Ecology and faunal dynamics

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Adequacy of the data in faunal and floral logs

The degree to which the data in the faunal and floral logs accurately represent the species distributions at Vattenfallet is affected by four main factors: (1) Variation in sample size, (2) variations in vertical spacing of sampled beds (sample density), (3) the nature of the rock, and (4) differences in collecting methods.

(1) One of the weaknesses of the present study is the poor control of sample size (in this context, the amount of rock from a bed examined for fossils). The sample size has varied from bed to bed and, since the number of taxa from a bed is normally a function of sample size, taxonomic data from different levels are not strictly comparable. In almost every bed examination of additional rock material would of course have increased the number of species recorded. A certain indirect measure of the sample size is the frequency of specimens collected from each bed. This parameter is dependent on the sample size as well as the density of fossils in the rock, but since most beds of the section are moderately to richly fossiliferous the importance of sample size in the variation of the number of collected specimens is probably greater than that of the density of fossils. The frequency of articulate brachiopods, rugose corals, pelecypods, and trilobites in various beds of the section is shown in Fig. 74, and in most parts of the section the variation in the frequencies reflects reasonably well the nature of the exposure.

Some portions of the section are exposed only in fairly steep walls from which large samples of macrofossils are difficult to obtain. Such portions are (1) the lower part of the Upper Visby Marl (up to about 4.5 m; see Fig. 3), (2) the upper part of Högklint *a* (c. 11.1 to 12.1 m) and (3) the lowermost part of Högklint *b* (about 13.5 to 17.0 m; see Fig. 13 and Hedström 1910, Fig. 60a). These intervals are also notably poorly represented in Liljevall's collections. A complication is that the lowermost Upper Visby Marl (up to about 3.8 m) and the lowermost Högklint *b* (between 13.3 and 16.7 m) consist predominantly of calcilutites which one would expect to be less rich in macrofossils than the calcarenitic parts of the sequence. It is difficult to estimate to what extent the poor representation of these intervals in the collection depends on the low density of macrofossils and to what extent this is a function of small sample size due to the nature of the exposure. At some levels extensive bedding surfaces were available for collecting (particularly at 13.0–13.1 m and 19.5–19.6

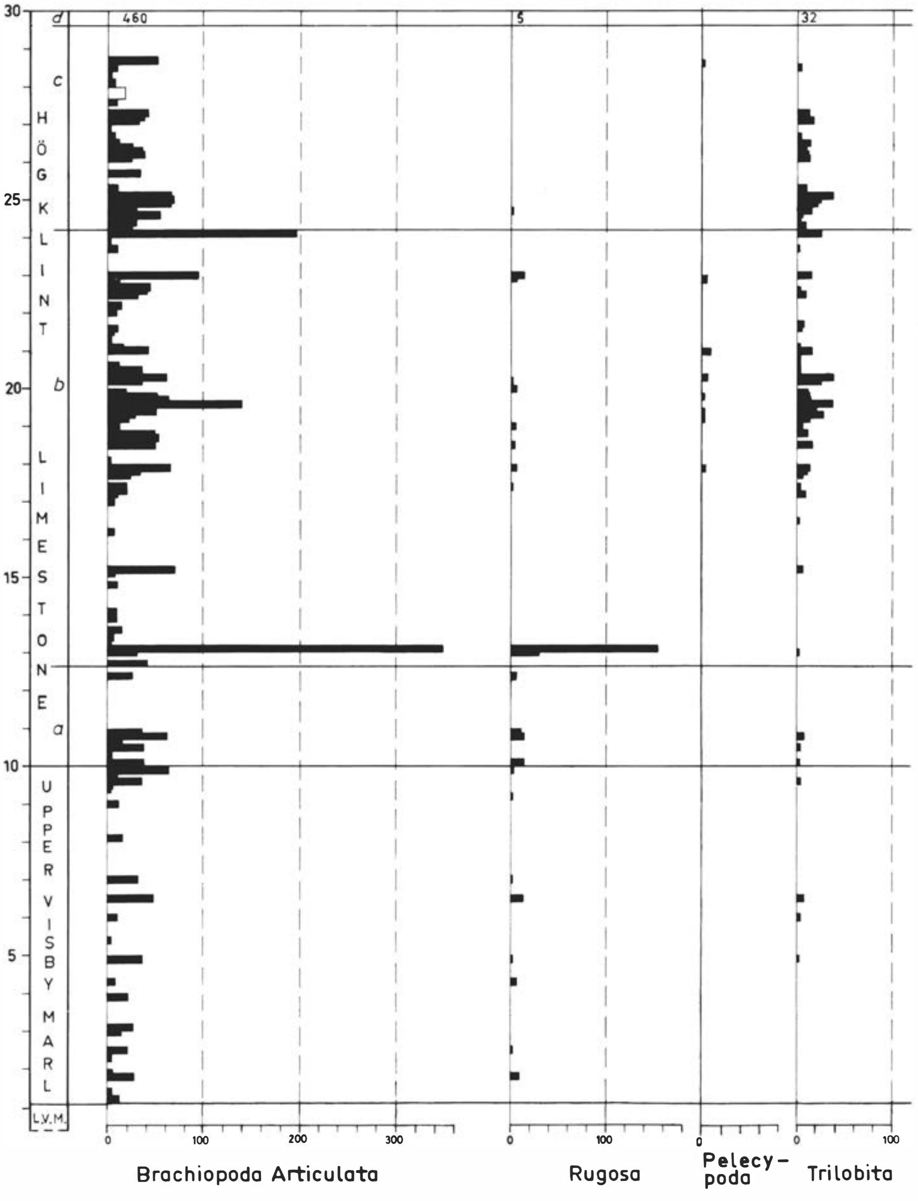


Fig. 74. Frequencies of articulate brachiopods, rugose corals, pelecypods, and trilobites in the Vattenfallet material (mainly Liljevall's collection). Only such data in which the precision of the level is within 20 cm are included, and levels with less than 3 specimens are not shown. The columns record the number of specimens in the collection (for brachiopods either separate valves or articulated shells); most of the specimens observed when counting valves in rock samples are not included.

m), and these levels coincide with the peaks in the brachiopod frequency. The level 13.1 m shows a high peak also for Rugosa (68 per cent of it formed by a single species, *Crassilasma* sp. *a*) but not for trilobites. The lack of a peak for Rugosa at 19.6 m is also due to real scarcity of this group in the fossil assemblage. The peak for brachiopods at 24.1–24.2 m is associated with the bed crowded with *Atrypa* sp. and it is not reflected in many other groups of macrofossils. The available sample from the "*Pterygotus*" Beds is proportionally larger than from any of the other levels. This is due to the particularly intense collecting in these beds. A more detailed discussion of specimen frequencies of macrofossils at different levels is hardly warranted because much of the collecting has been selective and the collections may not reflect the true proportions between different groups.

(2) The data in Fig. 74 also give a fair impression of sample density, S. This term is defined as the total thickness of sampled individual beds divided by thickness of the sampled unit (Jaanusson 1976:303). Fig. 74 shows that in some portions of the section the sampled beds are fairly widely spaced, whereas in some other portions the sampling has been continuous, from bed to bed. In the Upper Visby Marl the sample density is low (S=0.1–0.2), except in the uppermost part (9.0–10.0 m) where it is much higher (S=0.4–0.5). In favourably exposed intervals of Högklint *b* (17.2–20.6 m) and Högklint *c* almost every bed has been sampled and the sample density is very high (S=0.7–1). The differences in sample density are clearly reflected in the faunal and floral logs.

(3) The nature of the rock varies within the section, and with it also the possibility to obtain identifiable specimens of several groups; marl samples, for example, normally yield a somewhat different set of identifiable specimens than beds of hard limestone. The data in the logs are thus somewhat lithology-dependent. Several contributors to this publication (see the chapters on bryozoans, tentaculitoids, echinoderms, and machaeridians) have stressed that in Högklint *c* the representation of the groups is incomplete because this interval lacks marly intercalations as well as argillaceous bedding planes, and identifiable specimens of these groups cannot be successfully collected from a hard limestone. Most data on these groups in the logs come either from marl samples or from scanning argillaceous bedding planes. Molluscs, on the other hand, are mostly poorly preserved in friable marl or argillaceous beds and yield in such beds a proportionally great number of unidentifiable specimens. The relative rarity of molluscs in the Upper Visby Marl is in part due to this factor.

(4) The material assembled from the Vattenfallet section has been collected in three main different ways: (a) selective collecting of macrofossils from a bed (or from an interval of the section, such as 8.6–9.2 and 9.2–10.0 m along the

exposure), (b) by systematic searching of washed marl samples or crushed limestone samples for fossils, and (c) by systematic searching for acid-resistant fossils in insoluble residues from well-defined series of samples. In the logs, data based on either of the first two collecting methods cannot be distinguished. The main difference between selective collecting from the exposure and systematic collecting from limited rock samples is that in the former case large samples of the rock have been examined but with preference for easily recognizable, large macrofossils. In the latter case the data on small macrofossils are reasonably complete relative to the size of the sample but the density of many large macrofossils in the rock is frequently too low to be found in samples of that size. For example, at many levels of the Upper Visby Marl a sample of 1 kg does not contain many identifiable brachiopods, not to mention tabulate or rugose corals, or stromatoporoids.

