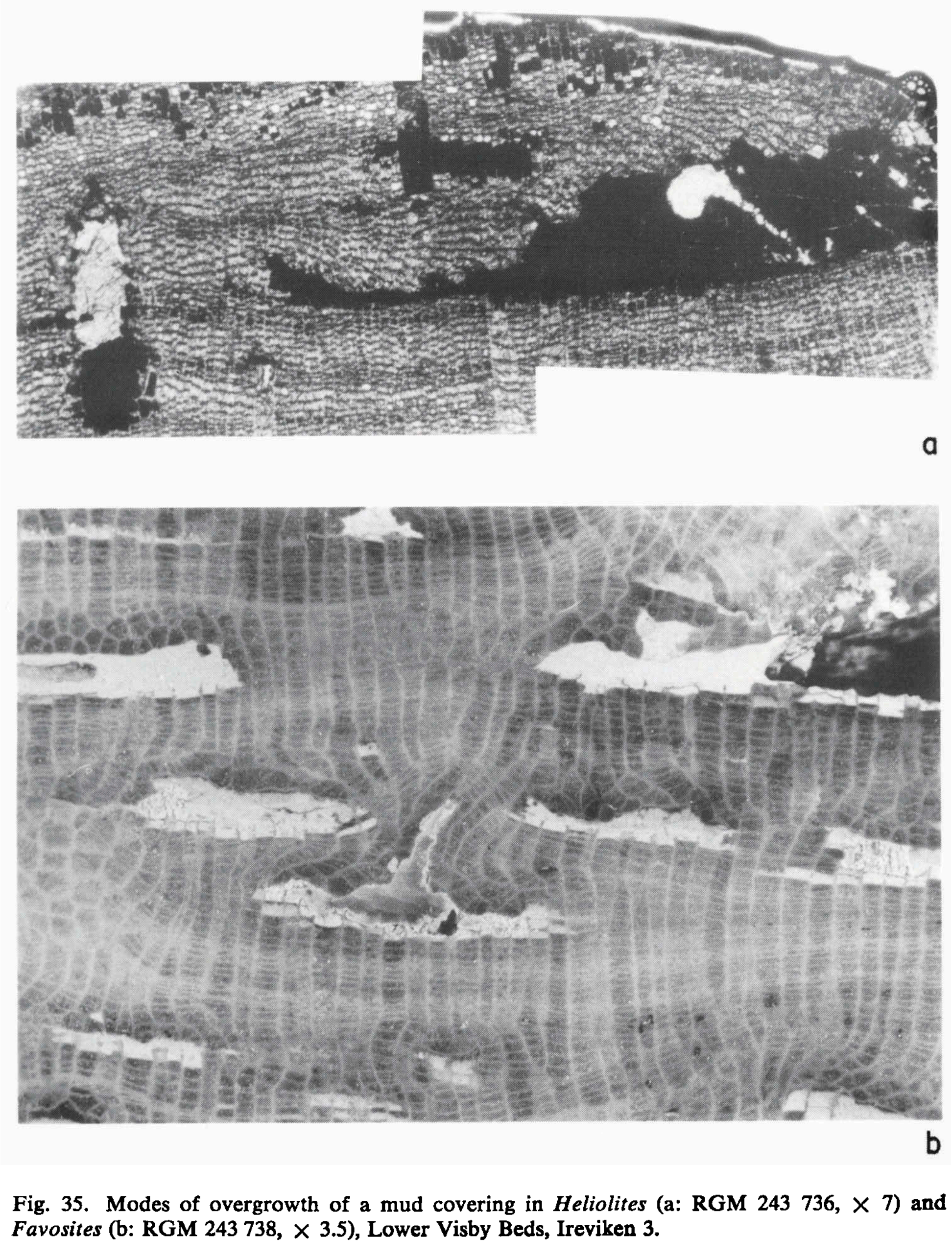

Fig. 35. Modes of overgrowth of a mud covering in *Heliolites* (a: RGM 243 736, × 7) and *Favosites* (b: RGM 243 738, × 3.5), Lower Visby Beds, Ireviken 3.

of the double-wall (Oekentorp & Schouppé, 1969) is not observed. Moreover, as the pores mostly are arranged in 1 - 3 rows, the present author considers these 'corner pores' as ordinary mural pores situated in the periphery of the wall. The diameter of these pores is about 0.15 mm.

In reptant parts of the colony, tabulae distance is mostly large, whereas in the other part of the colony, zones with closely spaced tabulae occur (Fig. 37). Larger spacing between the tabulae is always accompanied by thinner double-walls and a less pronounced development of the septal formations. In zones with closely spaced tabulae a luxuriant development of the septal spines sometimes occurs and causes a thick double-wall. These observations confirm Sokolov's (1962) correlation between growth rate and tabulae distance. The correlation between thickness of the double-wall and the intensity of the septal spines is the result of a comparatively low growth rate. This is indicated by the coinciding distribution of zones with closely spaced tabulae. As such zones with closely spaced tabulae always are related — even if a repetitive sequence of such zones occurs — to mud-coverings, the author supposes that this zonation is caused by ecological factors, and genetical control (Klaamann, 1970) is considered to be unlikely.

Chaetosalpinx huismani Stel is sometimes found in *F. hisingeri.* It is a striking fact that this endobiont is infrequently noticed in this tabulate while it is found in almost every heliolitid (Fig. 9) from the same biostrome. Borings, which are very common in stromatoporoids and heliolitids, sometimes also occur in *F. hisingeri.* Some rare colonies (Fig. 38) are intensively bored; these borings are starlike because of the honeycomb character of the surface of the colony. Pyrite cubes are frequently observed within the colonies.

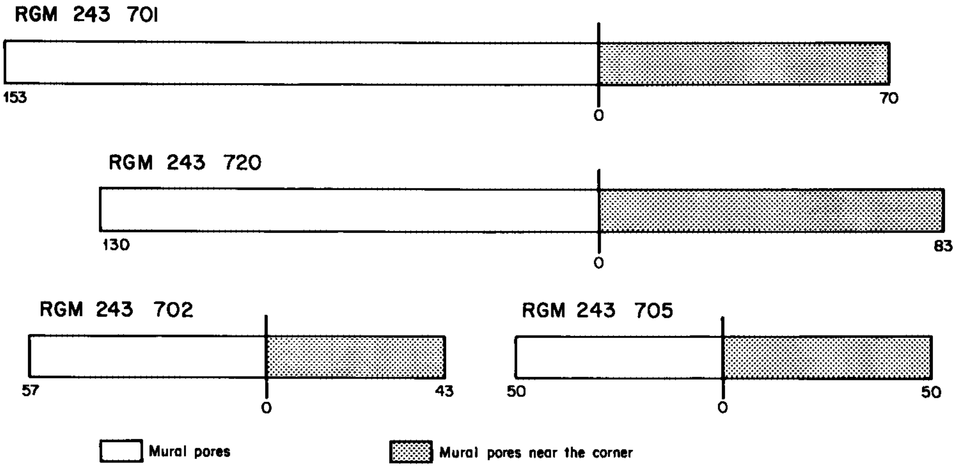

Fig. 36. Diagrams of countings of mural pores and pores near a corner in four *Favosites hisingeri* colonies, Lower Visby Beds, Ireviken 3.

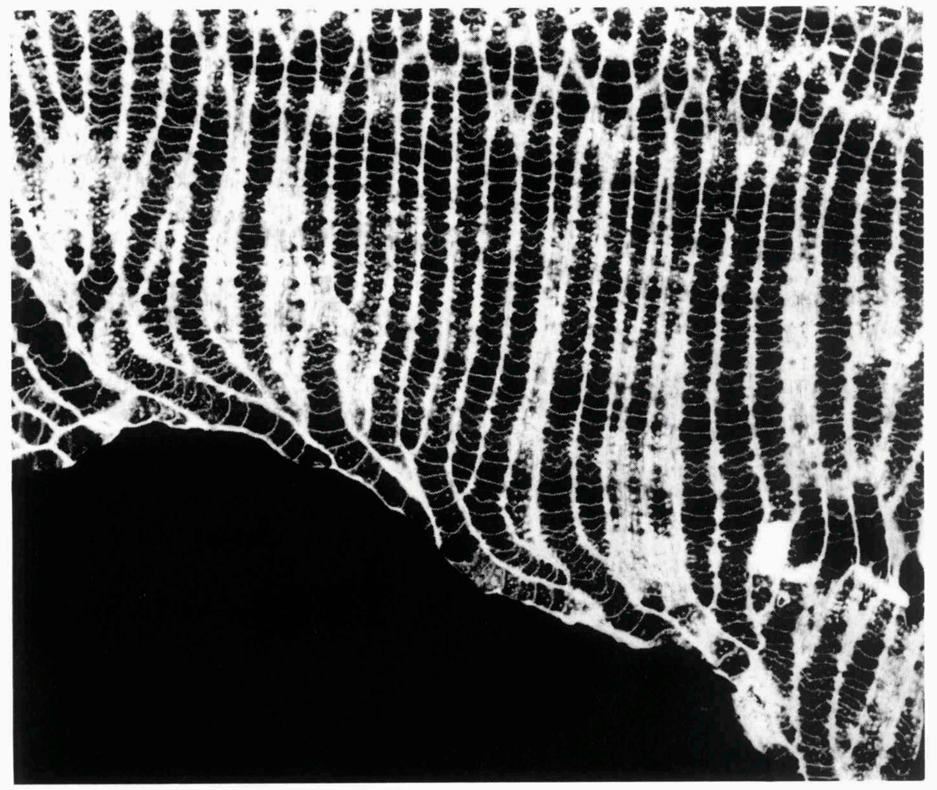

Fig. 37. Variation in distance of tabulae, wall thickness and development of spines in a longitudinal section of a *Favosites hisingeri* colony, Visby Beds, Nyhamn 7, RGM 243735, × 5.

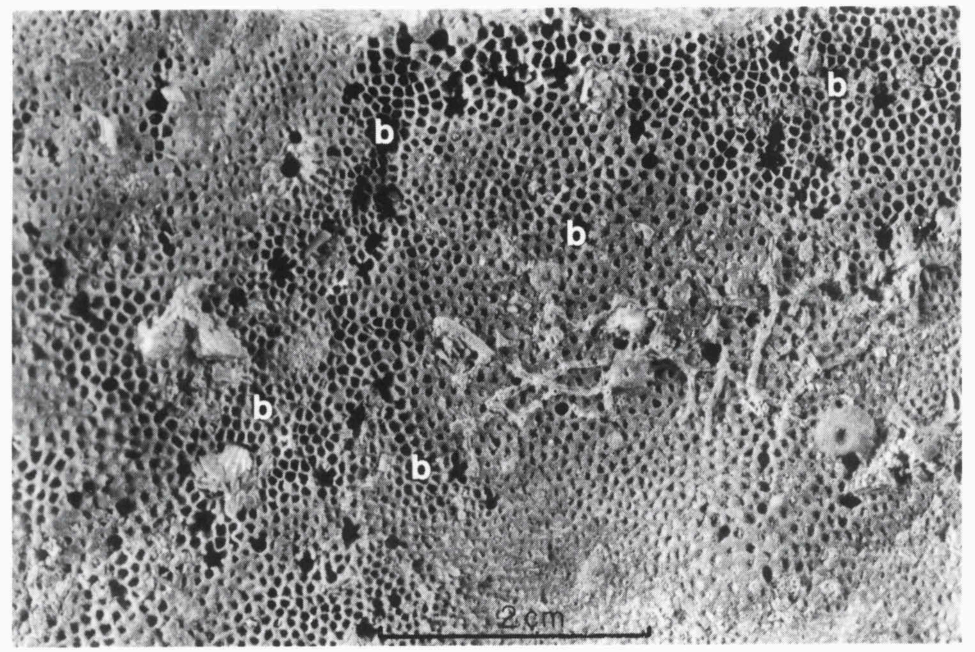

Fig. 38. Borings in a *Favosites hisingeri* colony, Lower Visby Beds, Ireviken 3, RGM 243 705.

Morphology of *Favosites obliquus* (Sokolov, 1951)

Sokolov (1951) established the genus *Mesofavosites* for favositids with both mural and corner pores. The author thinks that most *Mesofavosites* should be classified as *Favosites,* because the undulation of the walls near the 'corner pores' is lacking. As this undulation is not observed in the colonies described below, the author assigned these colonies to *Favosites.*

A dozen colonies of *F. obliquus* were collected from beach-rubble between Nyhamn and Ireviken. These colonies probably were derived from the reefs and mixed clastic carbonates of the Högklint Beds.

Favosites obliquus (Sokolov, 1951)

1951b *Mesofavosites obliquus* sp. nov. — Sokolov, p. 70 - 72, pl. 30, figs. 1 - 4.
1952a *Mesofavosites obliquus* Sokolov — Sokolov, p. 21 - 22, pl. 6, figs. 3 - 5.
1952a *Mesofavosites obliquus* var. *major* var. nov. — Sokolov, p. 22 - 23, pl. 7, figs. 1 - 2.
1952a *Mesofavosites bonus* sp. nov. — Sokolov, p. 23 - 24, pl. 7, figs. 3 - 4.
1962a *Mesofavosites obliquus secundus* subsp. nov. — Klaamann, p. 80, pl. 7, figs. 1 - 3, 6.
1964 *Mesofavosites obliquus* Sokolov — Klaamann, p. 54 - 56, pl. 16, figs. 1 - 5.
1964 *Mesofavosites bonus* Sokolov — Klaamann, p. 56.
1964 *Mesofavosites major* Sokolov — Klaamann, p. 57.
1964 *Mesofavosites secundus* Klaamann — Klaamann, p. 57 - 58, pl. 16, figs. 8 - 10.
1975 *Mesofavosites obliquus* Sokolov — Stel, p. 66, pl. 25.

Diagnosis of Sokolov (1951b, p. 70 - 72; translated by Dr P. Oprsal) — The form of the colony is flat or disc-like. The corallites are uniform; the diameter is 1.4 - 1.9 mm. The double-wall is thick and shows large septal spines. Pores are arranged in 1 - 2 rows; the diameter is 0.14 - 0.17 mm. Zones of closely spaced (0.15 - 0.40 mm) and widely spaced (0.6 - 1.0 mm) tabulae are found.

Description — The form of the colony is hemispherical or platy. The corallites are polygonal and of about equal size. Some extremely large corallites, with an area of 8 mm² are found in sample RGM 243 707. These corallites are scattered at random between the other corallites and the grounds leading to the devolopment of these corallites are difficult to guess. However, such corallites might be a result of dissolution of the wall during diagenesis.

The graphs shown in Figure 39 were constructed from the data of three coherent parts of one colony. The statistic parameters of the characters are summarized in Table 8. The striking difference between these graphs is also indicated by the Sudent's t distribution of the samples. This test would again suggest inequivalency of the three samples. The difference, which could partly be due to sectioning effects, indicates that ecophenotypic variation of corallites within *F. obliquus* is not easily delimited, even when size distribution graphs of the corallite diameter are constructed. If only a limited number of measurings can be done, it should be realized that the graph constructed from these data gives the real phenotypic variation only by approximation. As a consequence small differences between such graphs do not necessarily prove (contrary to Klaamann, 1962, 1964, and Schouppé & Oekentorp, 1974) that the sample data reflect a difference on the species level.

When discussing the affinities of his *M. obliquus* and morphologically related forms as *M. bonus,* Klaamann (1964) considered the small differences

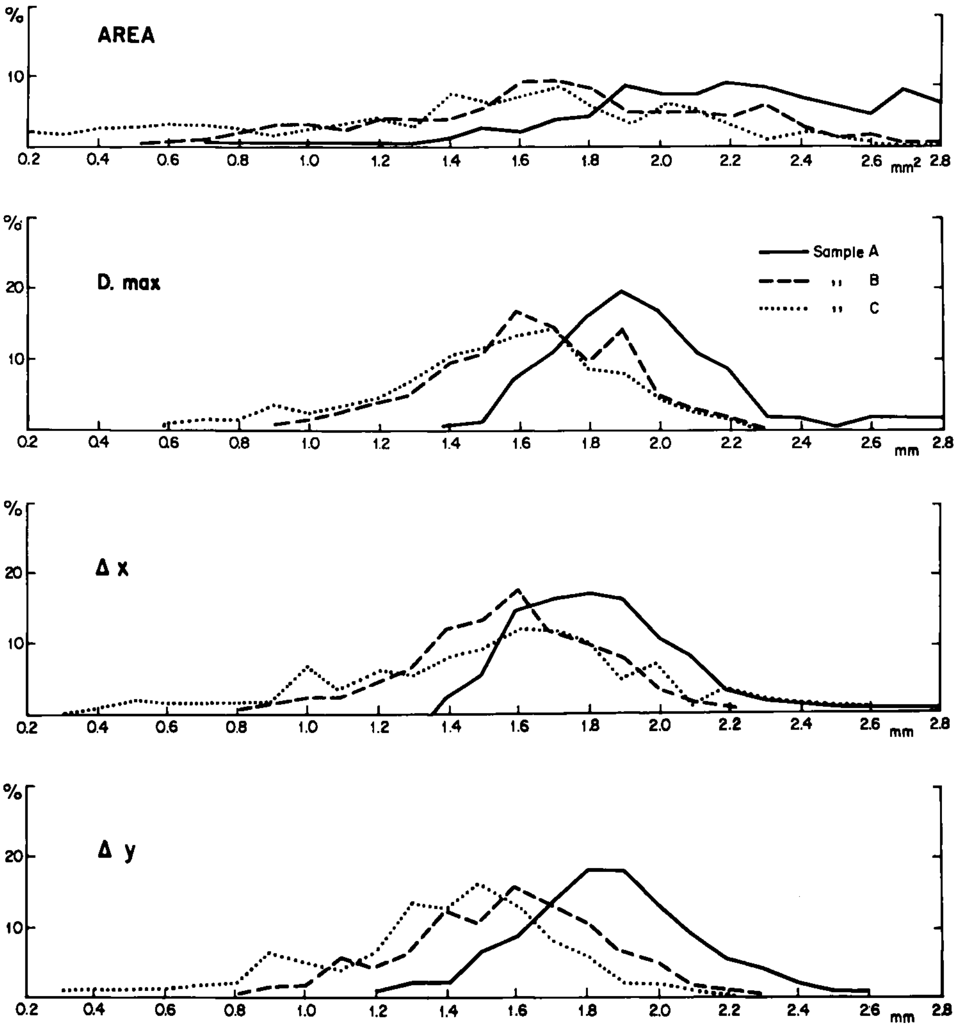

Fig. 39. Frequency distribution in measurings on a peel from a *Favosites obliquus* colony, Högklint Beds, Lundsklint, RGM 243 707.