Quantitative methods

Quantitative data are essential for any analysis of ecology and faunal dynamics, and for this reason a quantitative approach has been attempted wherever possible in the present study. The selective nature of Liljevall's collections inevitably places restrictions on a quantitative evaluation of the material in terms of individuals, particularly with respect to comparison of the relative frequencies of various groups in the total material from each bed. For the most common macrofossil groups in which individuals can be distinguished (articulate brachiopods, rugose corals, pelecypods, and trilobites), a general impression of relative frequencies can be obtained by comparing the absolute frequencies from each level shown in Fig. 74.

The most common quantitative approach is to count the number of individuals of various species in a sample and then to calculate their relative frequencies. Depending on the properties of the rock and the composition of the skeleton, four different sampling methods are normally available.

(1) In friable marls the rock can be broken down and the fossils washed out, picked and counted. Conditions in which the shells became so clean that the frequency of various taxa can be determined by weight (Imbrie 1955) are extremely rare. In the Vattenfallet section marls occur at many levels in the Lower and Upper Visby Marl and in Högklint *b*. Some of the data on the relative frequency of palaeocope ostracode species are based on such samples (Fig. 44).

(2) On exposed bedding surfaces with a sufficiently large area to yield an adequate sample size all visible specimens can be identified and counted (Sloan 1955; Ager 1963). At Vattenfallet some such surfaces were available in parts of Högklint *b* and *d* (see Bassett, this volume).

(3) The only possibility of obtaining quantitative data in terms of individuals from a rock which cannot be broken down by some mild treatment is to crush the rock of a bed into small pieces and count all specimens observed (cf. also Ziegler et al. 1968). Much of the Vattenfallet section consists of such rock. Most of the data on frequencies of palaeocope ostracode species (Fig. 44, left) were obtained by scanning chips of hard limestone under a binocular microscope. The relative frequencies of palaeocopes and "non-palaeocopes" were obtained in the same way (Fig. 44, right) but, because of difficulties in identifying many "non-palaeocope" species in such material, reliable relative frequencies of species among "non-palaeocopes" were difficult to determine. From the Upper Visby Marl and Högklint *a* a series of reasonably adequate limestone samples were available, and these were used for estimating relative frequencies of articulate brachiopod species (Fig. 61). The density of other macrofossils in which individuals can be recognized or estimated was too low for reliable quantitative estimations. With bivalved organisms the usual procedure is to regard the sum of articulated shells and the commonest separate valve as the total number of individuals. However, the assumption that all specimens of the less common valve belonged to individuals represented by the commonest valve is seldom correct. With brachiopods there is also the problem that for specimens still in the rock it is not always possible to determine which valve is represented without tedious preparation, or even whether the visible valve is separate or belongs to an articulated shell. For ostracodes and brachiopods simple counting of the number of valves was therefore deemed sufficient. Differences from results based on more sophisticated calculations of the probable number of individuals proved to be negligible.

(4) For acid resistant skeletons reliable quantitative data are easy to obtain by dissolving a sample, preferably of a standard weight, in a suitable acid and by counting the number of specimens of various taxa. In this study such data have been obtained separately for chitinozoans (Fig. 23), polychaete jaws (Fig. 27), conodonts (Fig. 70), and to some extent also for acritarchs (Cramer, Díez & Kjellström, this volume).

Volumetric determinations of skeletal constituents of various taxa, either in terms of skeletal material (grain-solid) or the total volume of the skeletons (grain-bulk), are particularly important because they give some impression of the relative production of the ostracomass. With the exception of a few groups the taxonomic level in identification of skeletal particles by point counting in peels or thin sections is normally seldom below phylum or class (Fig. 77), and thus the taxonomic resolution is very low. For bryozoans and coenitids the relative grain-bulk volume has been determined at species level (Fig. 56).

In all these cases, except when volume is concerned, the data must be presented in terms of individuals or, when dealing with colonial organisms, separate colonies *(individual-based frequencies)*. This presents no problems in groups in which the skeleton of every individual or colony is normally preserved as a single specimen (rugose corals, many tabulates and stromatoporoids, gastropods, cornulitids, etc.). Relatively slight complications are involved with bivalved skeletons, such as those of brachiopods and pelecypods which occur as articulated shells as well as separate valves. The problem becomes more complicated in arthropods, such as trilobites, in which a single individual has produced a number of carapaces which, in turn, mostly occur disarticulated into many individual pieces.

In addition, a fossil fauna normally contains many other constituents that once belonged to macro-organisms but in which individuals are mostly no longer recognizable. Most echinoderms, bryozoans, coenitids, tentaculitoids, and "chitinous" hydroids occur in a very fragmented state. Machaeridians became disarticulated into many individual plates. In some groups of macro-organisms individual skeletal constituents disarticulate rapidly after the decay of soft tissue and form skeletal particles of the size range of microfossils. Examples include sponge spicules, melanosclerites, ossicles of holothurians, and jaw components of annelid worms. Conodonts also fall in this category but it is not known for certain whether their mode of life was benthic or planktic. In all such fossils estimation of the number of individuals in a sample is either difficult or virtually impossible.

Previous reconstructions of Silurian fossil "communities" (e.g. Ziegler 1965; Ziegler et al. 1968; Calef & Hancock 1974; Hurst 1975a) are individual-based, that is, with few exceptions only such groups were considered in which the frequency of individuals could be counted or estimated. In these "communities" brachiopods are mostly considered to dominate (for quantitative data from Gotland, see Hurst 1975b). It is notable that the composition of such individual-based "communities" differs considerably from that of the skeletal sand, that is, the production of ostracomass by various groups.

The exclusion of many groups of macro-organisms in making reconstructions of ancient biotic relationships is, of course, unsatisfactory. In a modern marine benthic community 10 to 70 per cent of macro-organism species are soft-bodied and have little potential for preservation (e.g., see Lawrence 1968). Exclusion from consideration of a large number of preserved species, the skeletons of which occur in a strongly fragmented or disintegrated state, would reduce the available information to such a degree that meaningful reconstructions of biotic relationships are scarcely possible.

In order also to take species with disintegrated skeletons into account the *sample-frequency method* is introduced here. This method is based on a series of samples and for each sample the presence or absence of various species is recorded, irrespective of whether the species are represented by complete skeletons belonging to single individuals or tiny fractions of individual skeletons. It is assumed that the frequency of samples in which a species occurs is proportional to the average frequency of the species. In other words, a species which is recorded from a greater number of samples is considered to be, on average, more common than a species that occurs in a smaller number of samples. The group of species with the highest frequencies is named here as the *Average Macro-organism Assemblage Nuclei* (abbreviated AMAN).

The sample-frequency method is related to Raunkiaer's (1913, 1916, 1918) method of vegetation analysis in which the presence or absence of different species is recorded on each of a number of sample areas of constant size, scattered over the vegetation to be analysed. For every species found, the number of hits is expressed in per cent of the total number of throws, and is taken to represent the frequency of the species.

When applying the sample-frequency method, some uniformity in sample size is required throughout the sampled section. The results are also dependent on sample size because with increasing size of the samples the number of high-frequency species increases (Romell 1930:590). Results from different sections based on different sizes of samples are difficult to compare because there is no safe way of correcting the results for another size of analysed sample (Romell 1930:593).

Even when the above requirements have been fulfilled some further factors should also be borne in mind. (1) With a sample size which is sufficient for obtaining representative data on species represented by skeletal fragments or small to medium-sized individual skeletons, large skeletons – such as those of tabulates and stromatoporoids–tend to be underrepresented in relation to their volumetric importance in the rock. (2) Conversion of data for species found in acid resistant residues–such as jawed annelids and "chitinous" hydroids–so that they become comparable with data on species with a carbonate skeleton collected in a different way may present problems. (3) Frequencies of species represented by individual skeletons may not be exactly comparable with the frequencies of species whose skeletons are preserved as numerous fragments; the chance of finding a piece of an individual skeleton disintegrated into numerous pieces may be greater than the probability of finding an individual represented by a single skeleton. These points show that additional methodological studies are needed in order to increase the precision of the sample-frequency method for thanatocoenotical purposes. However, in general the method appears to be an important tool for studying ancient biotic relationships.

Species size in an ecological context

In a random sample of an organism group from a habitat the majority of individuals belongs to only one or a few species, whereas many species are represented by one or a few individuals. This species abundance relationship (Fisher et al. 1943) has been discussed in numerous papers, most recently by May (1975). Similar relative abundances of species also characterize many standing crops of soft-bottom communities where one or a few species are dominant. In a palaeoecological context this species abundance relationship has been discussed by Johnson (1964), who found that similar circumstances do occur in fossil assemblages but do not necessarily reflect the relationships of a living community. At best, a fossil assemblage reflects the total productions of preservable individuals and not a standing crop.

A similar quantitative relationship also exists with respect to relative frequencies of species in terms of biomass. In a standing crop one or a few specimens commonly comprise the bulk of the biomass, whereas many species make up the remainder. Quantitative analyses of soft-bottom communities, in which not only the number but also the weight of individuals is given for each species (e.g., Molander 1930), show that the species which dominate by biomass are frequently not those that dominate by the number of individuals. Thus, if the importance of a species in a community is judged from its biomass, then the most important species are not necessarily the most abundant.

The above generalisations are based on quantitative analyses of either a single major size group of organisms, or two groups. However, in a standing crop the range of species sizes is considerable, from, say, a large sea-urchin to an ostracode. Normally in a habitat the size of the organisms is inversely proportional to the frequency of individuals, that is, with decreasing size of organisms the number of individuals increases considerably (Elton 1927), a relationship which is now commonly known as the Eltonian Pyramid. Instructive examples for a marine benthic community have been given by Mare (1942). An important factor is that each size group of species generally has the type of species abundance relationsship discussed above. But if several size groups are lumped it is the group with smallest species that provides the dominant species, because its most common species tend to vastly outnumber the commonest species in next largest size group. It is important to remember this trend when interpreting species frequency data. For brevity, this trend is here termed *the frequency dominance of the smallest.*

For understanding ecological relationships within a community the pyramid of numbers is not very fundamental or instructive since a great many small units are required to equal the mass of one large unit (Odum 1959:60). In this respect the pyramid of biomass is of more fundamental interest. This pyramid is mostly inverted relative to the pyramid of numbers, that is, with increasing size of the organisms the relative importance ot their total biomass increases (Odum 1959:60–61; for marine benthic organisms see Mare 1942). This is the main reason why in a standing crop the most common but relatively small species has frequently a smaller biomass than a less abundant large species.

Differences in the numbers of individuals between different size groups of organisms should also be reflected in the production of a community. That similar abundance relationships also exist in fossil assemblages is known to everyone who has picked samples for fossils of all sizes.

In the Upper Visby Marl at Vattenfallet rough estimates of abundance of various groups per kilogram of rock at different levels give the following maximum and minimum figures for the samples examined: 20,000 to 440,000 acritarchs (G. Kjellström, personal communication), 5000 to 100,000 chitinozoans (Fig. 22), 8000 to 25,000 ostracode valves, 80 to 300 gastropods, 60 to 200 brachiopod valves, 20 to 100 jawed polychaete worms (Fig. 27), 0 to 20 rugose corals, 0 to 10 tabulate and heliotitid corals and 0 to 5 stromatoporoids. Most of the macrofossils were represented by juvenile specimens. For echinoderms, bryozoans, trilobites, sponges, tentaculitoids, and several other groups such individual-based estimates were difficult or impossible. With regard to conodonts see Fig. 70. The data for acritarchs were based on counts of the number of specimens in the insoluble residue of 5 g of rock from each sample and then multiplying the results by 200. Estimation of the frequency of ostracode valves per kilogram of rock was based on counting separate valves in thin sections, and then allowing data from each section to be representative of a rock slice with the surface area of the thin section. The frequency data were then multiplied by a factor equal to that obtained by dividing one kilogram with the weight of the rock slice. More than one hundred cross-sections of ostracode valves in a thin section (2×2.5 cm) were not uncommon. The data are not corrected for carapaces nor for the potential production of several carapaces by the same individual. Frequency of brachiopod valves and gastropod shells was estimated from peels in the same way.

Of particular interest is the relatively high frequency of gastropods which is not reflected in collections from the Upper Visby Marl. With few exceptions the cross-sections of shells observed in peels are very small, mainly 0.7 to 1.3 mm in diameter—a size approaching that of protoconchs. The specimens may represent larval or early postlarval individuals, but the possibility cannot be excluded that undescribed small gastropod species are involved.

The frequency data give a rough impression of the partial pyramid of numbers in an Upper Visby assemblage of fossils. They may also serve as an example of the frequency dominance of the smallest, because it can be easily seen that in a sample a numerically dominant meio-organism species, such as an ostracode, would vastly outnumber a dominating small macro-organism species, such as a brachiopod.

The great differences between different size groups in a sample, not only in the number of individuals but also in rational sampling methods for organisms of widely different sizes, makes it necessary to treat each size group separately for ecological purposes. However, even then some size-dependent effects remain, because each size group still includes a range of different sizes of species. There is a tendency within each size group for many species with the adult size close to the lower size limit of the group to be represented by a larger number of individuals than large species of the group. For example, among pedunculate articulate brachiopods at Vattenfallet several of the dominant species are small for brachiopods (e.g., *Dicoelosia verneuili,* average adult length 6–7 mm; *Eocoelia angelini,* 8–9 mm; *Microsphaeridiorhynchus* sp., 6–8 mm) and their small size may have contributed to their relatively high frequency. Conversely, large fossils, such as many species of tabulate and heliolitid corals and stromatoporoid colonies, are rarely even represented in small random samples; the data in the Vattenfallet logs are based mostly on selectively collected specimens. In a bed such fossils are sparsely spaced (Fig. 7) and in order to get a fair coverage of them from a series of samples, the sample size has to be increased considerably, which imposes problems for rational sampling. Such large fossils have a relatively large "minimum area", to use a term borrowed from phytocoenology.

Species frequency

The material from Vattenfallet has a surprisingly high total number of species. Some 485 separate species of animals have been distinguished from the Upper Visby Marl and Högklint Limestone, while in addition in some small groups ("chitinous" hydroids, melanoscleritoids and partly in foraminifers) species have not been differentiated and in some other groups (cephalopods, echinoderms) indeterminate material includes a substantial number of additional species (Mutvei and Franzén, respectively, this volume). One of the factors contributing to the high total taxonomic diversity is that the sequence reflects a variety of different environments, each with a set of distinctive species. For example, Högklint *d,* only 40 cm thick and deposited in an unusual environment, has yielded 37 species which are restricted to this division, and many of them have not even been found elsewhere. It is also possible that during some period of the deposition of the sequence the fauna at Vattenfallet belonged to an ecotone, having been influenced by the relative proximity of reef mounds, and that for this reason some edge effect was involved. This possibility cannot be tested before comparable data become available from contemporaneous reef mounds and the bedded limestone sequence farther away from the reefs.

The variation in species frequency within the section is shown for most groups in Figs. 75 and 76. The groups excluded are either represented by only a small number of species (inarticulate brachiopods, coenitids, *Allonema,* conulariids, sponges, tentaculitoids, machaeridians, eurypterids, etc.) or lack reliable data on the number of species (cephalopods, echinoderms, foraminifers).

The data are presented separately for each lithologically distinguishable subdivision, and in some cases these are further subdivided in order to obtain a roughly comparable thickness for each unit. The lowermost beds of Högklint *b* (12.65–13.2 m), although forming a thin subdivision, are treated as a separate unit because they have yielded a large sample of fossils (Fig. 74) and possess distinctive lithological features. In the uppermost Högklint *c* (28.8–29.6 m) the material collected is so limited that no meaningful frequency data are available.

Species frequency is partly a function of sample size, in this context the quantity of rock available for collecting from each unit. With increased sample size probability of finding additional species increases. As discussed elsewhere in this volume, the sample size as well as the sample density varies in the material collected, which certainly distorts the data on the real taxonomic diversity in various ways. In particular, the sample size appears to have been small in the lowermost Upper Visby Marl (1.1–3.8 m) and in lower Högklint *b* (13.3–16.8 m). Both these units are calcilutitic and the total taxonomic diversity there would be expected to have been at least somewhat lower than in the calcarenitic portions of the sequence. However, to what extent the low taxonomic diversity in Liljevall's collection from these units is real or due to small sample size is difficult to prove. Conversely, the middle Högklint *b* is not only highly fossiliferous but also among the best exposed portions of the section. The peak in species frequency in this interval may depend partly on larger than average sample size. It should also be remembered that for macrofossils the sample density is far lower in the Upper Visby Marl than in most of the Högklint Limestone. With all these uncertainties in mind, it is still possible to draw some interesting conclusions from the histograms.

Several microfossil groups with an organic skeleton (acritarchs, chitinozoans and "chitinous" foraminifers) show a striking decrease from the upper Högklint *b* to Högklint *d,* not only in species frequency but also in general abundance, and several samples in Högklint *c* and *d* are barren. The rarity of chitinozoans in extremely shallow-water and high-carbonate sediments agrees with the general pattern of occurrence of this group on Gotland (Laufeld 1974a).

In the alternating calcarenitic and calcilutitic middle and upper part of the Upper Visby Marl the species frequency of tabulate and heliolitid corals is far greater than in the Högklint Beds. The diversity of these groups in the lower, calcilutitic part of Högklint *b* (13.3–16.7 m) is extremely low and although a larger sample size from this unit might have increased the number of species somewhat, it is clear that there the environment was unsuitable for these groups. The species frequency of rugose corals and stromatoporoids also follows the same pattern but not so markedly.