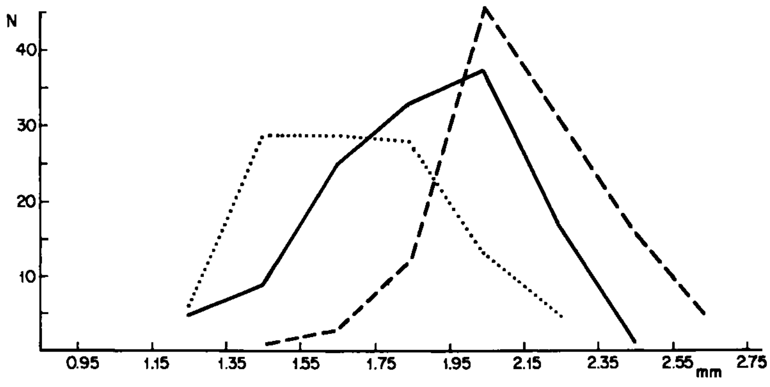

Fig. 40. Comparison of the corallite diameter of *Mesofavosites bonus* (stippled line), *Mesofavosites obliquus* (solid line) and *Mesofavosites major* (dashed line) (from Klaamann, 1964, p. 56).

Table 8. Parameters of corallites in three united samples of an acetate peel of a *Favosites obliquus* colony (RGM 243 707) and in a thin section of another colony (RGM 243 721).

Sample RGM 243 707 Högklint Beds, Lundsklint

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	2.36	0.68	1.65	9.92	0.20	6.10	2.28	249
Dmax	1.97	0.30	1.75	7.52	1.40	3.30	1.93	249
Δx	1.87	0.29	1.37	9.07	1.20	3.50	1.85	249
Δy	1.89	0.40	2.80	14.43	1.20	4.30	1.82	249
Area	1.73	0.64	1.42	9.87	0.30	5.90	1.70	385
Dmax	1.66	0.33	1.10	8.73	0.80	3.70	1.65	385
Δx	1.58	0.31	0.11	3.89	0.40	2.70	1.59	385
Δy	1.60	0.35	1.65	10.57	0.60	3.80	1.59	385
Area	1.47	0.67	0.09	3.02	0.10	3.60	1.53	216
Dmax	1.52	0.39	—0.21	4.26	0.40	2.80	1.56	216
Δx	1.37	0.36	—0.36	3.90	0.30	2.70	1.42	216
Δy	1.53	0.46	0.21	4.77	0.40	3.70	1.57	216

Sample RGM 243 721 Hamra oncolite, Uddvide 1

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	1.71	0.55	—0.65	3.00	0.30	3.10	1.80	153
Dmax	1.63	0.27	—1.03	4.26	0.70	2.20	1.66	153
Δx	1.53	0.27	—0.86	3.90	0.60	2.00	1.57	153
Δy	1.62	0.31	—0.49	4.90	0.60	2.80	1.65	153

between the variation of the corallite diameters (Fig. 40) as decisive. Therefore the latter two were not described as variants of *M. obliquus* (Sokolov, 1952) but as independent species. However, as such differences are within the range of the variability described above, the author considers these species as junior synonyms of *F. obliquus*. *M. secundus,* in which no septal spines are found (Klaamann, 1964), also is a junior synonym of *F. obliquus*.

The double-wall is 0.12 - 0.16 mm thick and possesses small (max. length 0.44 mm) septal spines. The pores are arranged in 1 - 3 rows; the diameter is about 0.20 mm. Alternating zones of closely and widely spaced tabulae are found.

Morphology of *Syringolites kunthianus* (Lindström, 1896)

In 1879 Hinde established the genus *Syringolites,* to which he assigned favositids with infundibuliform tabulae forming a central tube. Although this new genus seems closely allied to *Roemeria* Edwards & Haime, Hinde — after having studied Goldfuss's type specimen of *'Calamopora' infundibulifera* — considered the type species *Syringolites huronensis* as different because:

(1) Corallites in *Roemeria* diverge peripherally; as a consequence they are cylindric in later stages.

(2) Corallites in *Roemeria* are thick-walled.

(3) No pores were observed by Hinde in *Roemeria* (although mentioned by Goldfuss).

(4) No axial tube was found in the holotype of the type species of *Roemeria*.

Nicholson (1879, 1889) follows Hinde and also considered *Roemeria* and *Syringolites* as distinct genera. Schlüter (1889), however, considered *Syringolites* as a junior synonym of *Roemeria*. Lindström (1896) described *Roemeria kunthiana* as a new species from the Silurian of Gotland. After comparison of *R. kunthiana* with some specimens of *S. huronensis*, Lindström concluded that these species were different.

These conflicting views have remained a subject of much discussion in the literature; for a historical review the reader is referred to Lecompte (1936). Sokolov (1955) assigned Lindström's *R. kunthiana* to *Syringolites*, a view followed by Klaamann (1964), Stasinska (1967) and the present author. Hill & Jell (1970) thought that *Syringolites* could more likely be referred to the favositids than to the syringoporids because most morphologic features of *Syringolites* would be favositoid. Such favositoid characters are the thin walls of the peripherally never diverging corallites, as well as the occurrence of numerous pores. The only syringoporoid feature in *Syringolites* is the presence of an axial tube, which does not (as in syringoporids) divert to communicate with the one of a neighbour through a pore. These authors consider *Roemeria* and related tabulates as syringoporids because the corallites more or less diverge peripherally and the axial tubes communicate through pores.

According to the present author, Hill & Jell's emphasis on the different morphological arrangement of the axial tube in *Syringolites* and *Roemeria* does not warrant their conclusions about the systematic position of these tabulates. The present author, moreover, labelled such favositids with an axial tube as *S. kunthianus*, because topotypical material of *Roemeria* is not available to present a detailed comparison of Gotland material and other morphologically related specimens.

Six colonies of *S. kunthianus* were collected from the beach rubble between Nyhamn and Ireviken, which is probably derived from the Upper Visby Beds and

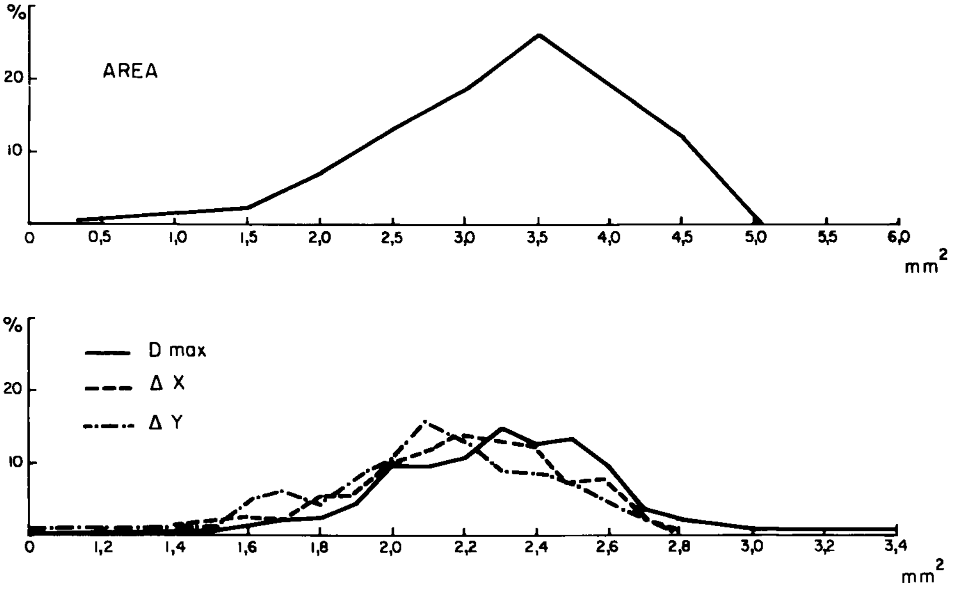

Fig. 41. Frequency distribution in measurings on two thin sections of a colony of *Syringolites kunthianus*, Högklint Beds, Nyhamn 10, RGM 243 708.

the Högklint Beds and one was collected from the Hemse Beds at Snoder 1. Additional observations were obtained from a dozen erratic boulders, found in the neighbourhood of Groningen, The Netherlands.

Syringolites kunthianus (Lindström, 1896)

1896 *Roemeria kunthiana* sp. nov. — Lindström, p. 14 - 17, pl. 2, figs. 19 - 25, pl. 3 figs. 26 - 29.
1933 *Roemeria kunthiana* Lindström — Tripp, p. 130 - 131, pl. 16, fig. 3.
1949 *Roemeria kunthiana* Lindström — Sokolov, p. 87, pl. 8, figs. 13 - 14.
1955 *Syringolites kunthianus* (Lindström) — Sokolov, p. 160 - 163, pl. 11, figs. 1 - 5.
1961 *Syringolites kunthianus* (Lindström) — Klaamann, p. 82 - 83, pl. 8, figs. 3 - 4.
1964 *Syringolites kunthianus* (Lindström) — Klaamann, p. 75 - 76, pl. 11, figs. 1 - 5.
1967 *Syringolites kunthianus* (Lindström) — Stasinska, p. 86 - 87, pl. 26, fig. 1.

Diagnosis of Lindström (1896, p. 14 - 17) — The form of the colony is discoidal, tuberiform, or hemispheroidal. The polygonal corallites have an average diameter of 2 mm. The double walls are thin, but show a distinct dark line. Spines are found on both the wall and on top of the tabulae. Funnel-shaped tabulae form an axial tube.

Description — The shape of the colonies varies from discoidal to hemispheroidal. Colonies of *Syringolites kunthianus* are easily recognized because of the regular

Table 9. Parameters of corallites in two thin sections of a *Syringolites kunthianus* colony from Gotland (RGM 243 708) and in thin sections of colonies found as erratic boulders in The Netherlands (RGM 243 709 - 243 710).

Sample RGM 243 708 I-II Högklint Beds, Nyhamn 10

		$\bar{x}$	S	Sk	K	min.	max.	G	N
I :	Area	3.17	0.73	—0.27	2.66	1.30	4.70	3.22	136
	Dmax	2.31	0.31	0.34	3.85	1.60	3.40	2.32	136
	Δx	2.18	0.28	—0.49	2.94	1.40	2.70	2.21	136
	Δy	2.16	0.37	0.81	5.52	1.40	3.60	2.17	136
II :	Area	3.20	0.86	—0.49	2.99	0.30	5.00	3.28	170
	Dmax	2.26	0.33	—0.78	4.94	0.80	3.10	2.28	170
	Δx	2.18	0.35	—0.79	4.29	0.70	2.90	2.22	170
	Δy	2.10	0.35	—0.76	4.25	0.70	2.80	2.12	170
I + II :	Area	3.18	0.80	—0.42	2.95	0.30	5.00	3.24	306
	Dmax	2.28	0.32	—0.35	4.72	0.80	3.40	2.30	306
	Δx	2.18	0.32	—0.71	4.13	0.70	2.90	2.21	306
	Δy	2.13	0.36	0.04	5.16	0.70	3.60	2.14	306

Sample RGM 243 709 Erratic boulder, Groningen

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	2.73	0.83	—0.82	3.04	0.20	4.30	3.01	127
Dmax	2.09	0.33	—1.24	5.78	0.60	2.60	2.13	127
Δx	1.97	0.35	—0.95	4.61	0.60	2.60	1.98	127
Δy	2.00	0.37	—0.97	3.98	0.60	2.70	2.09	127

Sample RGM 243 710 Erratic boulder, Groningen

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	1.47	0.50	—0.40	2.78	0.20	2.80	1.52	297
Dmax	1.52	0.28	—0.73	3.73	0.60	2.20	1.57	297
Δx	1.44	0.29	—0.54	3.52	0.60	2.10	1.47	297
Δy	1.44	0.27	—0.63	3.23	0.50	2.00	1.48	297

arrangement of apparently equally large, polygonal corallites. The graphs in Figure 41 are constructed from the data of 305 measurings from two samples of a colony (RGM 243 708). The data of the corallite area measurings vary considerably: they range from 0.3 - 5.6 mm^2, more frequently from 2.2 - 4.5 mm^2. The corallite diameter measurings are almost normally distributed; they range from 1.30 - 3.0 mm, but a diameter of 2.0 - 2.5 mm predominates. The statistic parameters of the data are listed in Table 9. Among the erratic boulders a fragment (Fig. 42) was found showing diverging data, but ecophenotypic variation of *S. kunthianus* is not well known.

In erratic syringolitids some corallites are noticed which temporarily joined. In such cases a joint axial tube (Fig. 43b) is sometimes formed, but more often cooperation in the secretion of tabulae is observed (Fig. 45). Such cooperative behaviour of neighbouring corallites is also seen in *S. kunthianus* colonies from Gotland. In longitudinal sections tabulae frequently are traced from one corallite to several neighbouring corallites (Fig. 44). In transverse sections the double-wall may be a straight or an undulating line. The thickness of the double-wall is 0.12 - 0.16 mm in places without septal spines, but varies from 0.24 - 0.30 mm (or even more) where these spines are also present (Fig. 46). The pores are extremely numerous and are arranged in 1 - 3 rows; the diameter is 0.16 - 0.24 mm, but in average 0.20 mm. When these mural pores are situated near the corner of the corallite, corner-like pores (Fig. 44) are observed. Both incomplete and complete tabulae occur. Incomplete tabulae only form a part of the axial tube. Complete tabulae also shut off the axial tube. Septal spines, with a maximum length of 0.60 mm, are found together with tabular spines.

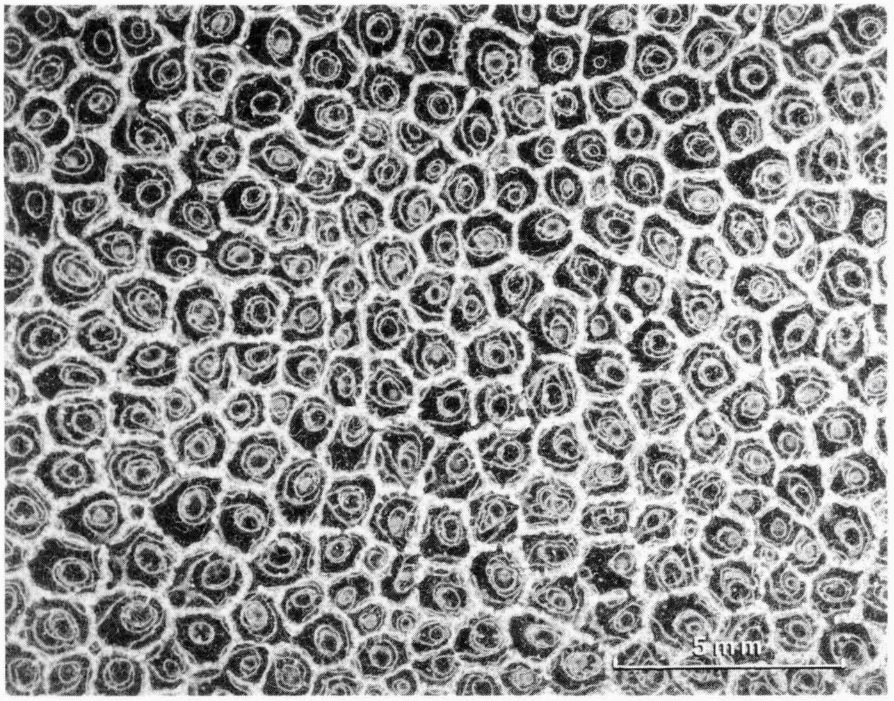

Fig. 42. Measured thin section of *Syringolites kunthianus*, erratic boulder, Groningen, The Netherlands, RGM 243 710, × 6.