An essentially opposite trend of species frequency is shown by some groups of vagile animals, such as gastropods and trilobites, and pelecypods have a comparable diversity pattern. These groups have the greatest species frequency in the middle and upper parts of Högklint *b* and in Högklint *c*, where the sea was shallowest and bahamitic sediments were deposited.

A particularly pronounced pattern of species frequency of the latter type is shown by palaeocope ostracodes. This group has a very distinct species frequency maximum in Högklint *c*, although it is almost certainly exaggerated to some extent by particularly intense collecting from these beds. The high diversity is also reflected in the data on relative frequency of various palaeocopes (Fig. 44). In the upper part of Högklint *b* and in Högklint *c* the number of species occurring with low frequencies increases considerably and this is also clearly reflected in the increase of the relative importance of the column for "others".

Unfortunately the taxonomic diversity of palaeocope and "non-palaeocope"

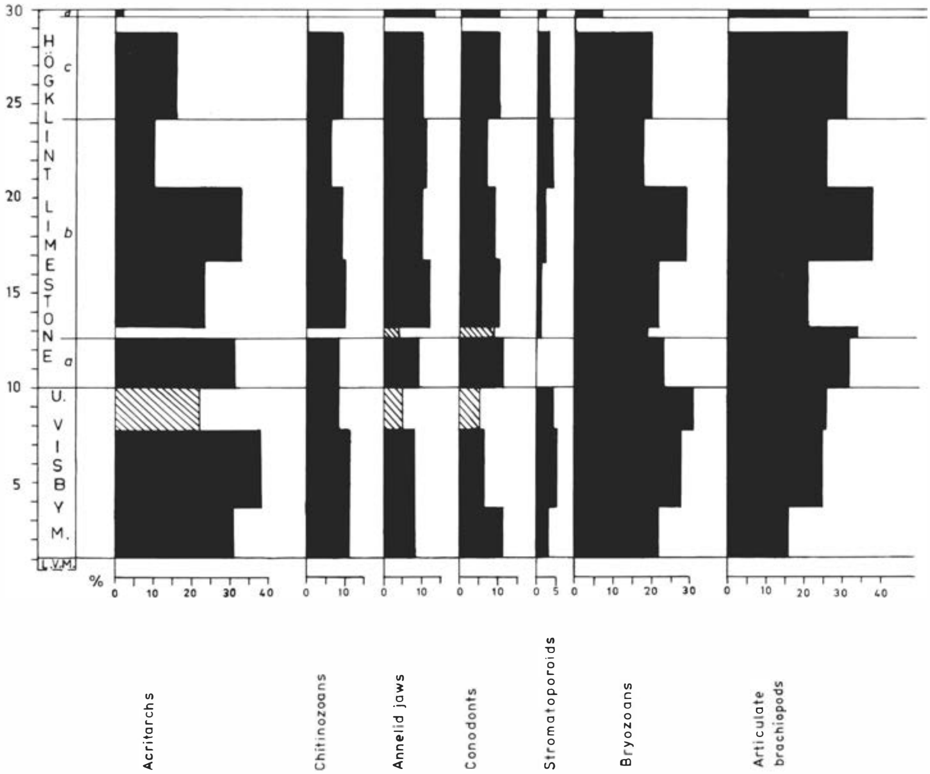


Fig. 75. Species frequencies in different parts of the Vattenfallet section. Continued on Fig. 76. From the lowermost beds of Högklint *b* (12.65–13.2 m) no samples have been analysed for acritarchs and chitinozoans. For a few groups some intervals have not been adequately sampled; such intervals are indicated by a pattern of diagonal lines. For further explanation see text.

(Podocopa, Metacopa and Platycopa) ostracodes is not always closely comparable in the faunal logs for the following reasons. (1) Most palaeocope ostracodes were collected from limestone chips, with only a minor portion of the material coming from marl samples; most of the "non-palaeocope" ostracodes were collected from marl samples or as articulated carapaces isolated from limestone. The problem is that while palaeocopes are readily identifiable from separate valves embedded in the rock, a safe identification of many "non-palaeocopes" requires some knowledge of overlap features and preferably also hinge structures (Lundin, this volume). (2) Because of patient collecting by Sethi over several years, the average sample size is far larger for palaeocopes than for "non-palaeocopes", especially in the portions of the section with few or no marl intercalations (upper Högklint *b* and Högklint *c*).

For comparison between palaeocopes and "non-palaeocopes" at Vattenfallet the relative frequencies of these groups (Fig. 44, right) are currently more

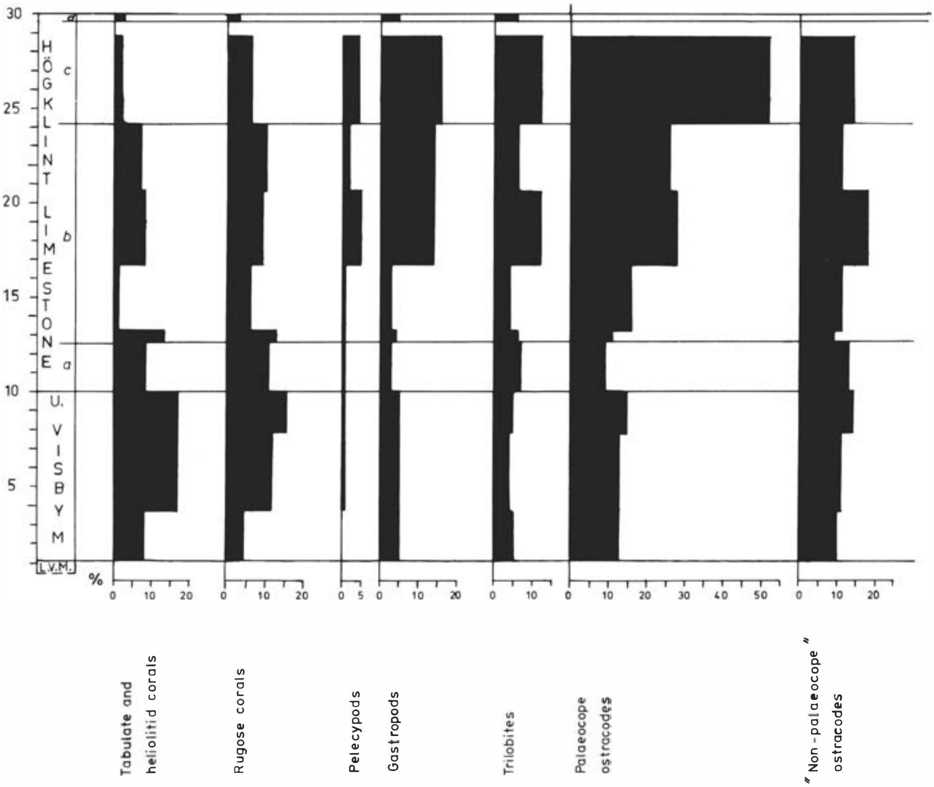


Fig. 76. Species frequencies in different parts of the Vattenfallet section. Continued from Fig. 75. Högklint *d* has not yet been searched exhaustively for ostracodes.

useful than their species frequencies. The former data show that in the Upper Visby Marl the "non-palaeocopes" dominate greatly over palaeocopes. In upper Högklint *b* and in Högklint *c*, on the other hand, the frequency of specimens of both groups is about equal. The data from the lower and middle parts of Högklint *b*, and also from the uppermost Lower Visby Marl, are intermediate between these extremes. It is interesting to note that in the Permian of Kansas the relative frequency of palaeocopes is also higher in extremely shallow-water environments than beds deposited at some depth (Kaessler & Peterson 1977).

A survey of published data on taxonomic diversity in modern benthic communities indicates that, provided other conditions (substrate, nutrients, etc.) are equal, species frequency does not vary much with depth of the sea down to at least 150–250 m. Thus differences in species frequency within the shelf region do not appear to be depth-dependent but are controlled mainly by other factors such as substrate and variety of niches.

At Vattenfallet the role of perishable benthic macroscopic algae in epibiontic communities is difficult to reconstruct but they must have formed an important constituent in the vegetation. Such algae increase the epibiontic stratification on the sea-floor and thus also the number of niches available for small animals. At Vattenfallet the importance of calcareous algae increases with decreasing water depth upwards through Högklint *b* and *c* (Fig. 20) and this trend would have also applied to non-calcareous forms. Some of the increase in species frequency of gastropods and palaeocope ostracodes in upper Högklint *b* and Högklint *c* might have been associated with the probable increase in density of algal vegetation, although for palaeocopes the autecological dependence on vegetation is difficult to prove.

The environmental conditions responsible for a high species frequency of corals in the middle and upper part of the Upper Visby Marl are not obvious. They may have been associated with subtle properties of the substrate and slight variations in the relative water energy level that are not clearly reflected in the rock. The skeletons of colonial organisms also increased epibiontic stratification on the sea-floor. Patches of hard bottom formed by corals and stromatoporoids were used by encrusting and attaching organisms and this may be reflected in the peak of bryozoan species frequency in the upper part of the Upper Visby Marl. The under sides of many colonies are covered by encrusting organisms, mainly bryozoans, coiled serpulids, cornulitids, and the enigmatic *Allonema*. These organisms were able to inhabit these surfaces because of the existence of a cavity beneath the colonies (Mori 1969; Spjeldnaes 1975). The most likely explanation of the origin of the cavities is that when the colonies began to grow laterally from the original attachment on top of some protruding patch of hard bottom they first extended free beyond the original attachment surface until they came to rest upon sediment surface

(Mori 1969:35). According to Spjeldnaes (1975) the encrusting bryozoans of what he terms the "shade fauna" consist mostly of species which are restricted to this specific cavity environment. This would imply that in beds where the "shade fauna" is present the species frequency of bryozoans would be increased by additional species. In the Vattenfallet material the "shade fauna" occurs at several levels of the Upper Visby Marl. The encrusting articulate brachiopod *Liljevallia gotlandica* was recorded only from this habitat but none of the bryozoan species was restricted to the under side of the skeletons of colonial organisms (K. Brood, personal communication). Similarly, most of the cornulitid and coiled serpulid species were also recorded encrusting skeletal particles outside the cavity environment.

Bionomic composition of the benthic fauna

The bionomic organisation of the Palaeozoic benthic fauna differs in several respects from that of its modern counterpart. This is due to the existence in the Palaeozoic of widespread types of adaptations which are rare or absent among modern benthic organisms, and vice-versa.

The benthic fauna at Vattenfallet can be divided into five bionomic groups: (1) hard-bottom epifauna, (2) hard-bottom endofauna, (3) soft-bottom epifauna, (4) soft-bottom endofauna, and (5) vagile benthos. The necessity of distinguishing between hard- and soft-bottom faunas should be especially stressed. On modern sea-floors these two faunas represent widely different adaptations, and the same conditions obviously existed in the past. A kind of transitional environment is formed on gravel bottoms where individual gravel particles represent small patches of hard bottom for attaching organisms, but where the interspaces can be inhabited by representatives of the soft bottom endofauna. Zoologists normally include gravel substrate in hard bottoms (for a modern example with brachiopods among dominant organisms see Dell 1951).

(1) Equivalents of the modern hard-bottom epifauna are common in the Vattenfallet section. No undoubted indications of hard-grounds have been observed, with the probable exception of the top surface of Högklint *c* which appears to be barren. However, throughout most of the section colonies of stromatoporoids, various corals, occasional cephalopod conchs, and large skeletons of other groups formed patches of hard bottom of varying size, scattered on the level sea-floor which consisted of soft sediment. Many of these patches were inhabited by an attached hard-bottom fauna. Encrusting organisms are still largely attached to the original hard substrate. Such organisms include encrusting bryozoans, small colonies of stromatoporoids and

corals, serpulid annelids, encrusting cornulitids, the enigmatic *Allonema,* the articulate brachiopod *Liljevallia,* and some craniacean brachiopods. The tabulate *Aulopora* and the enigmatic fossil *Condranema capillare* (Ulrich and Bassler) which are common encrusting organisms elsewhere in the Upper Visby Marl did not happen to be found at Vattenfallet. Among other hard-bottom organisms many had holdfasts (bryozoans, coenitids, crinoids) which can still be found attached to the hard substrate, whereas the rest of the skeleton has broken off and been distributed as skeletal grains in the adjacent soft sediment. And lastly, there is a group of hard-bottom organisms in which the association with the original habitat is not preserved since after death the organisms became completely disassociated from their substrate and their skeletons were deposited in the adjacent soft sediment where they occasionally formed small additional patches of hard bottom. Such organisms include many pedunculate brachiopods, byssate bivalves and "chitinous" hydroids. A few modern pedunculate brachiopods are capable of attaching themselves to small shell-fragments in a fine shell gravel (for a summary see Rudwick 1961) and it is possible that some thin-shelled Silurian pedunculate brachiopods had the same mode of attachment. In other cases, particularly in thick-shelled forms with a large pedicle opening, such as in most rhynchonellaceans, orthaceans and enteletaceans, attachment on a firm substrate is likely.

For attached organisms the substrate did not necessarily need to have been restricted to calcium carbonate skeletons. In modern environments small sedentary organisms, such as bryozoans, brachiopods and hydrozoans, are also found attached to firm but perishable organic substrates, such as tunicates or algae, and there are indications that this was also the case in the Silurian of Gotland. In the Vattenfallet material there are examples of encrusting bryozoan zoaria which were obviously attached to an organism that has perished without trace (Brood, this volume). Numerous similar examples are known among Ordovician bryozoans (Hecker 1928; Modzalevskaya 1955; Männil 1961).

The occurrence of patches of hard-bottom, formed by large dead shells and skeletons of various animals and occupied by a hard-bottom epifauna is a common phenomenon on the modern sea-floor. A special case has been described by Allen (1953), dealing with living pectinid bivalves which form patches of hard substrate for attached epifauna within a soft-bottom environment.

(2) Massive colonies and skeletons were also the habitat for a boring endofauna (calciobiocavicoles, Carriker & Smith 1969). At Vattenfallet many stromatoporoids and tabulate corals were bored, as well as some massive trepostome bryozoans. From the evidence of diameter and shape of the borings this habitat was occupied by several different animals. The borings are all that

are preserved of these organisms, but since they were not studied in detail the boring endofauna is not further considered in this volume.

(3) The sedentary soft-bottom epifauna of the Vattenfallet section is rich and diverse. In the Palaeozoic several groups of brachiopods had developed a type of adaptation that is not known in modern representatives of the phylum. In these groups the animal either lacked a pedicle or the pedicle atrophied during ontogeny. The animal lived resting free on the sea-floor either throughout its life or in the adult stage. This type of adaptation, immovable but not attached, is termed here *recumbent* (liberosessile, Remane 1940:50). Among brachiopods that lacked a pedicle are the possible lingulacean *Craniops* and pentameraceans. With the type of construction of the articulating devices and closure of the shell that pentameraceans have (Jaanusson 1971), it is difficult to see how this group could have possibly had a pedicle even during the earliest post-larval stage. Many plectambonitaceans (Williams 1953:2), such as *Eoplectodonta,* and chonetaceans lost the pedicle very early in ontogeny whereas in many strophomenaceans (see also Crickmay 1966) and davidsoniaceans the pedicle mostly atrophied at a later stage. Plectambonitaceans probably lived with the convex valve downwards (Cocks 1970) and this was probably also the case with other concavo-convex shells.

Sedentary organisms which were attached during early growth stages – and then belonged to the hard-bottom fauna – but were capable of resting free on the sea-floor during later stages, and then belonged to the soft-bottom epifauna, are here termed *ambitopic*. In additon to several brachiopod groups there existed numerous other ambitopic organisms. The size and shape of the skeletal grains used for the original attachment varied widely but many were small. When the attached animal grew in size its weight may sooner or later have surpassed the carrying capacity of the grain used as a hard substrate. Many Palaeozoic organisms were capable of continuing to grow over the soft sediment surface far beyond the area of the initial skeletal grain or the patch of firm substrate. Thus during most of their life-time these organisms had a recumbent mode of life. This ability is displayed by many stromatoporoids (Hadding 1941) and tabulate corals. At Vattenfallet a particularly illustrative example is provided by the colonies of *Planalveolites fougti* which could grow as a thin veneer over carbonate mud and skeletal sand. Other groups which included many representatives with an initially attached but later recumbent mode of life are massive trepostome bryozoans (cf. Männil 1961) and rugose corals. In many such organisms the original substrate is mostly preserved but in some cases only a mould of some unknown, perished organic material is discernible. In a few cases, such as in the rugose corals *Palaeocyclus porpita* and *Holophragma calceoloides,* no clear scar of the original attachment can normally be recognized, and it is possible that they started to grow directly upon the sediment, that is, that for attachment of their larvae a sedimentary grain of average size was sufficient. A modern analogue may be the larval attachment of the cheilostome bryozoans *Discoporella* and *Cupulandria* on sand grains (Driscoll et al. 1971).

The capability of stromatoporoids and tabulate corals to grow free upon soft sediment is an important factor in the construction of Palaeozoic reef-like mounds, such as the Gotland reefs. Contrary to most modern reefs, which are firmly anchored to a rocky bottom, Silurian organic reefs developed on a soft substrate (Hadding 1941, 1950; Lowenstam 1950, 1957).

Among the echinoderms from Vattenfallet the edrioasteroid *Pyrgocystis* belonged to the recumbent epifauna of the soft bottom (Franzén, this volume).

In modern marine environments a recumbent mode of life appears to be rare. Hard-bottom organisms may begin to grow attached to skeletal fragments that later prove to be too small to carry the weight of organism when it increases in size. When the organism falls over, its further growth is normally inhibited. However, some exceptions are known (e.g. Savilov 1961:15–16). The exceptions scarcely bridge the profound adaptional differences between modern hard- and soft-bottom faunas. It is also interesting to note that several of the modern free-living scleractinian corals which inhabit soft bottoms (Goreau & Yonge 1968; Hubbard 1972) and some unattached bryozoans (Marcus & Marcus 1962) are capable of some movement over the substrate on which they live. Thus these animals are not strictly sedentary.