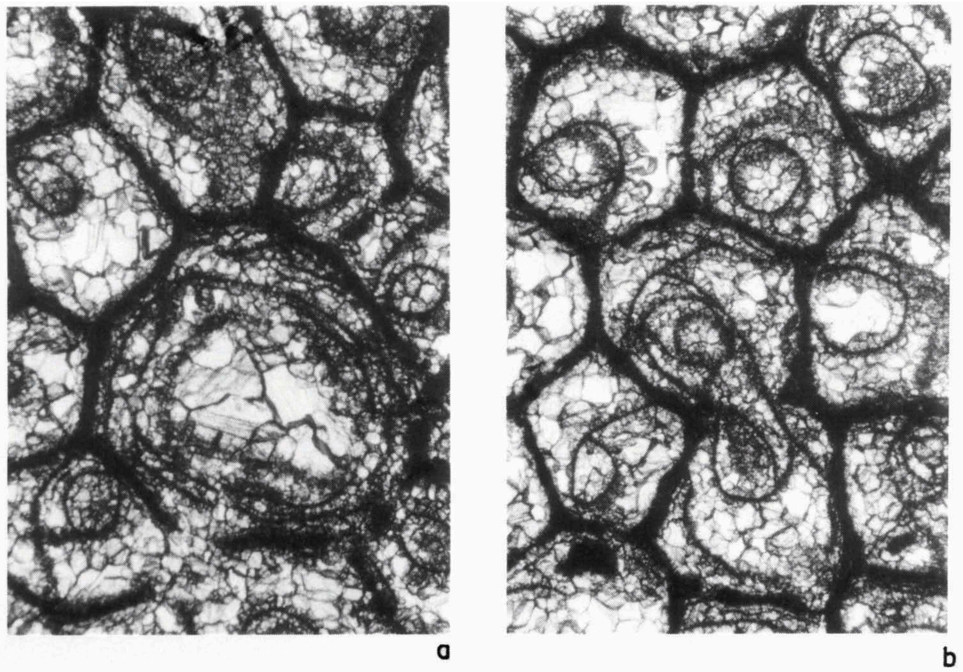

Fig. 43. Transverse section of *Syringolites kunthianus* with a large corallite (a) and **fusion** of tabulae in neighbouring corallites (b). Note the presence of thin double-walls and the lack of spines. Erratic boulder, Groningen, The Netherlands, RGM 243 740, × 14.

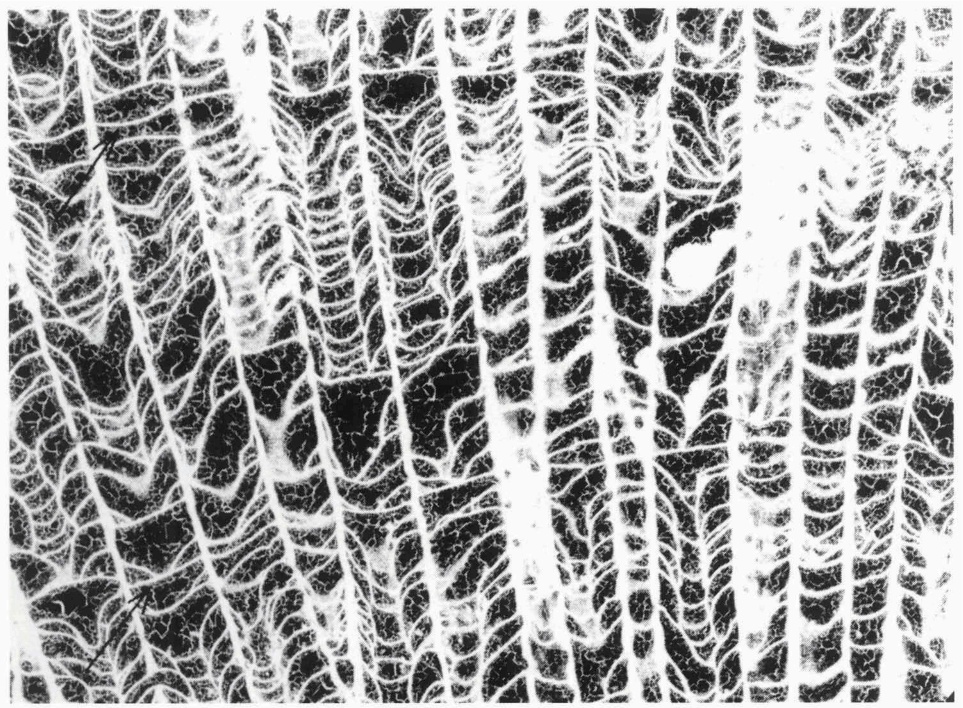

Fig. 44. Longitudinal section of *Syringolites kunthianus* with simultaneous formation of tabulae in different corallites. Up to three rows of mural pores are seen. Erratic boulder, Groningen, The Netherlands, RGM 243 741, × 6.

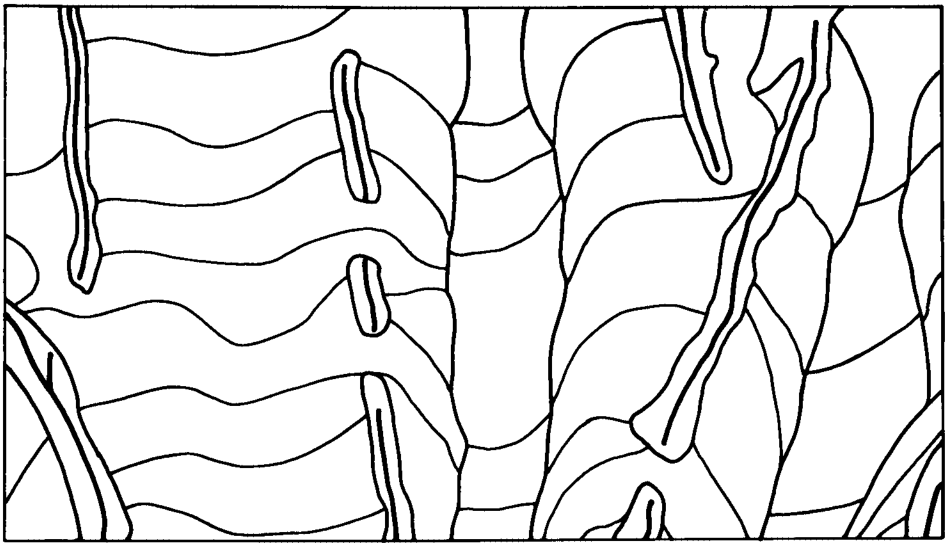

Fig. 45. Longitudinal section of *Syringolites kunthianus* with tabulae in mural and apical pores, erratic boulder, Groningen, The Netherlands, RGM 243 744, × 20.

Serial sections of a *S. kunthianus* colony revealed, that the so-called intermural increase in this tabulate actually is lateral increase.

Comparison of the specimens of *S. kunthianus* described by Klaamann (Estonia), Stasinska (Gotland) and those mentioned above with the morphologic data observed by Hill & Jell (1970) in their *S. huronensis,* suggest that they most likely are synonymous.

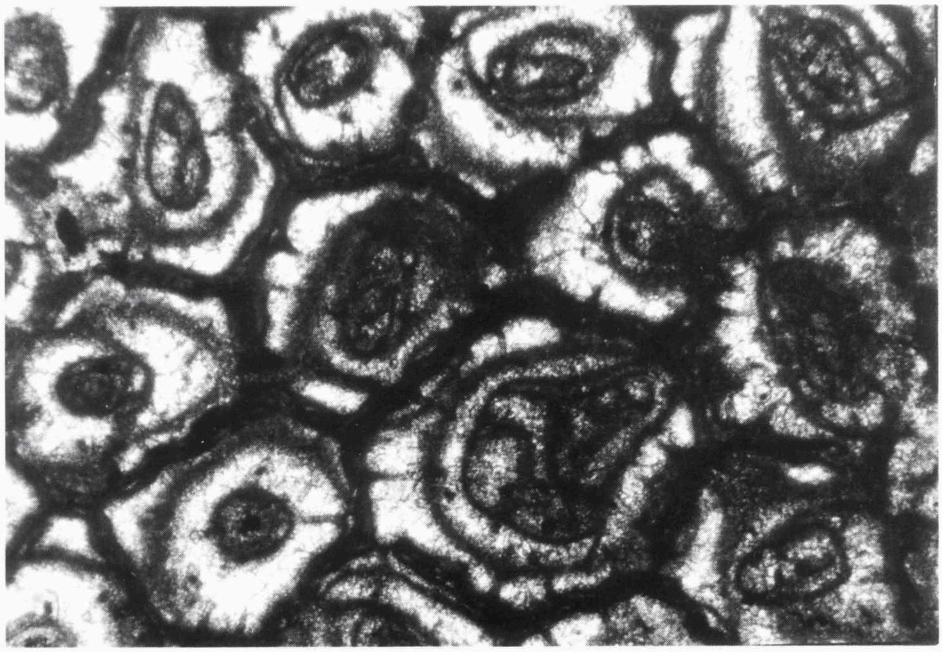

Fig. 46. Transverse section of *Syringolites kunthianus* with thick double-walls and spines, Högklint Beds, Nyhamn 10, RGM 243 708, × 16.

Morphology of *Favosites gothlandicus* Lamarck, 1816

Lamarck (1816) established *Favosites gothlandicus* upon material from Gotland, since then lost. He described this species as follows: '*Favosites* prismis solidis, hexaedris, contiguis. Les prismes petits, parallèles et réunis comme des prismes de basalte, paraissent, dans des parties cassées de leur masse, offrir des cubes anguleux, remplis de matière pierreuse, et divisés par des cloisons transversales'. Although nowadays this description is insufficient, Lamarck probably also referred to a favositid figured in Linnaeus' thesis (1745). Fought (1749), to which Linnaeus had submitted this thesis, was the first (see Sokolov, 1952a) to describe and figure a favositid under the name *Corallium gothlandicum.* Edwards & Haime (1855) ranged this specimen under *Favosites gothlandicus.* Goldfuss (1826 - 1833) gives a description and a lithograph of *Calamopora gothlandica,* chosen later by Jones (1936) as the neotype of the species and the lectotype of the genus. Nicholson (1879) stressed the characteristic uniform size and the occurrence of thin walls in *Favosites gothlandicus* while, in contrast, a conspicuous inequality of the size of the corallites was typical of *Favosites forbesi* Edwards & Haime. Tripp (1933) described an extensive 'form complex' of *F. gothlandicus* from Gotland, in which all variations from colonies with small corallites towards colonies with large corallites are found. When studying Tripp's collections (Senckenberg Museum, Frankfurt am Main, Federal Republic of Germany) the present author noticed that several species, such as *F. forbesi,* are within Tripp's *F. gothlandicus* 'form complex'.

Jones (1936) studied the environmental effects upon favositid colonies. As a result of this study Jones concluded that *F. gothlandicus, F. forbesi* and *F. multipora* Lonsdale were in fact ecophenotypes of the same species. Although in the neotype of *F. gothlandicus* uniform corallites occur, Jones supposed that these grade into such colonies with differentiated corallites, which Edwards & Haime (1851) labelled as *F. forbesi.* Size differentiation was, according to Jones, caused by growth of the colony because within the same colony both types were observed. Jones founded this view on the fact that even in colonies of *F. gothlandicus,* with uniform corallites at the surface, differentiated corallites occur when these colonies are sectioned parallel to their flat bases. From the changes in size and position of some corallites in a *F. forbesi* colony Jones concluded that this differentiation in size is related to the rate of offset formation. The degree of uniformity of the corallites depends upon the environment, just as the presence or absence of septal spines. As a consequence, Jones considered *F. forbesi* and *F. multipora* as 'formae' (ecophenotypes) of *F. gothlandicus.*

Sokolov (1952a) rejects Jones's artificial 'formae' and considers such a differentiation in corallite size as the result of fast offset formation which is typical of *F. forbesi.* On the other hand uniform size of the corallites in *F. gothlandicus* is a characteristic feature of this species. So far the present author agrees with Sokolov's views, but he thinks that the variants of *F. gothlandicus,* described by Sokolov, are artificial because they are founded on features such as distance between the tabulae, which are influenced to a high degree by the environment. The views of Sokolov (1950 - 1955) were followed by Klaamann (1962, 1964), Stasinska (1967) and Stel (1975).

Sutton (1966) found that the morphological characters which Jones used to distinguish his 'formae' actually were caused by environmental factors. Although Sutton thought that environmental conditions had little effect upon the size of adult corallites, he did not reject Jones's large range of the corallite diameter in *F. gothlandicus*.

The author collected two typical *F. gothlandicus* colonies from the Hemse Marl at Snoder 1, 2 (Laufeld, 1974a). Part of the colony surface of one colony has been measured. The lithology and palaeoecology of the Hemse Beds were discussed before (p. 17).

Favosites gothlandicus Lamarck, 1816

1816 *Favosites gothlandicus* sp. nov. — Lamarck, p. 206.
1829 *Calamopora gothlandica* sp. nov. — Goldfuss, p. 78, pl. 26, figs. 3a, 3c.
1851 *Favosites gothlandica* Lamarck — Edwards & Haime, p. 232 - 233.
1855 *Favosites gothlandica* Lamarck — Edwards & Haime, p. 256, pl. 60, figs. 1, 1a.
1879 *Favosites gothlandica* Lamarck — Nicholson, p. 46 - 56, fig. 14, pl. 1, figs. 1 - 6.
1933 *Favosites gothlandicus* Lamarck — Tripp, p. 101.
1936 *Favosites gothlandicus* Lamarck — Jones, p. 2 - 14, pl. 1, figs. 1 - 12.
1951b *Favosites gothlandicus* Lamarck — Sokolov, p. 78 - 86, pl. 31, figs. 4 - 6.
1952a *Favosites gothlandicus* Lamarck — Sokolov, p. 29 - 31, pl. 10, figs. 1 - 2.
1964 *Favosites gothlandicus* Lamarck — Klaamann, p. 59 - 60, pl. 17, figs. 3 - 4.
1967 *Favosites gothlandicus* Lamarck — Stasinska, p. 80, pl. 23, fig. 3.
1975 *Favosites gothlandicus* Lamarck — Stel, p. 79 - 81, pl. 42.

Diagnosis of Sokolov (1952a, p. 29 - 31 translated by Dr P. Oprsal) — The colonies are massive and mostly hemispherical or oblate ellipsoidal. The uniform polygonal corallites have a diameter of 2.0 - 3.0 mm; mostly 2.5 - 3.0 mm. The double-wall is thin. The distance between the tabulae is more or less the half of the corallite diameter. Pores are arranged in two rows; the diameter is 0.2 - 0.3 mm. Septal spines are short.

Description — The colonies are hemispherical, but somewhat flattened. Preferential growth of the colonies is indicated by the excentric position of the first corallites.

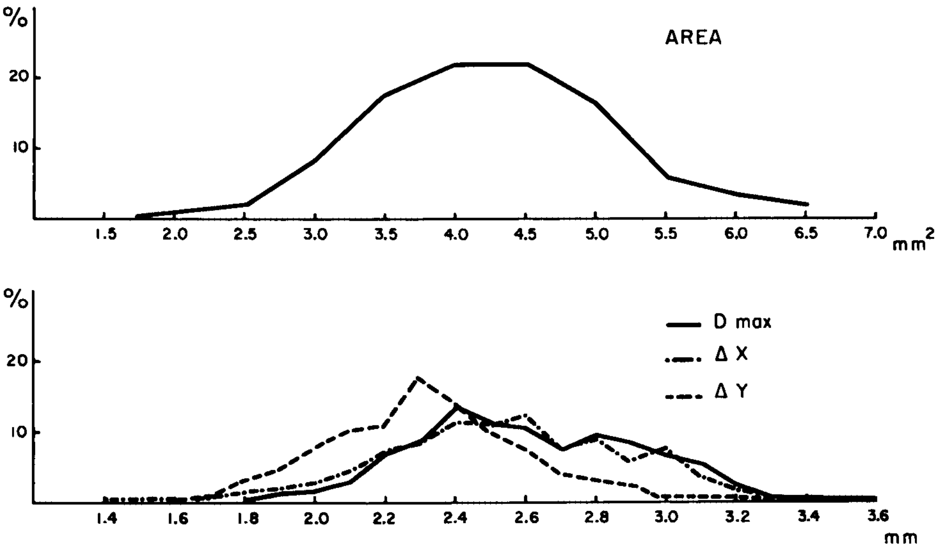

Fig. 47. Frequency distribution in measurings on scan micrographs of samples of a *Favosites gothlandicus* colony, Hemse Beds, Snoder 1, RGM 243 711.

Table 10. Parameters of corallites in scan micrographs of surface samples of a *Favosites gothlandicus* colony, RGM 243 711.