Among Silurian soft-bottom epifaunal organisms there were also some which anchored with a holdfast directly into the soft substrate (rhizosessile attachment; Remane 1940). Among modern benthic organisms such a mode of attachment is known in several groups, such as many algae, some crinoids, brachiopods and sponges, but also in bryozoans (*Cellaria fistulosa,* Nicolić 1963:433). In the Vattenfallet section a rhizosessile attachment has been proved for some crinoids (Franzén, this volume) but it is difficult to say how wide-spread this mode of life was. Dendroid graptolites probably had a rhizosessile attachment, as possibly did some "chitinous" hydroids. The sponge *Atractosella* may also have been anchored directly into the sediment because it is particularly common in calcilutites.

(4) The preserved evidence of Silurian soft-bottom endofaunas is far more fragmentary than that of epifaunas. A comparison with the composition of a modern soft-bottom endofauna (see also Craig & Jones 1966) also indicates that the Silurian endofauna may have included proportionally more perishable soft-bodied organisms than the epifauna.

At Vattenfallet intense bioturbation in many beds reflects the activities of the endofauna, some of which may have been caused by vagile benthos. Apart from the epibyssate and thus epifaunal *Mytilacra,* all pelecypods from Vattenfallet were endobyssate, that is, semi-infaunal (Pojeta, this volume). Among brachiopods lingulids belong to the soft-bottom endofauna. Further possible endofaunal organisms were tentaculitoids but their mode of life is uncertain (Larsson, this volume). Some representatives of the endofauna are known only from their organic (Brood, this volume) or phosphatic (Bengtson, this volume) tubes.

(5) Many vagile organisms from Vattenfallet are difficult to refer to their correct bionomic group and for this reason these animals are here treated separately. The activities of some vagile organisms may have covered the soft bottom as well as the patches of hard bottom. This is particularly the case with carnivores or scavengers, such as jawed polychaete worms which formed an important component in the fauna. Other carnivores or scavengers were the asteroid *Urasterella* and possibly also several cephalopods and the snail *Cyclonema*. Another reason for difficulties in making a correct bionomic reference of fossil vagile organisms is that among such organisms the distinction between soft-bottom epi- and endofauna is not always clear-cut, and particularly on mud bottoms (Remane 1940). Many vagile benthic organisms spend part of their time resting or searching for food partly or completely buried in the sediment and then behaving like endofaunal organisms.

Trilobites probably included deposit feeders, filtering suspension-feeders and possibly even some carnivores (Bergström 1973b). Calymenids were capable of burrowing in the sediment and an Ordovician calymenid has actually been found in its own burrow (Osgood 1970). Bergström (1973a, b) suggested that illaenids appear to have dug burrows in which they sat with the pygidium downwards and the cephalon at least partly above the sediment surface. However, this may not have applied to many bumastines in which the cephalon is normally not so highly vaulted as in the illaenines. Some cybelines have been inferred to have been able to conceal themselves in the substrate (Ingham 1968:312–313; Bergström 1973a) and this might have applied also to other encrinurids. Odontopleurids were probably strictly epifaunal, lying and crawling on the sediment surface (for a discussion, see Bergström 1973a). The mode of life of the rest of the Vattenfallet trilobites is less understood but they too may have been epifaunal animals which had the ability to burrow or hide themselves temporarily in the sediment. Many eurypterids may also have had the same mode of life.

Most gastropods from Vattenfallet were probably epifaunal deposit feeding microherbivores, and some show possible adaptations to life on a soft bottom (Peel & Wängberg-Eriksson, this volume). The echinoids *Aptilechinus* and *Neobothriocidaris* were probably epifaunal browsers. The unusual crinoid *Myelodactylus* was a suspension feeder and was probably capable of some movement over the sea-floor. The machaeridians too belonged to the vagile epifauna but their adaptations are not yet understood (Bengtson, this volume).

On the modern sea-floor, faunas of hard (rocky) and soft bottoms are normally totally different (for a discussion, see Gislén 1930). In the Silurian the distinction was not so sharp because the faunas were bridged by the capability of many organisms to inhabit both types of bottom and by the abundance of organisms with a recumbent mode of life, which generated autochthonous patches of hard ground in a soft-bottom environment. This type of organisation of the soft bottom epifauna developed in the Middle Ordovician and lasted, with few changes, up to the Permian. At the transition from the Palaeozoic to the Mesozoic the groups with a capability of adopting a recumbent mode of life mostly became extinct, and the organisation of the Mesozoic soft bottom epifauna appears to have been largely similar to the modern pattern (for Triassic see Fürsich & Wendt 1977).

A conspicuous difference between the Silurian and modern benthic faunas is also the poor development of the boring endofauna in the Silurian. Although, as in the Vattenfallet section, many corals, stromatoporoids and occasional large skeletons of other groups were bored by calciobiocavicole organisms, the diversity in the diameter and shape of the borings is extremely low compared to the modern bored skeletons. The density of borings is just a small fraction of that in almost any comparable modern bored skeleton. It is obvious that the boring habitat is occupied far more intensely in the modern sea-floor than it was during the Silurian. This also has important consequences with respect to the preservation of organic reef structures. In the modern environment boring organisms form a powerful destructive agency for disintegration of exposed portions of organic reefs, whereas in the Silurian the destructive capacity of boring organisms on reefs was low (Lowenstam 1950).

Composition of the skeletal sand

The volumetric composition of the skeletal sand gives a rough measure of the production of ostracomass (total skeletal material, Jaanusson 1972) by various groups of organisms. This has also some relationship, in terms of production, to the importance of these groups in the composition of communities. Only a few groups, most notably bryozoans, can be identified in sand-sized particles more exactly than to phylum or class level, and many of the other recognizable genera or species are rare in relation to the total volume of sand grains. Thus the taxonomic resolution in constituent analyses of skeletal sand is mostly very low.

The composition of skeletal sand in the section is shown in Fig. 77 based on modal analysis by point counting in thin sections (for a general discussion of the method, see Jaanusson 1972). All thin sections were cut perpendicular to

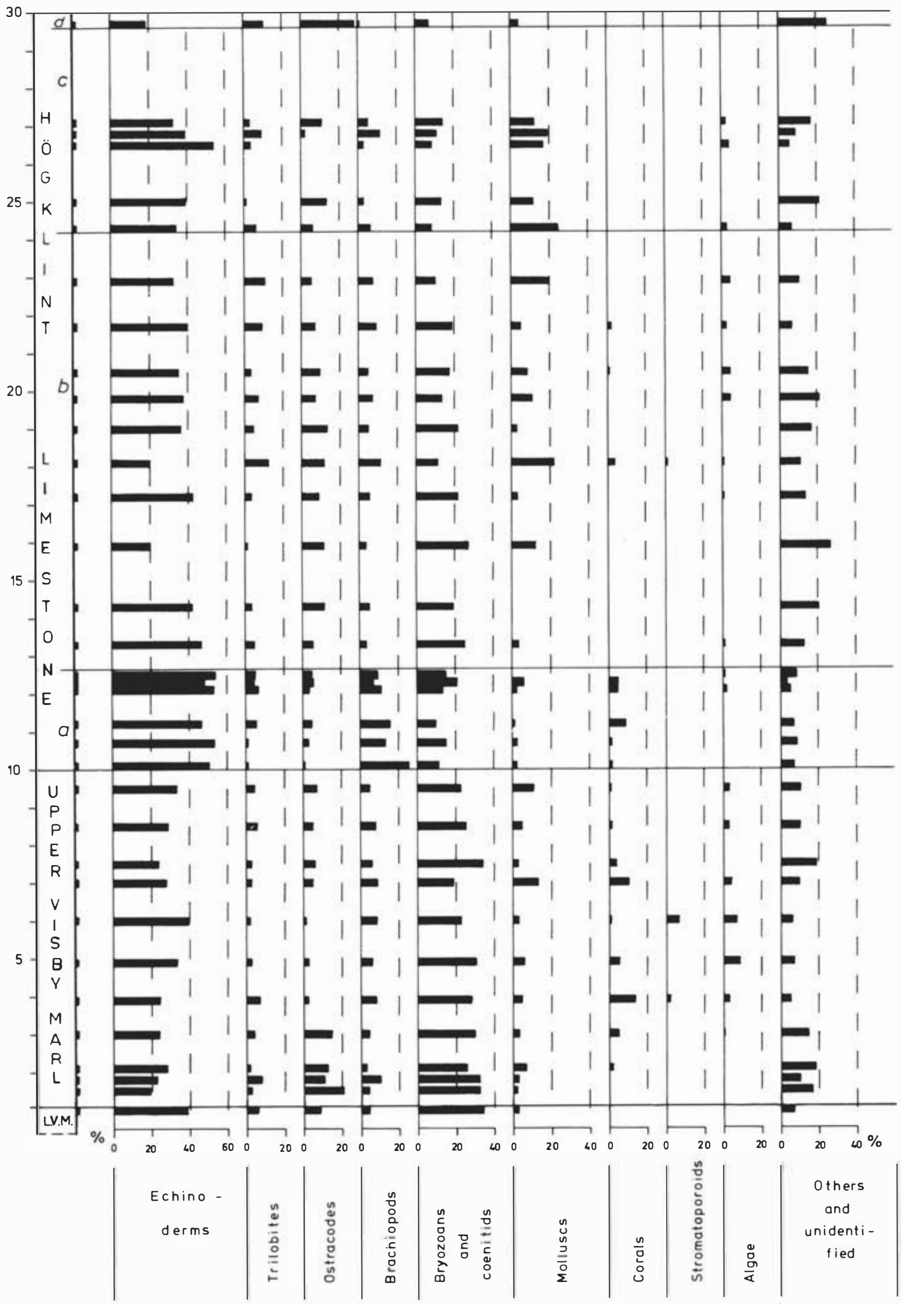


Fig. 77. Composition of skeletal sand in selected limestone beds. For full explanation see text. Compare also Fig. 5 for the content of skeletal sand in the rock.

the bedding. When point counting, the grain-solid definition of skeletal grains was applied. It should be stressed that, because of the limited area of a standard thin section (2×2.5 cm), the modal analysis gives reasonably representative data only for grains in the size range between 0.1 and about 2 mm. If grains larger than about 2 mm are involved, a considerable element of chance is introduced because a single large fragment of an organism that happened to be cut by the thin section may give the group represented by the grain an unduly large proportion of the total volume of skeletal sand. For this reason calciruditic beds were excluded, and the area to be cut for thin section in other beds located so that it would not include large skeletal particles.

Point counting of thin sections was done at a fairly early stage of the Project. At that time the importance of the sponge *Atractosella* for the production of skeletal sand in the Upper Visby Marl was not known, nor did I know how to distinguish the spicules of this animal in thin section. The majority of such grains were included in the category "others and unidentified". Subsequent checks on thin sections from the Upper Visby Marl indicate that *Atractosella* is present at several levels (see Fig. 6A) but its quantitative importance is low.

Bryozoans and coenitids are lumped in the diagram into one category although they were counted separately. The importance by grain-bulk volume of coenitids relative to the bryozoans is shown in Figs. 56 and 57.

As expected, echinoderms form the dominant group in terms of production of skeletal sand. According to sample-frequency data (Fig. 78), echinoids appear to form an important group in the production of ostracomass in the Upper Visby Marl. Cross-sections of echinoid spines occur in almost every thin section of Upper Visby Marl and in some from lower Högklint *b*, but the relative volumetric proportion of echinoids cannot be determined because, in our present state of knowledge, it is difficult to distinguish the microstructure or shape of echinoid plates from those of other echinoderms. As also expected, echinoderms are volumetrically more important in Högklint *a* than in other parts of the section, but compared to Högklint *b* and *c* the difference in the echinoderm content is not larger than some 10 to 15 per cent.

Bryozoans and coenitids form another important constituent in the skeletal sand and they even dominate volumetrically in parts of the Upper Visby Marl. Coenitids mostly form a small fraction of the total quantity of bryozoans and coenitids together, but they form a very important constituent in the calcirudites at the top of Högklint *c* (Figs. 56, 57).

With some volumetrically quite insignificant exceptions the recorded brachiopod fragments belong to the articulates. In terms of identifiable individuals articulate brachiopods form the most important group of macrofossils in the section, but in terms of production of skeletal sand their importance is low. This agrees with the experience from several Ordovician limestones. It is possible that, in terms of the total production of ostracomass, articulate brachiopods are somewhat underrepresented in the skeletal sand. Because of the tough finely fibrous construction of the shell, articulate brachiopods do not appear to have become easily crushed into sand-sized grains. It is also significant that in Högklint *a,* where – with the exception of the top of Högklint *c* (28.8–29.6 m) – the average grain size is the greatest, the importance of brachiopods in the skeletal sand is greater than in other parts of the section.

Fragments of molluscan shells are, on average, more common in uppermost Högklint *b* and in Högklint *c* than lower down in the section. Some of the difference may be the effect of differential solution, because in the upper Högklint Limestone aragonite became dissolved after lithification of the sediment had begun, whereas in preponderantly argillaceous portions of the section some of the aragonite was demonstrably dissolved when the sediment was still soft. On the other hand, the association of a relatively high proportion of molluscan fragments with the bahamitic sediment type may turn out to have some environmental significance because the increased content of molluscan fragments also increases the original content of aragonite in skeletal sand, and this might be temperature controlled (Jaanusson 1972:232–233). In this respect further studies are needed.

Data on the composition of skeletal sand are somewhat blurred because of a variable, and in some beds high, content of unidentified skeletal grains. The importance of "other groups" in this category is low (*Atractosella* in the Upper Visby Marl, and a single tentaculitid or scolecodont in some thin sections). The high content of unidentified grains depends mainly on two factors: (1) The relatively high quantity of very small grains (close to 0.1 mm) with unclear optical properties in calcilutitic beds, and (2) recrystallisation phenomena in sparitic calcarenites, particularly when their average grain size is comparatively small. The unidentified grains probably include proportionally less echinoderms than other groups because optical characteristics of an echinoderm particle tend to be relatively well defined even in grains close to the lower limit of the sand fraction.

The question remains as to how representative are data on the composition of skeletal sand in relation to that of the ostracomass in general. There is no information on the importance of various groups in the composition of carbonate mud, and groups whose skeletons disintegrated more readily into clay-sized particles than those of other groups are probably under-represented in the skeletal sand, particularly in the calcilutitic portions of the sections. Differential breakage may also result in differences in the composition of the skeletal sand relative to the total production of ostracomass. That articulate brachiopods may be somewhat under-represented in the skeletal sand has been mentioned above. The same may be the case also with many corals, particularly with the relatively massive Rugosa. Mori (1970) has attempted to estimate the importance of various large macrofossils by determining their grain-bulk volume by point counting in the field in a number of Gotland localities. He found that in the Upper Visby Marl tabulate corals form, on average, 1.5 per cent of the rock volume, stromatoporoids 1.1 per cent, and solitary rugose corals 0.5 per cent. This shows that the skeletal material incorporated in large fossils may attain significant proportions of the total ostracomass. For this reason, it is useful to complement the thin section analyses with modal analyses on large surfaces.

Average Macro-organism Assemblage Nuclei (AMAN) in the Vattenfallet succession

The Vattenfallet material was not collected originally for sample-frequency studies of the fauna and the poor control of sample size together with insufficient integration of different collecting methods may affect the results. The composition of an AMAN assemblage obtained here may not therefore be always correct for species with low frequency numbers. Only those beds were included in sample-frequency analysis from which all important groups of macro-organisms with a carbonate skeleton had been sampled. Beds from which, for example, sampling for bryozoans is demonstrably inadequate have been excluded. Only three intervals of the section are considered to have yielded meaningful data, viz. Upper Visby Marl, Högklint *b* between 16.9 and 20.5 m, and Högklint *c* between 24.2 and 28.8 m. In each interval the sample-frequency data have been based on at least ten samples. The analysis is confined to macro-organisms, that is, to species of animals and plants that attained a minimum size of 0.5 cm as complete organisms.

The soft- and hard-bottom epifaunas are assessed separately, although in the organisation of the Silurian benthic fauna this imposes some problems. It is not always clear whether a stromatoporoid or a coral was still attached and formed a constituent of the hard-bottom fauna, or had attained a recumbent mode of life and was thus a member of the soft-bottom fauna. For this reason ambitopic corals and stromatoporoids are listed separately. The correct biotic reference of some forms, such as the sponge *Atractosella,* is still uncertain because of insufficient knowledge of their autecology. Vagile benthos are included in the soft-bottom fauna because this probably formed their main substrate. For each species the frequency number is given (percentage of samples in which the species is present). The minimum frequency number for inclusion in AMAN is tentatively put at more than 50. Those commonly occurring species which have too low frequency numbers to be included in AMAN, but are confined to or have their maximum frequency in the interval under consideration, are termed accessory species.

Based on the sample-frequency analysis the following AMAN assemblages with their accessory species can be distinguished in the section.

Upper Visby Marl

Soft-bottom epifauna, AMAN

Aptilechinus sp. (frequency number 100), *Atractosella* n.sp. (100), *Encrinurus laevis* (64), *Neobothriocidaris* sp. (64). Accessory species: *Calymene frontosa, Seretites? exilis* (possibly semi-infaunal, see Larsson, this volume).