Sample RGM 243 711 Hemse marl, Snoder 1

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	4.03	0.86	0.17	2.95	1.70	6.50	4.03	336
Dmax	2.62	0.34	0.30	2.85	1.80	3.60	2.58	336
Δx	2.54	0.35	—0.15	2.77	1.40	3.40	2.55	336
Δy	2.33	0.30	0.78	5.74	1.60	4.00	2.31	336

The graphs, shown in Figure 47, were constructed from the data of 336 measurings of samples from the surface of a *F. gothlandicus* colony (RGM 243 711). The data of the area measurings are normally distributed and range from 2.5 - 6.0 mm^2. The ranges of the corallite diameters vary to some extent as a result of different methods. The graphs of Dmax and Δx are almost identical, whereas the graph of Δy differs from the former two. This indicates that the polygonal corallites are somewhat compressed. The statistic parameters of the characters are listed in Table 10.

The range of the corallite diameters corresponds with the variation Sokolov (1952a) and Klamann (1962) observed in Estonian specimens of *F. gothlandicus*. However, the data differ considerably from the size ranges Sutton (1966) found in specimens from the British Wenlock Limestone. Sutton founded his concept of *F. gothlandicus* on Jones's (1936) paper and the favositids studied by this author must be ascribed to *F. forbesi*, as defined in the present paper.

Variation in the other morphological features fits with the descriptions of Sokolov (1952a), Klaamann (1962) and Stel (1975).

Morphology of *Favosites forbesi* Edwards & Haime, 1851

In 1851 Milne-Edwards & Haime described favositids with a differentiation of large, almost round corallites between small, polygonal corallites as *Favosites forbesi*. Nicholson (1879) also characterized *F. forbesi* by the conspicuous inequality of the corallites: the smaller corallites are polygonal whereas the larger ones are cylindrical. Nicholson also noticed marked differences between young and old colonies. In young, generally discoidal, colonies large corallites predominate, whilst in old, generally hemispherical, colonies the size differentiation is less conspicuous because few small corallites occur.

Girty (1895), in studying the ontogeny of *F. forbesi*, noticed that a colony is founded by a single corallite in the so-called auloporoid stage. This process is also observed in other tabulates like *Michelinia convexa* d'Orbigny, described by Beecher (1891).

Jones (1936) considered (see also p. 53) *F. forbesi* as an ecophenotype of *F. gothlandicus*, a view rejected by Sokolov (1952a). Sokolov only assigned to *F. forbesi* such favositids with differentiated corallites and a diameter of 0.6 - 2.0 mm. As a result of Sokolov's more or less biometric approach several new species and variants recently have been established.

Stel (1978a) presents proof that in *F. forbesi* both asexual and sexual reproduction could occur; a situation which is compared with gemmule formation in recent sponges.

A hundred colonies of *F. forbesi* were collected from the beach between Nyhamn and Ireviken (Upper Visby and Högklint Beds) and from the Hamra oncolite at Southern Gotland. The Upper Visby and Högklint Beds were laid down in a period during which shoaling of the deposition area occurred. This led to the development of reefs and related environments. The Hamra oncolite is part of a transgressive sequence and was, according to Stel & de Coo (1977), formed in a shallow-marine-current environment.

Favosites forbesi Edwards & Haime, 1851

1851 *Favosites forbesi* sp. nov. — Edwards & Haime, p. 238.
1855 *Favosites forbesi* Edwards & Haime — Edwards & Haime, p. 258, pl. 60, fig. 2.
1879 *Favosites forbesi* Edwards & Haime — Nicholson, p. 57 - 60, pl. 1, fig. 7, pl. 2, figs. 1 - 3, pl. 3, figs. 1 - 2.
1879 *Favosites forbesi* var. *waldronensis* var. nov. — Nicholson, p. 60 - 61, pl. 2, fig. 2.
?1879 *Favosites forbesi* var. *eifelensis* var. nov. — Nicholson, p. 61 - 62, pl. 2, fig. 3, pl. 3, fig. 1.
1879 *Favosites forbesi var. tuberosa* var. nov. — Nicholson, p. 62 - 67, pl. 3, fig. 2.
1895 *Favosites forbesi* Edwards & Haime — Girty, p. 131 - 136, pl. 7, pl. 8 figs. 1 - 5, 23 - 25.
1933 *Favosites forbesi* Edwards & Haime — Tripp, p. 128 - 130, pl. 16, figs. 1 - 2.
1936 *Favosites gothlandicus* forma *forbesi* Edwards & Haime — Jones, p. 9 - 12, pl. 1, figs. 5 - 7.
1951b *Favosites fallax* sp. nov. — Sokolov, p. 90 - 92, pl. 36, figs. 1 - 3.
1952a *Favosites subforbesi* sp. nov. — Sokolov, p. 36 - 38, pl. 13, figs. 3 - 4.
1952a *Favosites multicarinatus* sp. nov. — Sokolov, p. 41 - 43, pl. 15, figs. 1 - 2.
1952a *Favosites forbesi* Edwards & Haime — Sokolov, p. 47 - 49, pl. 17, figs. 3 - 5, pl. 18, figs. 1 - 2.
1952a *Favosites forbesi* var. *similis* var. nov. — Sokolov, p. 49 - 50, pl. 18, figs. 3 - 4.
1952a *Favosites pseudoforbesi* sp. nov. — Sokolov, p. 50 - 52, pl. 19, figs. 1 - 4.
1952a *Favosites pseudoforbesi* var. *muratsiensis* var. nov. — Sokolov, p. 52, pl. 19, figs. 5 - 6.
1952a *Favosites kogulaensis* sp. nov. — Sokolov, p. 52 - 53, pl. 20, figs. 1 - 2.
1952a *Favosites humilis* sp. nov. — Sokolov, p. 57 - 58, pl. 22, figs. 3 - 6.
?1962a *Favosites opinabilis* sp. nov. — Klaamann, p. 35 - 36, pl. 4, figs. 3 - 4.
1962a *Favosites similis* Sokolov — Klaamann, p. 36 - 38, pl. 6, figs. 1 - 6.
1962a *Favosites pseudoforbesi pseudoforbesi* Sokolov — Klaamann, p. 38 - 40, pl. 7, figs. 1 - 3.
1962a *Favosites pseudoforbesi muratsiensis* Sokolov — Klaamann, p. 40 - 41, pl. 8, figs. 1 - 4.
1962a *Favosites pseudoforbesi ohesaarensis* subsp. nov. — Klaamann, p. 41 - 42, pl. 9, figs. 1 - 4, pl. 10, figs. 1 - 2.
1964 *Favosites fallax* Sokolov — Klaamann, p. 66.
1964 *Favosites subforbesi* Sokolov — Klaamann, p. 71.
1966 *Favosites gothlandicus* Lamarck — Sutton, p. 255 - 258, pl. 16.
1967 *Favosites similis* Sokolov — Stasinska, p. 84, pl. 25, fig. 2.
1967 *Favosites pseudoforbesi pseudoforbesi* Sokolov — Stasinska, p. 83 - 84, pl. 24, fig. 4.
1967 *Favosites pseudoforbesi ohesaarensis* Klaamann — Stasinska, p. 84, pl. 25, fig. 3.
1967 *Favosites kogulaensis* Sokolov — Stasinska, p. 81, pl. 23, fig. 1.
1967 *Favosites opinabilis* Klaamann — Stasinska, p. 83, pl. 24, fig. 1.
1975 *Favosites pseudoforbesi* Sokolov — Stel, p. 73, pl. 33.
1975 *Favosites pseudoforbesi muratsiensis* Sokolov — Stel, p. 73 - 75, pls. 34 - 36.
1975 *Favosites pseudoforbesi ohesaarensis* Klaamann — Stel, p. 75 - 76, pl. 37.
1975 *Favosites kogulaensis* Sokolov — Stel, p. 78, pl. 41.

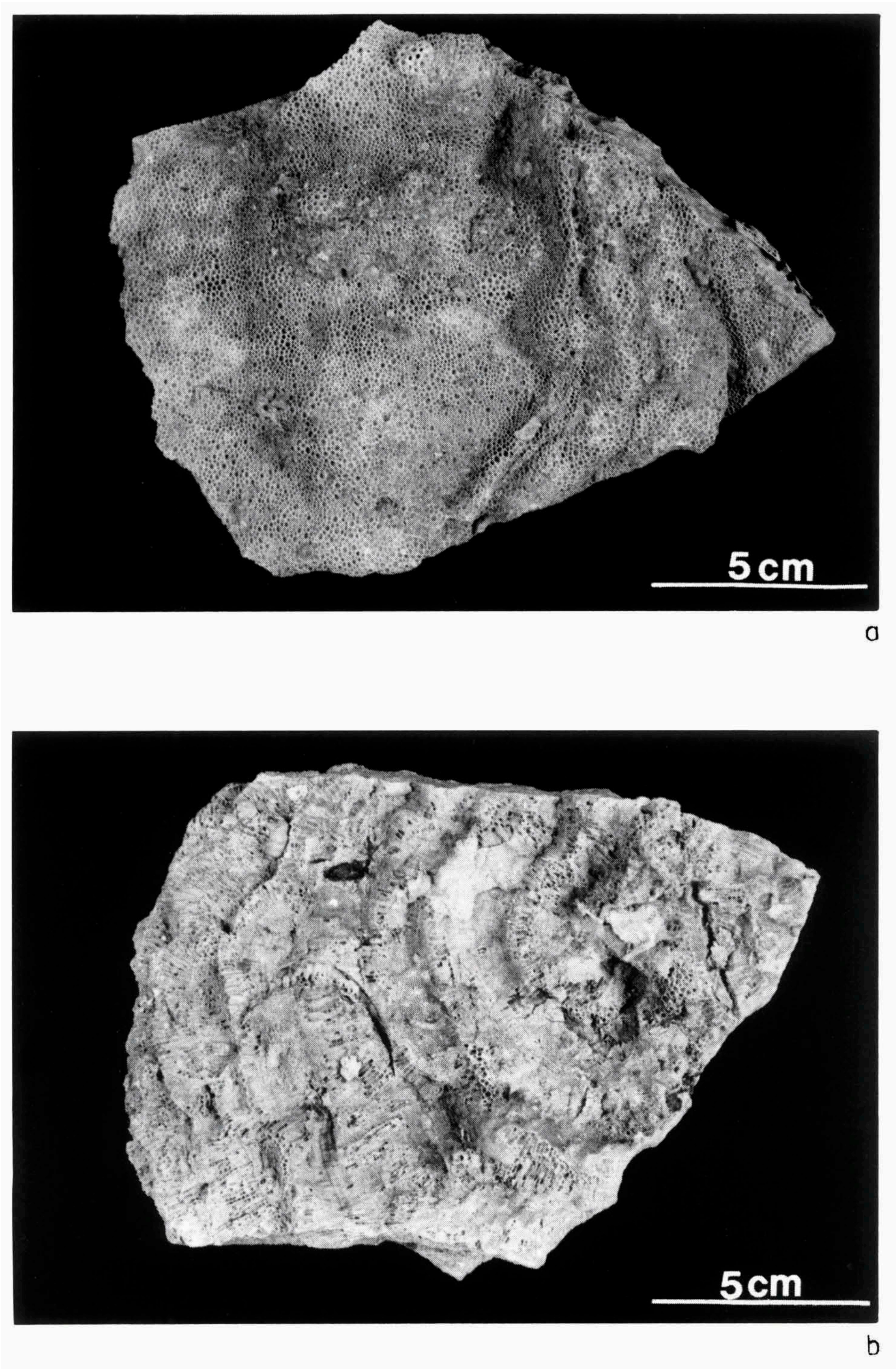

Fig. 48. Foliaceous colony of *Favosites forbesi* with knobs and ridges at its upper surface (a). The pattern of large corallites between smaller ones is absent in the valleys. At the lower surface (b) growth bands and epibionts are seen. Högklint Beds, Ireviken 3 (Snipklint), RGM 243 743.

Diagnosis of Edwards & Haime (1851, p. 239) — Polypier en masse convexe ou subgibbeuse, médiocrement élevée; calices extrêmement inégaux: les plus grands sont ordinairement espacés au milieu des plus petits et souvent presque arrondis, ils ont deux millimètres de diamètre ou rarement plus; les plus petits n'ont que deux tiers de millimètre ou même moins, et on trouve tous les intermédiaires entre ces deux grandeurs, de même qu'on observe tous les passages entre des exemplaires à calices très-inégaux, et d'autres dont les polygones calicinaux sont beaucoup moins différents et moins irréguliers; une section verticale montre des murailles assez minces et des planchers horizontaux, en général serrés mais très-inégalement.

Description — The form of the colonies is hemispheroidal, subhemispheroidal, oblate ellipsoidal, or foliaceous. No striking differences in colony shape were observed between colonies derived from the Upper Visby and Högklint Beds and from the Hamra-Sundre Beds. *F. forbesi* colonies from the Hamra oncolite, however, are mostly smaller than such colonies from the reef and interreef deposits of the area between Nyhamn and Ireviken. In the Högklint reefs large (at least with a diameter of 30 cm), foliaceous (Fig. 48) colonies are found; a growth form never observed in the Hamra oncolite. In all these colonies the differentiation in

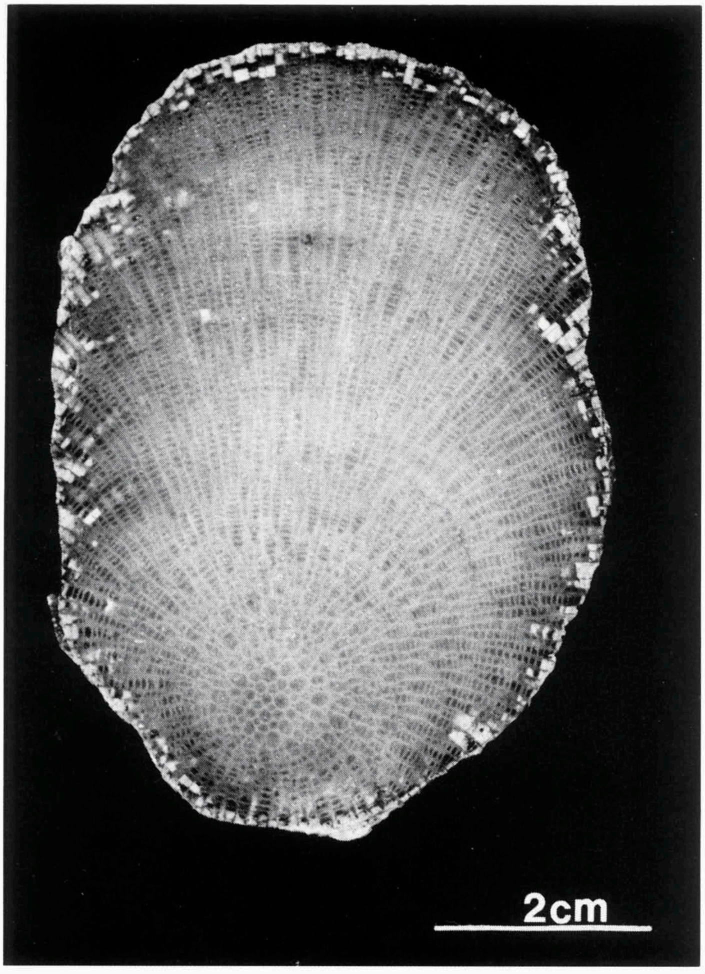

Fig. 49. Circumrotatory colony of *Favosites forbesi*, Hamra-Sundre Beds, Uddvide 2, RGM 243 689.

corallite size is seen. The form of the colony is influenced by both biotic and abiotic factors. Biotic factors, like the interaction of algae or grazing organisms, are described from the Hamra oncolite by Stel & de Coo (1977). Some colonies of *F. forbesi* (Fig. 49) in the Hamra oncolite start growing circumrotatory (Stel, 1978b). The maximum diameter in this growth stage is about 3 cm and is similar to the medium size of oncoids among which they occur. The circumrotatory growth stage is succeeded by a stabilization stage, as the colony grew too heavy to be rolled about. Later preferential growth, caused by currents that favoured growth (increased food supply) at the upstream side of the colony, produced ellipsoidal colonies. The occurrence of currents is also indicated by the form of the colonies found on the beach between Nyhamn and Ireviken.

The size variation of the corallites of *F. forbesi* is considered a characteristic feature of this favositid. Based on such a bimodal distribution (dimetrism) of the corallites, dimorphism of the colonial organisms (Stumm, 1965) is sometimes assumed. Ross (1953) noticed that dimetrism is related to crowding of the corallites; some attain the adult size, others do not. The larger corallites usually project slightly above the surrounding surface suggesting that they grew faster. However, in colonies of *F. forbesi* this is unlikely as is indicated by the rounded-polygonal shape (Fig. 50) of the larger corallites. If these corallites indeed had grown above the surrounding surface, cylindrical corallites would have developed.

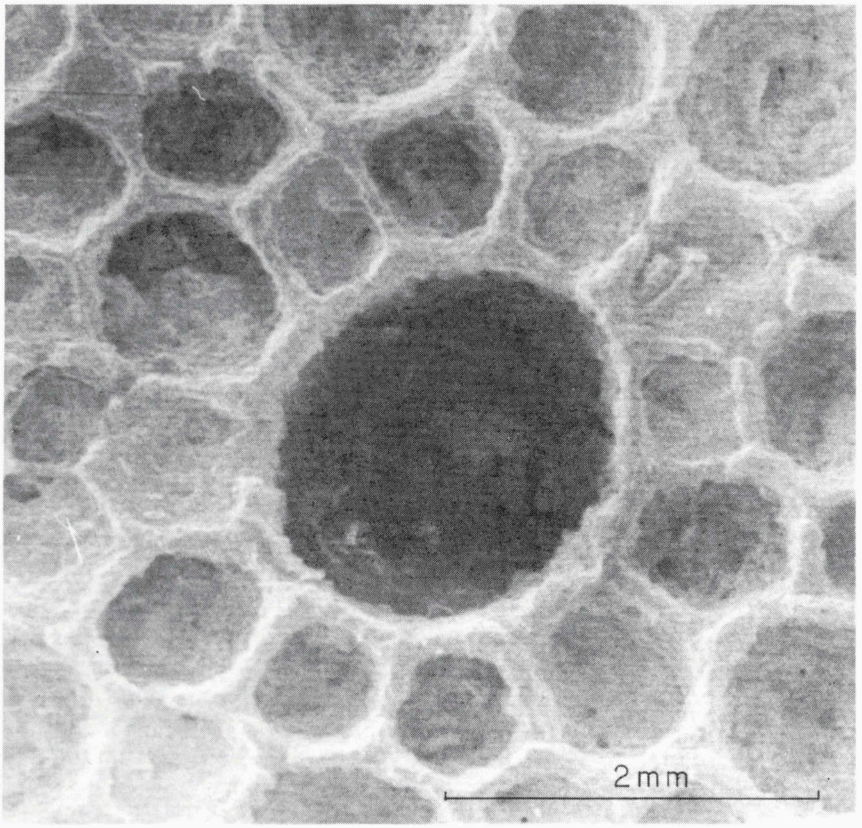

Fig. 50. Scan micrograph of a large polygonal corallite at the surface of a *Favosites forbesi* colony, Högklint Beds, Ireviken 3, RGM 243 713.

Such round corallites are described by Oliver (1975) in *Lecfedites canadensis* (Billings), but they are not seen in *F. oculiporoides* Sokolov.

Discussing dimorphism with regard to tabulates Sokolov (1955) concluded that this feature does not occur. Sokolov considered dimetrism a result of ontogeny, because early growth stages of both large and small corallites are identical. Oliver (1966) described dimorphism in *Striatopora flexuosa* Hall, a branching tabulate with thick dileted double-walls near the surface. Oliver distinguished two types of corallites in this tabulate: (1) A-corallites, which arise in the thin walled axial part of the colony and reproduce asexually, and (2) B-corallites, which develop (from the former) in the periphery of the colony and did not reproduce asexually. As a consequence of this way of growth an alternating succession of A- and B-corallites develops. These features were interpreted by Oliver as dimorphism. The present author regards this as questionable because the succession of A- to B-corallites and the related difference in reproduction could depend on the tiny branching growth form of the colony. B-corallites most likely developed by space-filling requirement.

Dimorphism as described by Oliver (1975) in his new genera *Lecfedites* and *Bractea* is also questionable because it is partly based on the occurrence of squamulae in the larger corallites while tabulae are found in the smaller ones. The development of squamulae, instead of tabulae, is well known (Philips, 1960), and probably an ecologically controlled feature. This development, probably was also connected with the diameter of the corallites because in small (young) corallites of *F. moniellensis* Oekentorp, squamulae replacement of tabulae was less pronounced than in adult corallites (Oekentorp, 1975). Nevertheless, as dimetrism is frequently found in favositids, some genetical and/or ecological factor determines that some corallites grew relatively large while others remained small.

The size variation of the corallites in *F. forbesi* also depends on the gross morphology of the colony. In flat, foliaceous or oblate ellipsoidal colonies the larger corallites are more or less regularly distributed between the smaller ones. In colonies with small knobs and ridges at their surface (Fig. 48) this regular pattern is sometimes obscured. In those with gently sloping surfaces the arrangement of larger (more or less rounded) corallites between smaller polygonal ones is still seen, but the latter tend to reduce more in size than the larger ones. Any differentiation generally is obliterated at the base of valleys between or around knobs; tiny polygonal corallites are found only. These phenomena are similar to variations in corallite size already described in *F. hisingeri* (p. 23 - 43).

The graphs shown in Figure 51 were constructed from 1307 measurings of samples from the surface of a *F. forbesi* colony, found in the mixed clastic carbonates near the reef of Nyhamn 9. In these graphs no distinction is made between larger and smaller corallites. The range of the corallite area is 0.1 - 2.4 mm^2; the area of about 76% of the corallites varies between 0.3 - 0.9 mm^2. In this graph two peaks are seen: the first at an area of 0.6 mm^2 and the second at 1.7 mm^2. This bimodal distribution corresponds with the striking size variation seen at the surface of the colony. In the distribution graphs of the corallite diameters this feature is hardly recorded. From these graphs (Fig. 51) it is concluded that by measuring the corallite diameters, pronounced size variation, like the one found in *F. forbesi,* is obscured.

In order to obtain an idea about the variation in the larger and smaller corallites, the data of the former were selected on account of their size and more or less rounded shape; 17.8% are large corallites. The graphs in Figure 52 were constructed from these groups of measurings. The statistic parameters of the characters are summarized in Table 11. Comparison of the graphs with those constructed before (Fig. 51) shows that the mode of the corallite area distribution of the smaller corallites indeed coincides with the first peak in the former graph, whilst the mode of the graph constructed from the area measurings of the larger corallites corresponds with the second peak. The modes of the graphs, constructed from the diameter measurings of the smaller corallites, more or less correspond with the first peaks in the graphs shown in Figure 51, but the variation of these measurings from the larger corallites is not at all reproduced in the graphs previously constructed. This is caused by the relatively small number of larger corallites.

Scan samples were also prepared from a colony, found in Snipklint at Ireviken (RGM 243 713). This colony differs from the one previously described by the occurrence of very large corallites with an area of about 5 mm² (Fig. 50). The graphs shown in Figure 53 were constructed from the data of these scan samples. The statistic parameters of the characteristics are listed in Table 11.

The range of the corallite area in the smaller corallites (83.9% of all measurements) is mostly 0.2 - 1.8 mm² and in the larger ones (16.1%) 1.2 - 3.2 mm². The corallite diameters vary from 0.6 - 1.8 mm in the smaller corallites and from 1.2 - 2.3 mm in the larger ones. The presence of the very large corallites is indicated by corallite diameters > 2.3 mm. Comparison of these graphs with those given in Figure 52 shows that both the smaller and the larger corallites of this sample are somewhat coarser. However, this feature is again less clear in the graphs of the corallite diameters.

From a *F. forbesi* colony, found in the Hamra oncolite at Uddvide 2, two sets of graphs were constructed. The graphs shown in Figure 54 are constructed from the data of all 740 measurings, whilst those in Figure 55 are made from the

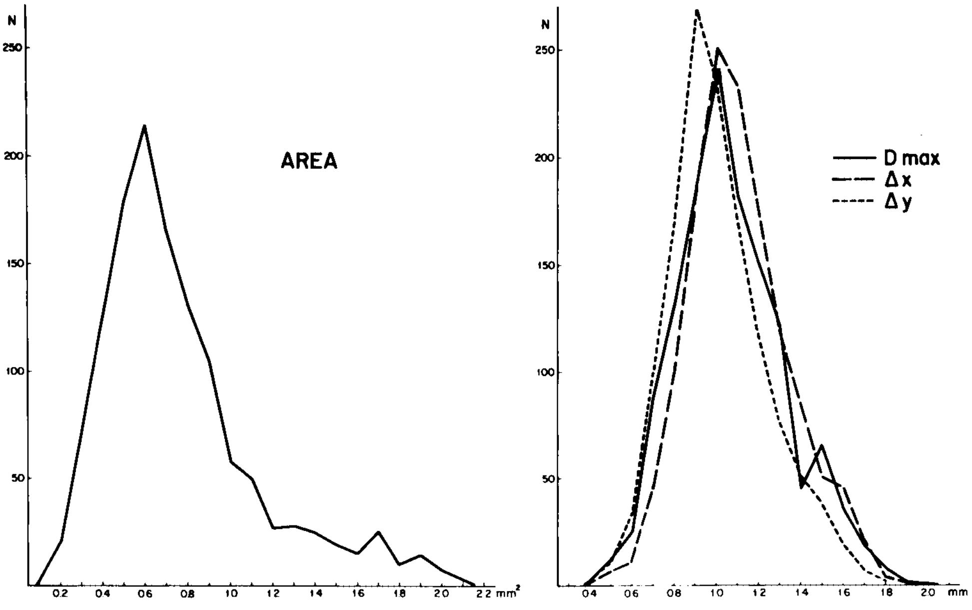

Fig. 51. Frequency distribution in measurings on scan micrographs of samples of a *Favosites forbesi* colony, Högklint Beds (mixed clastic carbonates), Nyhamn 9, RGM 243 712.

selected data: 23.1% are larger corallites and 76.9% are smaller ones. The statistic parameters of the characteristics are given in Table 11. Comparison of these graphs shows that graphs constructed from all data hardly give any information about the variation of the corallites. Similar graphs were constructed from all samples measured, but these graphs are not presented because, more or less the same variation was always observed (see Table 11).

The three samples dicussed above are representatives only of *F. forbesi* colonies out of three different environments: an interreef, a reef and a shallow marine current environment. The characteristic size differentiation of the corallites is seen in all these samples, although small differences in size occur (Table 12). As the characteristic pattern of larger corallites among smaller ones did not

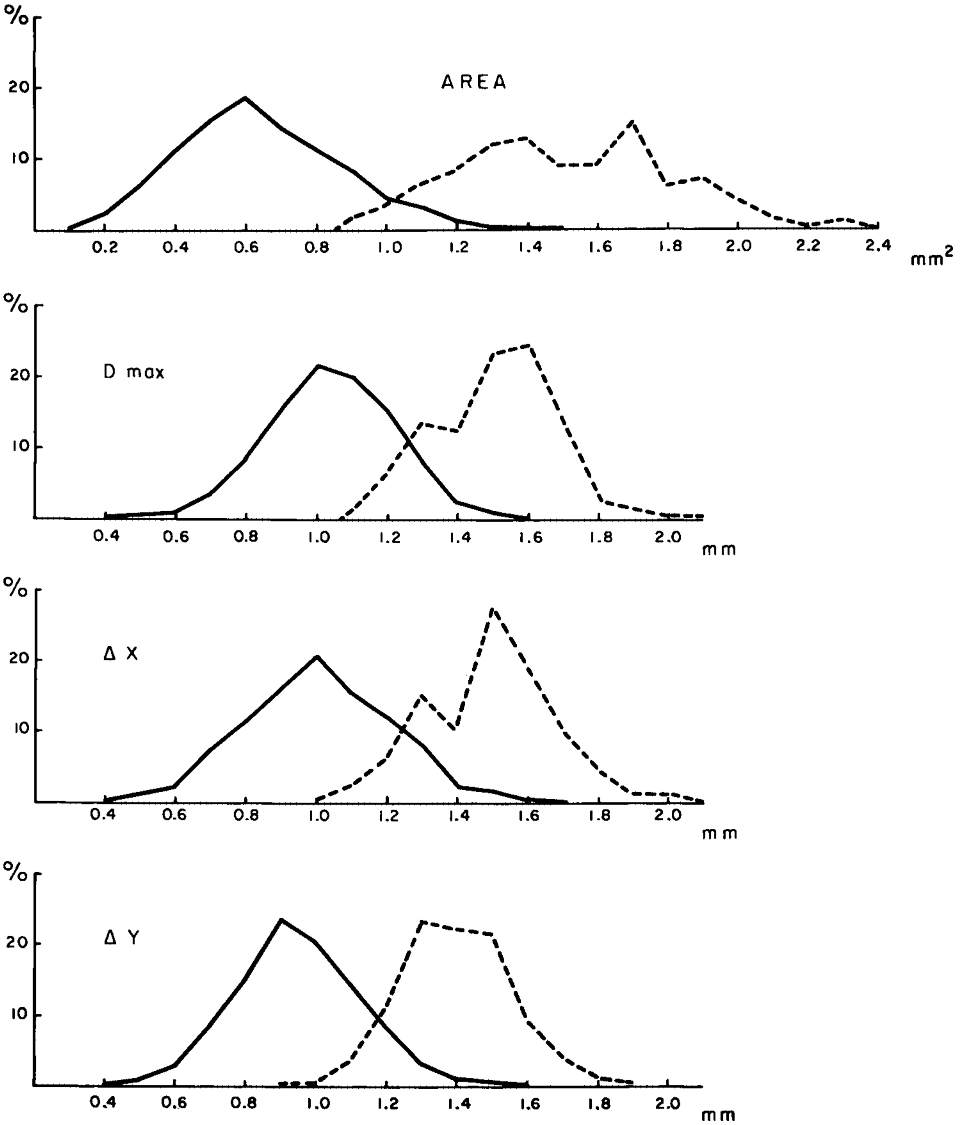

Fig. 52. Frequency distribution in measurings of selected larger and smaller corallites of scan micropraphs of samples of a *Favosites forbesi* colony, Högklint Beds (mixed clastic carbonates), Nyhamn 9, RGM 243 712.

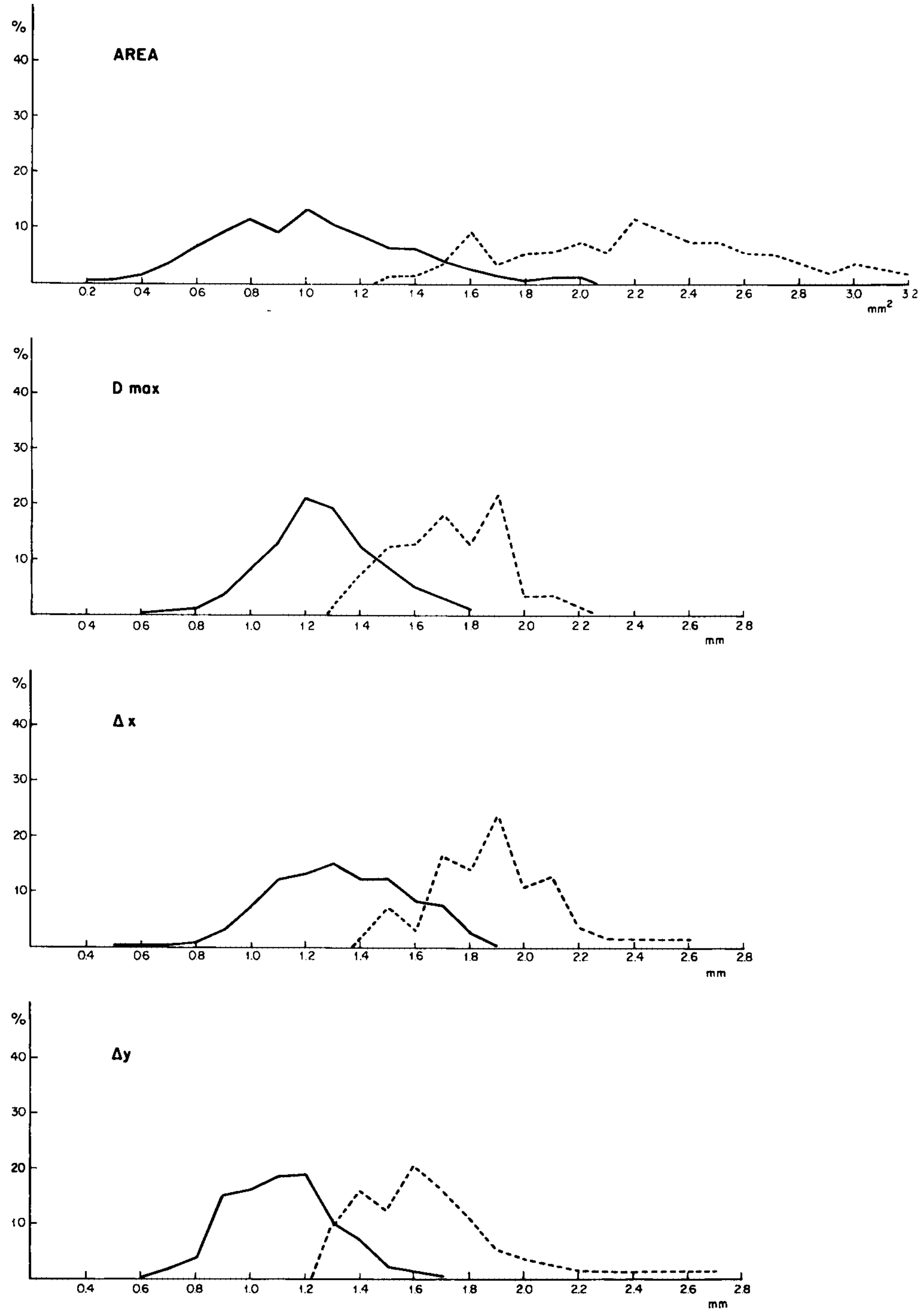

Fig. 53. Frequency distribution in measurings of selected larger and smaller corallites of scan micrographs of samples of a *Favosites forbesi* colony, Högklint Beds (reef), Ireviken 3 (Snipklint), RGM 243 713.

change in the three environments mentioned above, and is also present in all growth stages of a colony, the present author considers this differentiation as genotypic. Ecological influences only cause size variations as described above.

The graphs shown in Figure 56 give the variation of the corallite diameters Klaamann (1962a) observed in three subspecies of *Favosites pseudoforbesi* Sokolov. The corallite diameters vary from 0.6 - 2.4 mm in *F. pseudoforbesi pseudoforbesi* Sokolov, from 0.6 - 2.0 mm in *F. pseudoforbesi muratsiensis* Sokolov and from 0.6 - 1.8 mm in *F. pseudoforbesi ohesaarensis Klaamann.* However, this variation is within the variability range which the present author noticed in his collection of *F. forbesi* colonies. Consequently, this species and the subspecies are considered to be junior synonyms of *F. forbesi.*

Because in the synonyms, listed above, the characteristic size differentiation of the corallites corresponds with the variation observed in *F. forbesi,* these are considered as junior synonyms or ecophenotypes of *F. forbesi.* Although such a size variation is also noticed in *Favosites oculiporoides, Lecfedites canadensis* and *Favosites obliquus* it is not clear whether these species are synonyms of

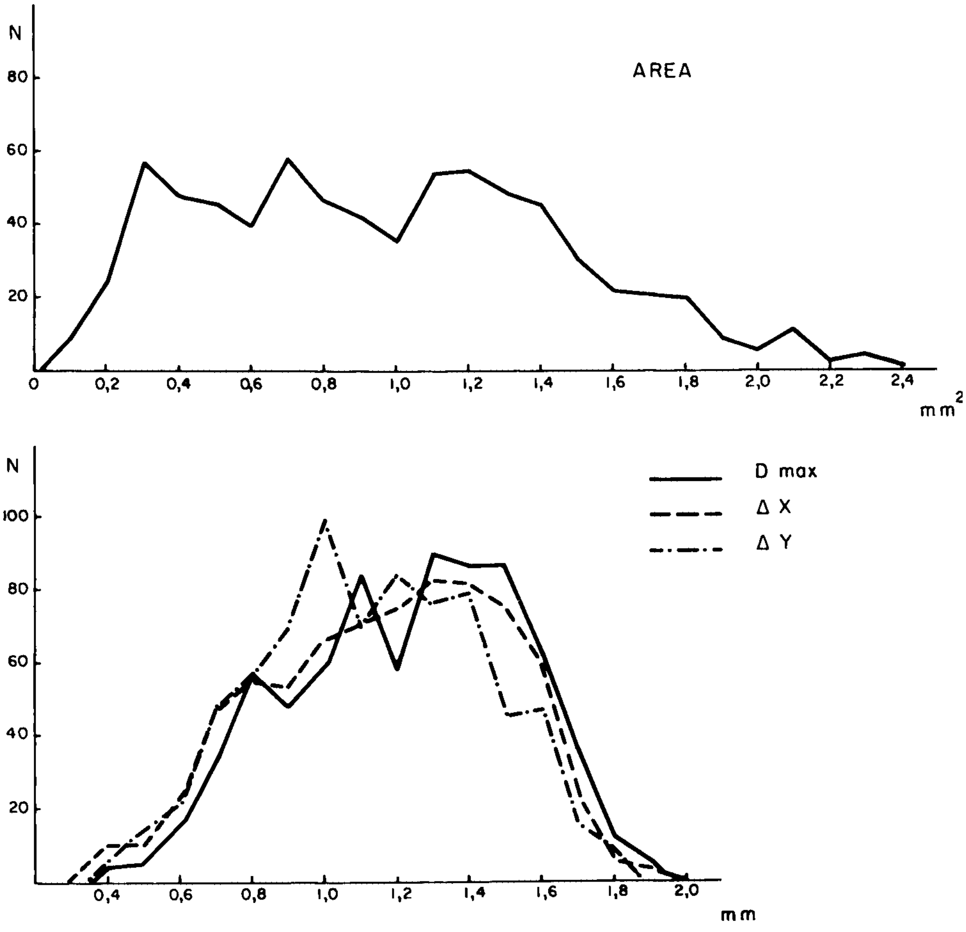

Fig. 54. Frequency distribution in measurings on a peel of a *Favosites forbesi* colony, Hamra-Sundre Beds, Uddvide 2, RGM 243 714.

F. forbesi. It also has to be investigated if such favositids like *F. jaanensis* Sokolov, *F. serratus* Sokolov and *F. ingens* Klaamann, are related to *F. forbesi*, as defined in this paper.

The tickness of the wall in *F. forbesi*, as defined in this paper, varies from 0.05 - 0.20 mm. Pores are arranged in 1 - 3 rows; the diameter is about 0.25 mm. Tabulae distance varies due to environmental influences.

In foliaceous or platy colonies two growth stages are sometimes seen: a reptant growth stage during which the shape is influenced by the morphology of the substrate, and a stage in which the corallites became vertical. This phenomenon is also noticed in such platy colonies of *F. hisingeri*. Colony growth occurred through lateral increase (Stel, 1978b).

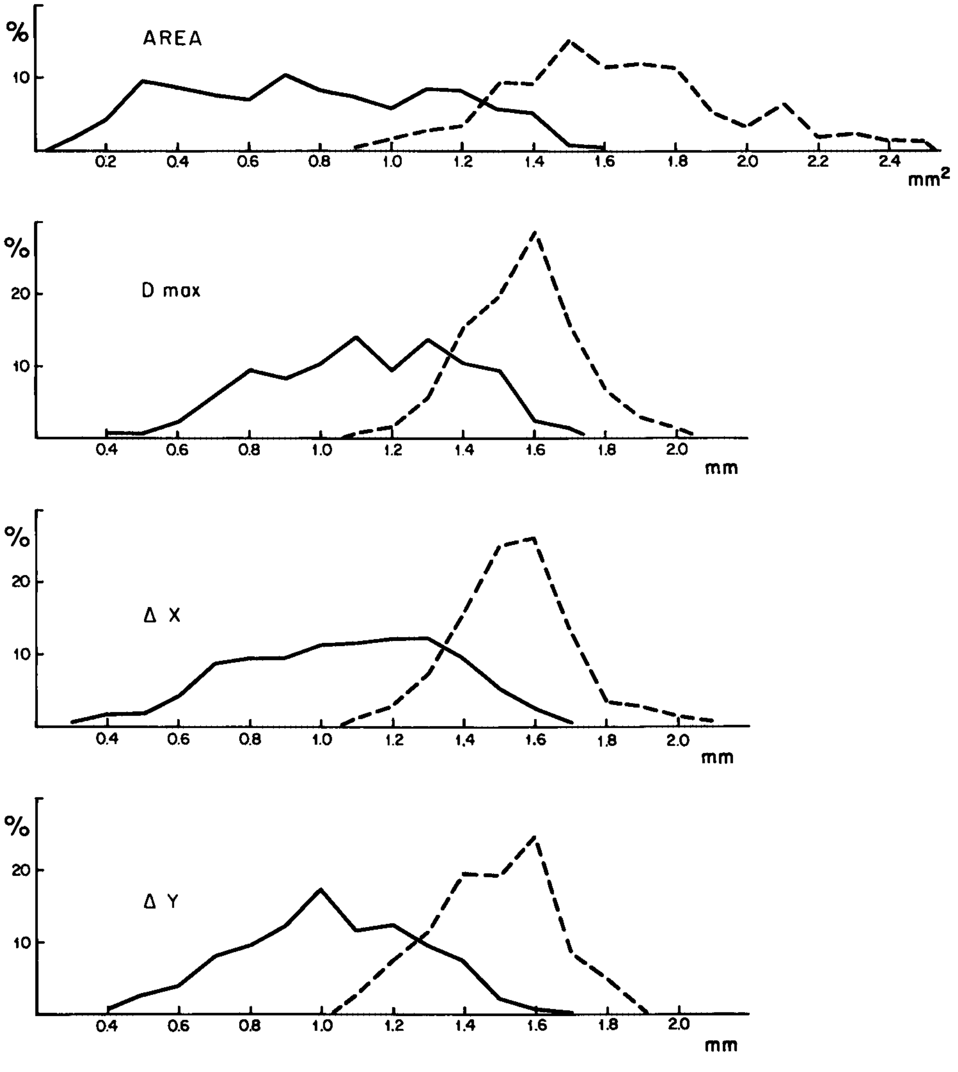

Fig. 55. Frequency distribution of measurings of selected larger and smaller corallites of a peel of a *Favosites forbesi* colony, Hamra-Sundre Beds, Uddvide 2, RGM 243 714.

Table 11. Parameters of corallites in three *Favosites forbesi* colonies from three different facies: mixed clastic carbonates (RGM 243 712), reef (RGM 243 713) and oncolite (RGM 243 714).

Scan sample RGM 243 712 Högklint, interreef, Nyhamn 9

	$\bar{x}$	S	Sk	K	min.	max.	G	N
S: Area	0.65	0.23	0.61	3.80	0.10	1.90	0.63	1141
Dmax	1.04	0.19	—0.04	3.15	0.40	1.60	1.04	1141
Δx	1.01	0.21	0.08	2.83	0.40	1.70	1.01	1141
Δy	0.95	0.18	0.17	3.20	0.40	1.60	0.99	1141
L: Area	1.52	0.32	0.41	3.25	0.90	2.70	1.50	166
Dmax	1.51	0.20	1.10	8.88	1.10	2.60	1.52	166
Δx	1.50	0.19	0.13	3.32	1.00	2.10	1.51	166
Δy	1.41	0.20	2.53	20.68	0.90	2.90	1.40	166

Scan sample RGM 243 713 Högklint, reef, Ireviken 3

	$\bar{x}$	S	Sk	K	min.	max.	G	N
S: Area	1.02	0.34	0.42	3.05	0.20	2.00	1.00	281
Dmax	1.27	0.21	0.17	2.98	0.60	1.80	1.26	281
Δx	1.33	0.25	—0.64	2.63	0.50	1.90	1.32	281
Δy	1.11	0.20	0.22	2.99	0.60	1.70	1.11	281
L: Area	2.23	0.62	2.44	13.75	1.30	5.40	2.20	54
Dmax	1.74	0.23	0.81	4.90	1.30	2.60	1.73	54
Δx	1.87	0.22	0.42	3.93	1.40	2.60	1.87	54
Δy	1.63	0.25	1.60	7.67	1.30	2.70	1.60	54

Sample RGM 243 714 Hamra, oncolite, Uddvide 2

	$\bar{x}$	S	Sk	K	min.	max.	G	N
S: Area	0.78	0.37	0.08	1.91	0.10	1.60	0.76	569
Dmax	1.13	0.28	—0.19	2.33	0.40	1.70	1.13	569
Δx	1.07	0.29	—0.22	2.34	0.30	1.70	1.08	569
Δy	1.02	0.26	—0.11	2.50	0.40	1.70	1.02	569
L: Area	1.64	0.32	0.37	2.96	0.90	2.50	1.61	171
Dmax	1.57	0.16	0.99	3.20	1.10	2.00	1.57	171
Δx	1.54	0.17	0.22	3.73	1.10	2.10	1.54	171
Δy	1.48	0.17	—0.13	2.54	1.10	1.90	1.49	171

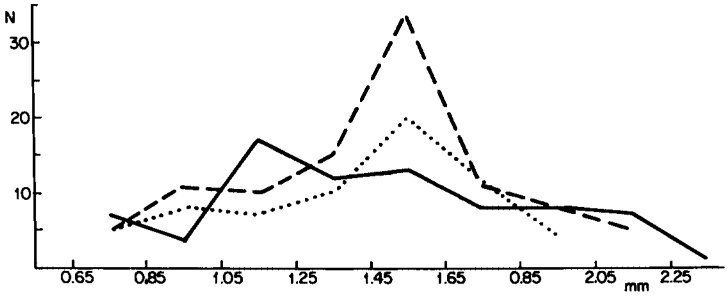

Fig. 56. Variation curves of the corallite diameters of some subspecies of *Favosites pseudoforbesi*. Solid line: *Favosites pseudoforbesi pseudoforbesi;* dashed line: *Favosites pseudoforbesi muratsiensis;* stippled line: *Favosites pseudoforbesi ohesaarensis* (from Klaamann, 1962a, p. 41).

Table 12. Parameters of corallites in peels from three *Favosites forbesi* colonies (RGM 243 715 - 243 717).

Sample RGM 243 715 Hamra oncolite, Uddvide 2

	x̄	S	Sk	K	min.	max.	G	N
S: Area	0.94	0.50	0.28	2.12	0.10	2.30	0.92	500
Dmax	1.20	0.31	—0.10	2.44	0.40	2.20	1.23	500
Δx	1.12	0.31	—0.15	2.40	0.40	2.00	1.15	500
Δy	1.17	0.35	—0.09	2.15	0.40	2.10	1.20	500
L: Area	2.24	0.56	0.87	3.34	1.10	3.80	2.14	108
Dmax	1.81	0.24	0.58	2.84	1.40	2.40	1.79	108
Δx	1.74	0.23	0.56	3.09	1.30	2.40	1.72	108
Δy	1.79	0.24	0.31	4.04	1.00	2.60	1.80	108

Sample RGM 243 716 Hamra oncolite, Uddvide 2

	x̄	S	Sk	K	min.	max.	G	N
S: Area	0.79	0.43	0.16	1.83	0.10	1.70	0.77	209
Dmax	1.11	0.30	—0.31	2.20	0.40	1.70	1.16	209
Δx	1.05	0.31	—0.09	2.22	0.40	1.70	1.06	209
Δy	1.05	0.30	—0.19	2.17	0.40	1.70	1.06	209
L: Area	2.05	0.45	0.90	2.95	1.50	3.20	1.94	49
Dmax	1.75	0.19	0.42	2.28	1.40	2.10	1.72	49
Δx	1.69	0.19	0.27	2.12	1.40	2.10	1.68	49
Δy	1.66	0.18	0.50	2.52	1.40	2.10	1.62	49

Sample RGM 243 717 Hamra oncolite, Uddvide 1

	x̄	S	Sk	K	min.	max.	G	N
S: Area	0.71	0.38	0.22	2.05	0.10	1.50	0.70	85
Dmax	1.04	0.28	—0.38	2.41	0.40	1.50	1.07	85
Δx	0.99	0.29	—0.24	2.41	0.30	1.50	0.99	85
Δy	0.98	0.29	—0.17	2.29	0.30	1.60	1.00	85
L: Area	1.88	0.41	—0.63	2.02	1.10	2.40	2.02	18
Dmax	1.63	0.18	—0.65	3.00	1.20	1.90	1.65	18
Δx	1.61	0.19	—0.53	2.49	1.20	1.90	1.65	18
Δy	1.58	0.24	—0.33	2.52	1.10	2.00	1.62	18

Morphology of *Alveolites suborbicularis* Lamarck, 1801

As the type specimen of Lamarck (1801) is lost, a neotype *(Calamopora spongites* var. *tuberosa* Goldfuss, 1829, pl. 28, Fig. 1d) was chosen by Smith (1933, p. 137) as the lectotype of *Alveolites suborbicularis* Lamarck. The reader is referred to Lecompte's (1933) paper on *Alveolites* Lamarck, for a detailed historical review and list of synonyms.

About fifty colonies of *A. suborbicularis* were collected from the Hamra oncolite in southern Gotland. Stel & de Coo (1977) found that this oncolite was deposited in a shallow-marine-current environment.

Alveolites suborbicularis Lamarck, 1801

1801 *Alveolites suborbicularis* sp. nov. — Lamarck, p. 375.
1829 *Calamopora spongites* var. *tuberosa* var. nov. — Goldfuss, p. 80 pl. 28, figs. 1a-e.
1853 *Alveolites suborbicularis* Lamarck — Edwards & Haime, p. 219 - 220, pl. 49, fig. 1.
1879 *Alveolites suborbicularis* Lamarck — Nicholson, p. 126 - 128, pl. 6, fig. 2.
1933 *Alveolites suborbicularis* Lamarck — Lecompte, p. 15 - 25, pl. 1, figs. 1 - 2.
1936 *Alveolites suborbicularis* Lamarck — Lecompte, p. 6 - 9, pl. 1, pl. 2, figs. 1 - 2.
1939 *Alveolites suborbicularis* Lamarck — Lecompte, p. 19 - 22, pl. 1.
1952b *Alveolites suborbicularis* Lamarck — Sokolov, p. 78 - 80, pl. 17, figs. 1 - 4.
1955 *Alveolites suborbicularis* Lamarck — Sokolov, p. 185, pl. 29, fig. 1.
1959 *Alveolites suborbicularis* Lamarck — Dubatolov, p. 142 - 143, pl. 48, fig. 4.

Diagnosis of Goldfuss (1826, p. 80) — Calamopora tuberosa vel ramosa, tubibus obconicis brevibus tenuibus imbricatis extus subprismaticis vel rhomboideis intus cylindricis vel compressis, dissepimentis planis remotiusculis, poris communicantibus (ad angulos dispositis?) alternantibus.
Var. tuberosa. Informis, hemisphaerica, placentaeformis, tuberosa, tubulis minimis imbricatis compressis, ostiolis rhomboideis.

Description — The shape of the colonies of *A. suborbicularis* generally is oblate ellipsoidal. Stel & de Coo (1977) noticed that the colony shape of this tabulate is influenced by discrete abiotic and biotic (Fig. 58) factors. Local currents favoured, through increased food supply, growth at the upstream side of the colony (Fig. 57), whilst growth was impeded by the competition of algae.

The graphs shown in Figure 59 were constructed from the data of two different colonies (RGM 243 718, 243 719) found at Uddvide 2. The range of the

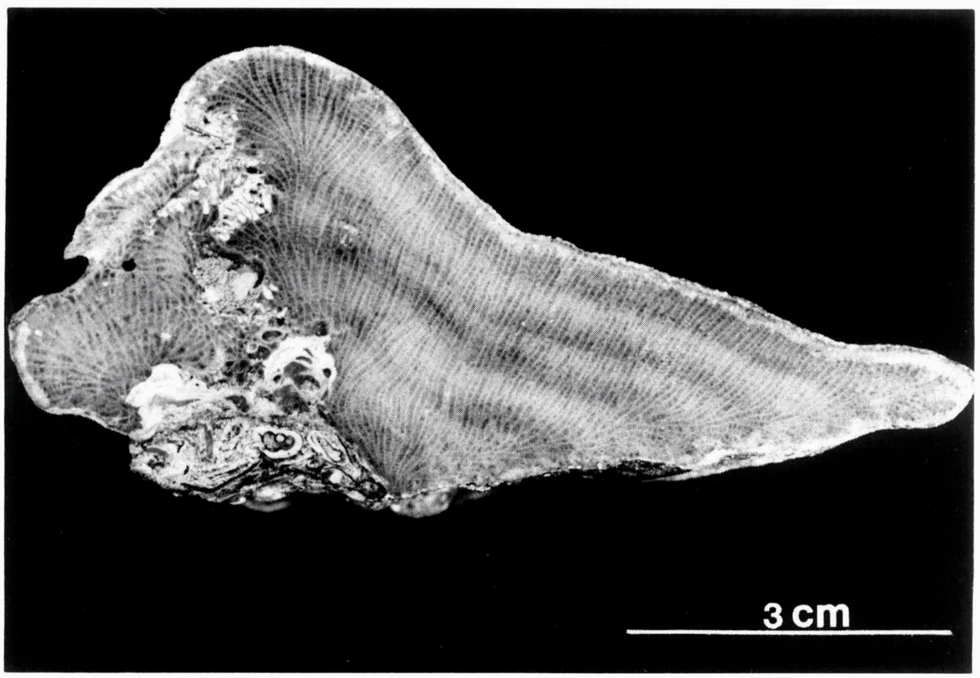

Fig. 57. Longitudinal section of an *Alveolites suborbicularis* colony with preferential upstream growth, Hamra-Sundre Beds, Uddvide 2, RGM 243 718.

Table 13. Parameters of corallites in thin sections of two *Alveolites suborbicularis* colonies (RGM 243 718 - 243 719).

Sample RGM 243 718 Hamra oncolite, Uddvide 2

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.46	0.14	—0.56	3.11	0.10	0.80	0.48	452
Dmax	0.87	0.16	—0.35	3.07	0.40	1.30	0.88	452
Δx	0.79	0.15	—0.27	2.86	0.40	1.10	0.79	452
Δy	0.89	0.18	—0.76	3.74	0.30	1.30	0.92	452

Sample RGM 243 719 Hamra oncolite, Uddvide 2

	$\bar{x}$	S	Sk	K	min.	max.	G	N
Area	0.60	0.15	—0.55	4.14	0.10	1.10	0.61	338
Dmax	1.04	0.17	—0.47	3.80	0.50	1.60	1.06	338
Δx	0.88	0.16	—0.00	2.82	0.50	1.30	0.87	338
Δy	1.00	0.17	—5.10	3.76	0.40	1.40	1.01	338

corallite area measurings in the first colony is somewhat narrower than that of the second one (Fig. 59). Small differences between the corallite diameters of these colonies are a result of this size difference. The differentiation between the three diameter measurings also is more pronounced than in the tabulates described before. This differentiation is caused by the more or less half-moon shaped corallites that are diagnostic for *Alveolites*. Statistical parameters are listed in Table 13. The data of the Δ x measurings in these colonies correspond to the dimensions given by Sokolov (1952b).

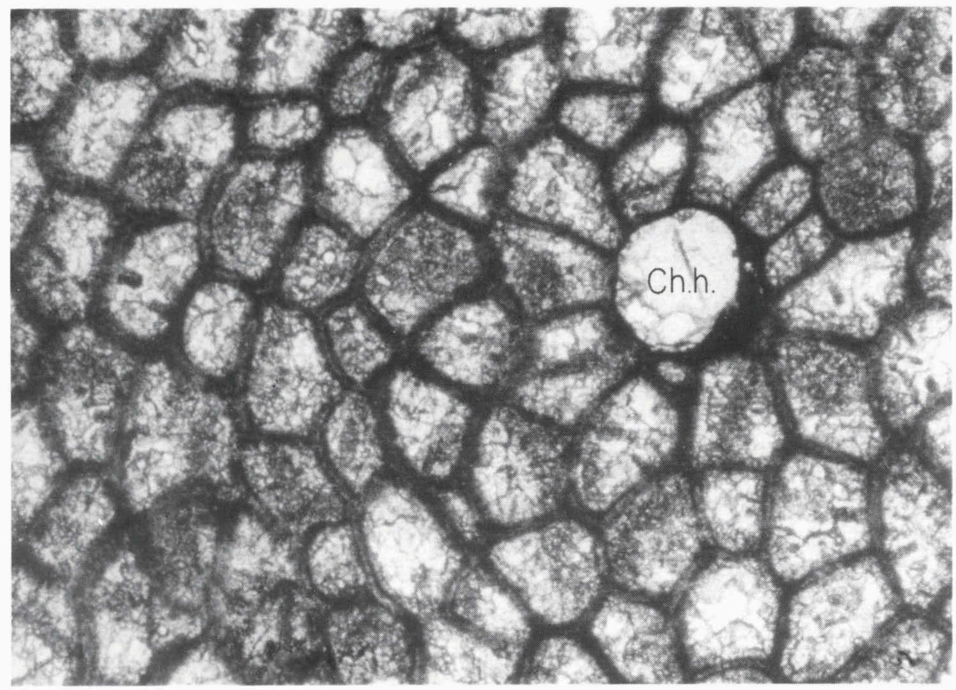

Fig. 58. Transverse section of an *Alveolites suborbicularis* colony with *Chaetosalpinx huismani*, (Ch.h.) Hamra-Sundre Beds, Uddvide 2, RGM 243 718, × 20.

The thickness of the double-wall is 0.12 - 0.24 mm. The pores are situated near the corners of the corallites (Fig. 58), the diameter is 0.12 - 0.16 mm. Some septal spines are observed. Increase in *A. suborbicularis* has not yet been sudied in detail.

Conclusions

The observations, described in this paper, indicate that the corallite diameter can only be considered as a characteristic at the species level if the ecophenotypic variation is known. Measuring this feature on samples of unknown ecophenotypic variation can only indicate statistical inequivalency of these samples. Therefore, such variation graphs do not necessarily represent different morphospecies. Unfortunately, construction of such graphs has frequently led to the description of morphospecies which actually are ecotypes of classical species. Current limitation of the range in corallite diameters at the species level often is too narrow and does not allow for ecophenotypic variation at all.

When interpreting differences between variation graphs, small deviations are seen, which are due to the method of measuring, e.g. differences between Δ x and Δ y graphs.

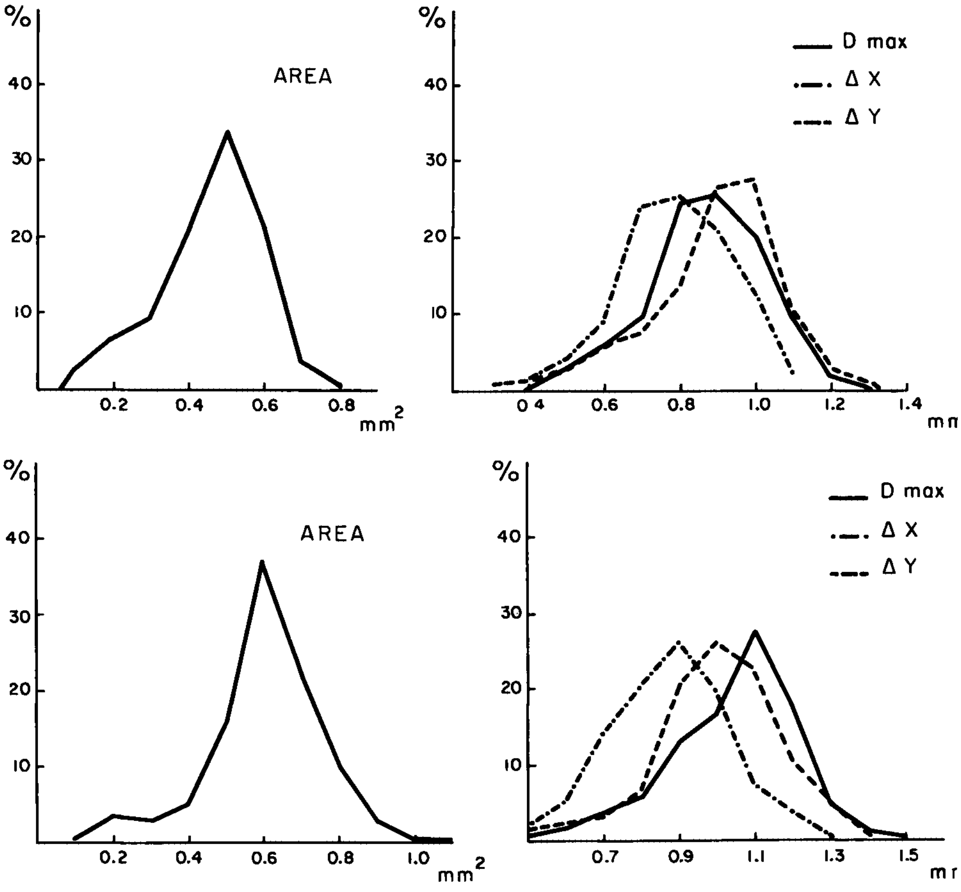

Fig. 59. Frequency distribution in measurings on thin sections of two *Alveolites suborbicularis* colonies, Hamra-Sundre Beds, Uddvide 2, RGM 243 718 - 243 719.

If the ecophenotypic variation is unknown, the corallite area is the better measure, although this parameter is less easily obtained. A disadvantage of the corallite area measuring is that, because the number of possibilities increases quadratic, an increasing number of measurements is needed when the corallites are large. On the other hand, important differences in corallite area are hardly visible in graphs of the variation of the corallite diameter, because in this case the number of possibilities increases linear. In Figure 60 the corallite diameter graphs are shown of *Favosites gothlandicus* (mean corallite area: 4.02 mm^2), *Syringolites kunthianus* (mean corallite area: 3.20 mm^2) and *Favosites obliquus* (mean corallite area: 2.30 mm^2). From these graphs it is seen that, although the mean corallite area increases in about the same degree, the difference between the graphs of *S. kunthianus* and *F. gothlandicus* is less pronounced than the one between *S. kunthianus* and *F. obliquus*.

Variability of the corallite size in *F. hisingeri* is influenced to a high degree by the environment. Small corallites near knobs may be degenerated larger corallites, as is shown in the astogenic series, described before.

Variability in *F. forbesi* corallites is apparently less influenced by the environment; the colony form on the contrary is dependant on ecological factors. The typical arrangement of larger corallites between smaller ones, is considered to be a genotypic feature of *F. forbesi*.

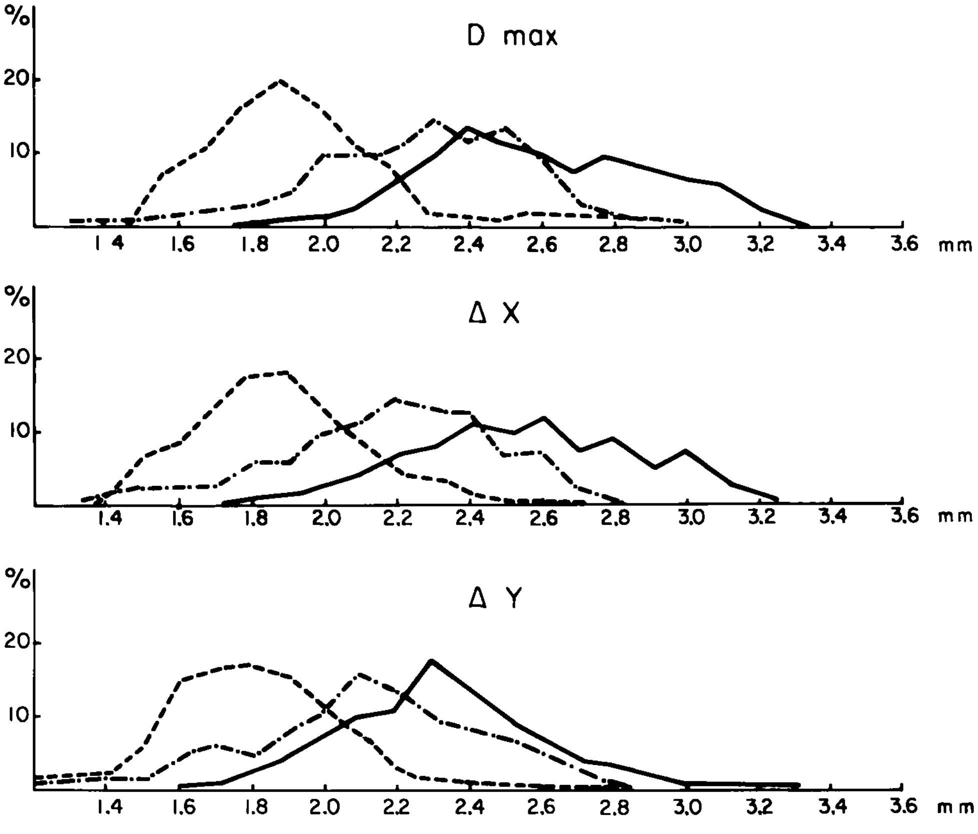

Fig. 60. Comparison of frequency distribution in *Favosites obliquus* (dashed line; RGM 243 707; cf. Fig. 39, Table 8), *Syringolites kunthianus* (dash-dot line; RGM 243 708; cf. Fig. 41, Table 9) and *Favosites gothlandicus* (solid line; RGM 243 711; cf. Fig. 47, Table 10).

References

Basset, M. G. & L. R. M. Cocks, 1974. A review of Silurian branchoipods from Gotland. — Fossils Strata, 3: 1 - 56.

Beecher, C. E., 1891. The development of a Paleozoic poriferous coral. — Trans. Connecticut Acad. Arts Sci., 8: 207 - 214.

Copper, P., 1974. Structure and development of Early Paleozoic reefs. — Proc. 2nd Int. Coral Reef Symp., Brisbane, 1973, 1: 365 - 387.

Dubatolov, V. N., 1959. Tabuljaty, Geliolitidy i Chetetidy Silura i Devona Kuzneckogo bassejna. — Trudy VNIGRI, 139: 1 - 292.

Edwards, H. M. & J. Haime, 1849. Mémoire sur les polypiers appartenant aux groupes naturels des Zoanthaires perforés et des Zoanthaires tabulés. (Extrait.) — C. R. Acad. Sci. Paris, 29: 257 - 363.

Edwards, H. M. & J. Haime, 1850. A monograph of the British fossil corals. — Monogr. Palaeont. Soc., 1: I - LXXXV, 1 - 71.

Edwards, H. M. & J. Haime, 1851, Monographie des polypiers fossiles des terrains paléozoiques. — Arch. Mus. Hist. Nat. Paris, 5: 1 - 502.

Edwards, H. M. & J. Haime, 1855. A monograph of the British fossil corals. — Monogr. Palaeont. Soc., 5: 245 - 299.

Eriksson, C. O. & S. Laufeld, 1978. Philip structures in the submarine Silurian of northwest Gotland. — Sver. Geol. Unders., C, 736: 1 - 30.

Fought, H. 1749. Dissertatio de coralliis balticis. In: C. Linnaei. Amoenitates Academicae seu dissertationes variae..... — C. Haak, Lugdunum Batavorum: 177 - 212.

Flügel, H. W., 1976. Ein Spongienmodell für die Favositidae. — Lethaia, 9: 405 - 419.

Girty, G. H., 1895. Development of the corallum in *Favosites forbesi* var. *occidentalis.* — Am. Geol., 15: 131 - 146.

Goldfuss, G. A., 1826 - 1833. Petrefacta Germaniae I. — Arnz & Co., Düsseldorf: 1 - 252; pls. 1 - 71.

Graus, R. R., 1977. Investigation of coral growth adaptation using computer modelling. — Proc. 3rd Int. Coral Reef Symp., Miami, 1977, 2: 463 - 469.

Graus, R. R. & J. G. MacIntyre, 1976. Light control of growth form in colonial reef corals: computer simulation. — Science, 193 (4256): 895 - 897.

Gray, J., S. Laufeld & A. J. Boucot, 1974. Silurian trilete spores and spore tetrads from Gotland: their implications for land plant evolution. — Science, 185: 260 - 262.

Hadding, A., 1950. Silurian reefs of Gotland. — Jour. Geol., 58: 402 - 409.

——, 1956. The lithological character of marine shallow water limestones. — Publ. Inst. Mineral. Paleont. Quaternary Geol. Univ. Lund, 33: 1 - 18.

Hall, J., 1852. Natural history of New York, Part VI. Palaeontology of New York II. — C. van Benthuyzen, Albany, 2: 1 - 363, pls. 1 - 85.

Hartman, W. D. & T. F. Goreau, 1975. A Pacific tabulate sponge, living representative of a new order of sclerosponges. — Postilla, 167: 1 - 13.

Heckel, P. H., 1974. Carbonate buildups in the geologic record: a review. In: L. F. Laporte (ed.). Reefs in time and space. — Soc. Econ. Paleont. Mineral., Spec. Publ., 18: 40 - 154.

Hede, J. E., 1919. Djupborrningen vid Burgsvik på Gotland, 1915. Paleontologisk stratigrafiska resultat. — Sver. Geol. Unders., C, 298: 1 - 59.

——, 1925. Berggrunden (Silursystemet). In: H. Munthe, J. E. Hede & L. von Post. Beskrivning till kartbladet Ronehamn. — Ibidem, Aa, 156: 1 - 96.

——, 1927. Berggrunden (Silursystemet). In: H. Munthe, J. E. Hede & L. von Post. Beskrivning till kartbladet Hemse. — Ibidem, Aa, 160: 1 - 155.

——, 1929. Berggrunden (Silursystemet). In: H. Munthe, J. E. Hede & G. Lundqvist. Beskrivning till kartbladet Katthammarsvik. — Ibidem, Aa, 170: 1 - 120.

——, 1940. Berggrunden. In: H. Munthe, J. E. Hede & N. Sundius. Beskrivning till kartbladen Visby och Lummelunda. — Ibidem, Aa, 183: 9 - 69.

——, 1960. The Silurian of Gotland. In: G. Regnéll & J. E. Hede (eds.). The Lower Palaeozoic of Scania. The Silurian of Gotland. — Excursion Guide 21st Int. Geol. Congr., Copenhagen, 1960: 44 - 89.

Hedström, H., 1910. The stratigraphy of the Silurian strata of the Visby district. — Geol. Fören. Stockh. Förh., 32: 1455 - 1484.

Hill, D. & J. S. Jell, 1970. The tabulate coral families Syringolitidae Hinde, Roemeriidae Pocta, Neoroemeriidae Radagin and Chonostegitidae Lecompte, and Australian species of Roemeripora Kraicz. — Proc. Roy. Soc. Vict., 84: 171 - 190.

Hill, D. & E. C. Stumm, 1956. Tabulata. In: R. C. Moore, Treatise on invertebrate paleontology, Pt. F. — Geol. Soc. Am. & Univ. Kansas Press: 444 - 447.

Hinde, D., 1879. On a new genus of favosite coral from the Niagara Formation (U. Silurian), Manitoulin Island, Lake Huron. — Geol. Mag., N. S., 2, 6: 244 - 246.

Hurst, J. M., 1975. Some observations on brachiopods and the level bottom community ecology of Gotland. — Geol. Fören. Stockh. Förh., 97: 250 - 264.

Jones, O. A., 1930. A revision of some Palaeozoic coral genera and species. — Thesis.

——, 1936. The controlling effect of environment upon the corallum in *Favosites;* with a revision of some massive species on this basis. — Ann. Mag. Nat. Hist., 10: 1 - 23.

Kirkpatrick, R., 1911. On *Merlia normani,* a sponge with a siliceous and calcareous skeleton. — Quart. Jour. Microsc. Sci., 56: 657 - 702.

Klaamann, E. R., 1961. Tabuljaty i geliolitidy venloka Estonii. — Trudy Inst. Geol. Akad. Nauk Est. SSR, 6: 69 - 110.

——, 1962a. Tabuljaty verkhnego silura Estonii. — Ibidem, 9: 25 - 74.

——, 1962b. Rasprostranenie ordovikskikh i silurijskikh tabuljat Estonii (s opisaniem nekotorykh novykh vidov). — Ibidem, 10: 149 - 172.

——, 1964. Pozdneordovikskie i ranne silurijskie Favositida Estonii. — Ibidem: 1 - 118.

——, 1970. Izmenuivost i taksonomicheskoe palozenie *Angopora hisingeri* (Jones). — Ibidem, 19: 62 -68.

——, 1971. Tabuljaty verkhnego korallovogo isvestnjaka Norvegii. — Ibidem, 20: 356 - 363.

——, 1977. Über die Silurischen Tabulatensukzessionen Estlands und der Insel Gotland. — Ibidem, 26: 203 - 210.

Lamarck, J. B. P. A. de, 1801. Système des animaux sans vertèbres. — Paris.

——, 1816. Histoire naturelle des animaux sans vertèbres, II. — Verdière, Paris: 1 - 568.

Larsson, K., 1975. Clastic dikes from the Burgsvik Beds of Gotland. — Geol. Fören. Stockh. Förh., 97: 125 - 134.

Laufeld, S., 1974a. Reference localities for palaeontology and geology in the Silurian of Gotland. — Sver. Geol. Unders., C, 705: 1 - 150.

——, 1974b. Preferred orientation of orthoconic nautiloids in the Ludlovian Hemse Beds of Gotland. — Geol. Fören. Stockh. Förh., 96: 157 - 162.

——, 1974c. Silurian Chitinozoa from Gotland. — Fossils Strata, 5: 1 - 130.

Laufeld, S. & L. Jeppsson, 1976. Silicification and bentonites in the Silurian of Gotland. — Inst. Mineral. Paleont. Quaternary Geol. Univ. Lund, 200: 31 - 44.

Lecompte, M., 1933. Le genre *Alveolites* Lamarck dans le Dévonien moyen et supérieur de l'Ardenne. — Mém. Mus. Roy. Hist. Nat. Belg., 55: 1 - 50.

——, 1936. Revision des tabulés dévoniens décrits par Goldfuss. — Ibidem, 75: 1 - 112.

——, 1939. Les tabulés du Dévonien moyen et supérieur du bord sud du Bassin de Dinant. — Ibidem, 90: 1 - 227.

——, 1970. Die Riffe im Devon der Ardennen und ihre Bildungsbedingungen. — Geol. Palaeont., 4: 25 - 71.

Lindström, G., 1896. Beschreibung einiger obersilurischer Korallen aus der Insel Gotland. — Bih. Kgl. Svensk Vetensk. Akad. Handl., 21: 4 - 50.

Linnaeus, C., 1745. Dissertatio, Corallia Baltica adumbrans, quam ..... submittet Henricus Fought. — Upsaliae.

Lowenstam, H. A., 1957. Niagaran reefs in the Great Lakes area. In: H. S. Ladd (ed.) Treatise on marine ecology and paleoecology, 2. — Mém. Geol. Soc. Am., 67: 215 - 248.

Manten, A. A., 1960. De groeivormen van koralen als milieu-indicatoren. — Grondboor Hamer, 5: 145 - 165.

——, 1962. Some Middle Silurian reefs of Gotland. — Sedimentology, 1: 211 - 234.

——, 1962. Silurian reefs on Gotland. Typology, palaeoecology and stratigraphical implications. — Developments sedimentology, 13: 1 - 539 (with maps).

Martinsson, A., 1962. Ostracods of the family Beyrichiidae from the Silurian of Gotland. — Bull. Geol. Inst. Univ. Uppsala, 41: 1 - 369.

——, 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. — Geol. Fören. Stockh. Förh., 89: 350 - 386.

Mori, K., 1969. Stromatoporoids from the Silurian of Gotland, I. — Stockh. Contr. Geol., 19: 1 - 100.

——, 1970. Stromatoporoids from the Silurian of Gotland, II. — Ibidem, 22: 1 - 152.

Morton, J., 1974. The coral reefs of the British Solomon Islands; a comparative study of their composition and ecology. — Proc. 2nd Int. Coral Reef Symp., Brisbane, 1973, 2: 31 - 55.

Munthe, H., 1910. On the sequence of strata within southern Gotland. — Geol. Fören. Stockh. Förh., 32: 1397 - 1453.

——, 1921. Beskrivning till kartbladet Burgsvik jämte Hoburgen och Ytterholmen. — Sver. Geol. Unders., Aa, 152: 1 - 172.

Murchison, R. J., 1846. On the Silurian and associated rocks in Dalecarlia and on the succession from Lower to Upper Silurian in Smoland, Öland, and Gothland, and in Scania. — Quart. Jour. Geol. Soc. London, 3: 1 - 48, pl. 1.

Nicholson, H. A., 1879. On the structure and affinities of the 'Tabulate corals' of the Palaeozoic Period. — Blackwood, Edinburgh: 1 - 342.

——, 1889. On the relations between the genera *Syringolites,* Hinde, and *Roemeria,* Edwards & Haime, and on the genus *Caliapora,* Schlüter. — Geol. Mag., N.S., 3, 6: 433 - 438.

Nowinski, A., 1976. Tabulata and Chaetetida from the Devonian and Carboniferous of southern Poland. — Palaeontol. Polon., 35: 1 - 125.

Oekentorp, K., 1970. Revision des Genus *Thecia* Edwards & Haime, 1849 (Coelenterata, Tabulata). — N. Jb. Geol. Paläont. Abh., 137: 103 - 173.

——, 1975. Beschreibung und Systematik devonischer Favositidae Asturiens und Betrachtungen zur Biogeographie nordspanischer Korallenfaunen. — Münster. Forsch. Geol. Paläont., 37: 1 - 129.

——, 1976. Revision und Typisierung des Genus *Paleofavosites* Twenhofel, 1914 (Coelenterata, Tabulata). — Paläont. Z., 50: 151 - 192.

Oekentorp, K. & A. von Schouppé, 1969. Kritische Bemerkungen über die Anordnung der Poren bei *Palaeofavosites* Twenhofel, 1914. — N. Jb Geol. Paläont. Abh., 133: 89 - 100.

Oliver, W. A. Jr., 1966. Description of dimorphism in *Striatopora flexuosa* Hall. — Palaeontology, 9: 448 - 454.

——, 1968. Some aspects of colony development in corals. — Jour. Paleont., 42: 16 - 34.

——, 1975. Dimorphism in two new genera of Devonian tabulate corals. — Geol. Surv. Prof. Paper, 743-D: 1 - 9.

Philips, G. M., 1960. The Middle Palaeozoic squamulate Favositids of Victoria. — Palaeontology, 3: 186 - 207.

Počta, Ph., 1902. Anthozoaires et Alcyonaires. In: J. Barrande. Système silurien du centre de la Bohême. — Prague, 8, 2: 1 - 347, pls. 20 - 118.

Ross, M. H., 1953. The Favositidae of the Hamilton Group (Middle Devonian of New York). — Buffalo Soc. Nat. Sci. Bull., 21: 32 - 89.

Rukhin, L. B., 1937. Verkhnesilurijskie Tabulata Turkestanskogo khrebta i Chan-Tengri. — Izd. Leningrad. Gosud. Univ.: 1 - 96.

Rutten, M. G., 1958. Detailuntersuchungen an Gotländischen Riffen. — Geol. Rundschau, 47: 359 - 384.

Schlüter, C., 1889. Anthozoen des rheinischen Mittel-Devon. — Abh. preuss. geol. Landesanst., 8: 261 - 465.

Schouppé, A. von & K. Oekentorp, 1974. Morphogenese und Bau der Tabulata unter besonderer Berücksichtigung der Favositida. — Palaeontographica, A, 145: 79 - 194.

Smith, S., 1933. Sur des espèces nouvelles d' *Alveolites* de l'Eifelien inférieur du Nord de la France et de la Belgique. — Ann. Soc. Géol. Nord, 57: 135 - 145, pls. 2 - 3.

Sokolov, B. S., 1949. Tabulata i Geliolitida silura SSSR. Atlas rukovodjashchikh form iskopaemykh faun SSSR II: Silur. — VSEGEI, Leningrad: 75 - 98.

——, 1950. Sistematika i istorija razvitija paleozojskikh korallov Anthozoa Tabulata. — Voprosy Paleont., 1: 134 - 210.

——, 1951a. Tabuljaty paleozoja evropejskoj chasti SSSR, I. Ordovik zapadnogo Urala i Pribaltiki (Favositidy llandoverskogo jarusa). — Trudy VNIGRI, N.S., 48: 1 - 132.

——, 1951b. Tabuljaty paleozoja evropesjskoj chasti SSSR, II. Silur Pribaltiki (Favositidy llandoverskogo jarusa). — Ibidem, 52: 1 - 124.

——, 1952a. Tabuljaty paleozoja evropejskoj chasti SSSR, III. Silur Pribaltiki (Favositidy venlokskogo i ludlovskogo jarusov). — Ibidem, 58: 1 - 85.

——, 1952b. Tabuljaty paleozoja evropejskoj chasti SSSR, IV. Devon Russkoj platformy i zapadnogo Urala. — Ibidem, 62: 1 - 208.

——, 1955. Tabuljaty paleozoja evropejskoj chasti SSSR. Vvedenie. Obshchye voprosy sistematiki i istorii razvitija tabuljat (s charakteristikoj morfologicheski blizkikh grupp). — Ibidem, 85: 1 - 528.

Sokolov, B. S., 1962. Tabulata. In: Y. A. Orlov (ed.). Osnovy paleontologii, II. — Akad. Nauk SSSR, Moskva: 192 - 254.

Sorauf, J. E., 1971. Microstructure in the exoskeleton of some Rugosa (Coelenterata). — Jour. Paleont., 45: 22 - 32.

——, 1974. Growth lines on tabulae of *Favosites* (Silurian, Iowa). — Ibidem, 48: 553 - 555.

Spjeldnaes, N., 1959. Silurian bentonites from Gotland, Sweden. — Geol. Fören. Stockh. Förh., 81: 582 - 587.

Stasinska, A., 1967. Tabulata from Norway, Sweden, and from the erratic boulders of Poland. — Paleontol. Polon., 18: 1 - 112.

Stel, J. H., 1975. Erratische Favositidae der nördlichen Niederlande. — Geschiebesammler, Sonderh. 2: 1 - 203.

——, 1976. The Paleozoic hard substrate trace fossils *Helicosalpinx, Chaetosalpinx* and *Torquaysalpinx.* — N. Jb. Geol. Paläont. Mh., 12: 726 - 744.

——, 1978a. Growth and reproduction in the tabulate *Favosites forbesi* from the Silurian of Gotland. — Geol. Fören. Stockh. Förh., 100 (in press).

——, 1978b. Studies on the palaeobiology of favositids. — Thesis, Groningen Univ.: 1 - 247.

——, 1979. Lateral increase in *Paleofavosites asper* (Tabulata). — Jour. Paleont., 52 (in press).

Stel, J. H. & J. C. M. de Coo, 1977. The Silurian Upper Burgsvik and Lower Hamra-Sundre Beds, Gotland. — Scripta Geol., 44: 1 - 43.

Stel, J. H. & K. Oekentorp, 1976. On the solenid growth habit of *Paleofavosites.* — Geol. Mijnb., 55: 163 - 174.

Stumm, E. C., 1965. Silurian and Devonian corals of the Falls of the Ohio. — Geol. Soc. Am. Mem., 93: 1 - 184.

Sutton, J. D., 1966. The value of corallite size in the specific determination of the Tabulate corals *Favosites* and *Palaeofavosites.* — Mercian Geol., 1: 255 - 263.

Swann, D. H., 1947. The *Favosites alpenensis* lineage in the Middle Devonian Traverse Group of Michigan. — Mich. Univ. Mus. Paleont. Contr., 6: 235 - 318.

Thompson, d'A. W., 1917. On growth and form. — Cambridge Univ. Press, Cambridge: 1 - 327.

Tripp, K., 1933. Die Favositiden Gotlands. — Palaeontographica, 79: 75 - 142.

Weele, L. T. van der, 1977. WESP. — Publ. Rekencentrum, 8.

Wijsman-Best, M., 1974. Habitat-induced modification of reef corals (Faviidae) and its consequences for taxonomy. — Proc. 2nd Int. Coral Reef Symp., Brisbane, 1973, 2: 217 - 228.

Ziegler, A. M., 1965. Silurian marine communities and their environmental significance. — Nature, 207: 270 - 272.

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