Ambitopic species, AMAN

Heliolites decipiens (82), *Clathrodictyon simplex* (64), *Catenipora quadrata* (55). Accessory species: *Stromatopora impexa, Densastroma pexisum, Angopora hisingeri, Pachypora lamellicornis, Phaulactis cyathophylloides, Kyphophyllum lindstroemi.*

Hard-bottom epifauna, AMAN

Dicoelosia verneuiliana (100), *Helopora lindstroemi* (100), *Nematopora visbyensis* (100), *Phaenopora lindstroemi* (91), *Atrypa* sp. (82), *Visbyella visbyensis* (73), *Fistulipora pusilla* (73), *Ceramoporella lindstroemi* (64), *Saffordotaxis gotlandicus* (55). Accessory species: *Asperopora asperum, Allonema* cf. *botelloides.*

Högklint b, *16.9–20.5 m*

Soft-bottom epifauna, AMAN

Acernaspis sp. *a* (80), *Eoplectodonta duvalii* (70), *Encrinurus punctatus* (70), *Coolinia pecten* (60), *Strophochonetes piptis* (60). Accessory species: *Lepidocoleus* cf. *britannicus* (50). Machaeridians are fairly common (for example, the marl sample at 17.0 m has yielded 88 plates of *T.* cf. *wrightiana;* S. Bengtson, personal communication) and it is probable that, if the sampling had been more consistent, *L.* cf. *britannicus* or *T.* cf. *wrightiana* would have been included in the AMAN of this interval.

Soft-bottom endofauna, accessory species

Grammysia cingulata, Pteronitella? sp. *a* (both species are semi-infaunal).

Ambitopic species, accessory

Phaulactis sp. a.

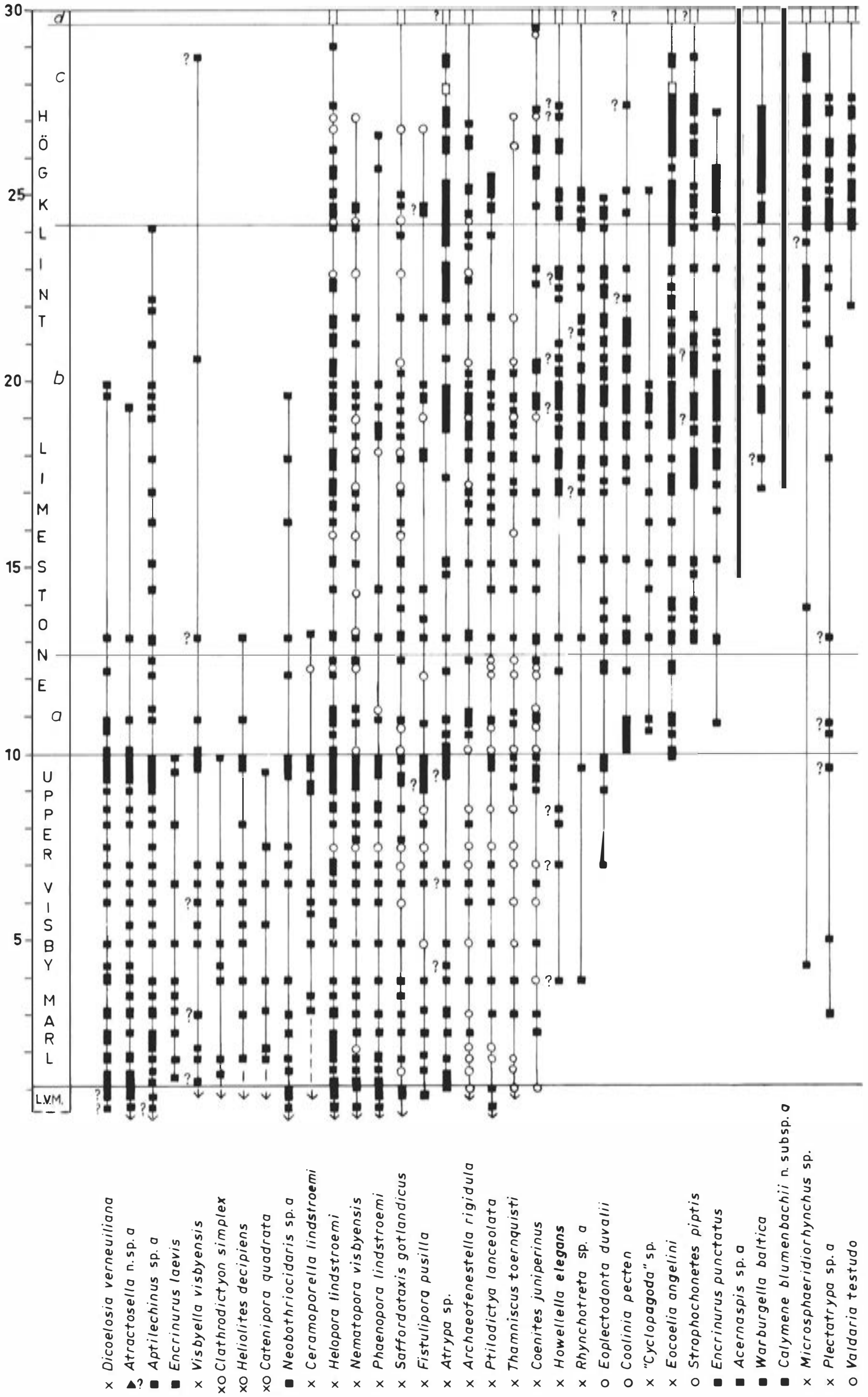
Hard-bottom epifauna, AMAN

Eocoelia angelini (100), *Howellella elegans* (80), *Helopora lindstroemi* (80), *Thamniscus toernquisti* (80), *Rhynchotreta* sp. *a* (70), *Nematopora visbyensis* (70), *Saffordotaxis gotlandicus* (70), *Ptilodictya lanceolata* (70), "*Cyclopagoda*" sp. (60; may include several species). Accessory species: *Estonirhynchia*? sp. *a.*

Högklint c, *24.2–28.8 m*

Soft-bottom epifauna, AMAN

Calymene blumenbachii n. subsp. *a* (80), *Warburgella baltica* (70), *Strophochonetes piptis* (60), *Valdaria testudo* (60). Accessory species: *Oriostoma globosum, Herrmannina phaseolus catarractensis, Proetus (Lacunoporaspis)* n.sp. *a.*


30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
× Dicoelosia verneuiliana
▲? Atractosella n. sp. a
■ Aptilechinus sp. a
■ Encrinurus laevis
× Visbyella visbyensis
×○ Clathrodictyon simplex
×○ Heliolites decipiens
×○ Catenipora quadrata
■ Neobothriocidaris sp. a
× Ceramoporella lindstroemi
× Helopora lindstroemi
× Nematopora visbyensis
× Phaenopora lindstroemi
× Saffordotaxis gotlandicus
× Fistulipora pusilla
× Atrypa sp.
× Archaeofenestella rigidula
× Ptilodictya lanceolata
× Thamniscus toernquisti
× Coenites juniperinus
× Howellella elegans
× Rhynchotreta sp. a
○ Eoplectodonta duvalii
○ Coolinia pecten
× "Cyclopagoda" sp.
× Eocoelia angelini
○ Strophochonetes piptis
■ Encrinurus punctatus
■ Acernaspis sp. a
■ Warburgella baltica
■ Calymene blumenbachii n. subsp. a
× Microsphaeridiorhynchus sp.
× Plectatrypa sp. a
○ Valdaria testudo

Ambitopic species, accessory

Vikingia tenuis (in part probably transported).

Hard-bottom epifauna, AMAN

Eocoelia angelini (90), *Helopora lindstroemi* (80), *Microsphaeridiorhynchus* sp. (70), *Atrypa* sp. (70), *Plectatrypa* sp. *a* (60), *Coenites juniperinus* (60) Accessory species: *Ptilodictya flabellatiformis*.

The above AMAN assemblages are incomplete in several respects. (1) The available data on polychaetes cannot be integrated with those of groups with a carbonate skeleton. However, the quantitative data indicate that all assemblages should include at least two jawed polychaete species, *Eunicites serrula* and *"Lumbriconereites" "obliquus"*. (2) Crinoid columnals are common in most samples and their morphology indicates a considerable taxonomic diversity. If crinoid columnals had been systematically sampled and differentiated taxonomically as far as possible, some probable additional high frequency species would have been added to the AMAN in all intervals analysed. (3) In parts of the section "chitinous" hydroids occur in almost every sample analysed for chitinozoans (Fig. 66). It is probable that when the taxonomy of this group has been worked out, at least one species will show a high sample-frequency number, at least in the Upper Visby Marl.

The distribution of species occurring in any of the three AMAN-assemblages is shown in a separate log (Fig. 78). Several species are members of several consecutive AMAN assemblages and thus their general abundance throughout the Upper Visby Marl and Högklint Limestone has a broad biotic implication. The same is true with respect to several other species, the frequency of which is relatively high throughout most of the section but not always sufficiently high to be included in AMAN.

And finally the AMAN for each analysed interval includes species which have their maximum frequency in this interval. These species, together with accessory species from the same interval, form the distinctive macrofaunal constituents of the interval. These still include members of several communities, at least one for hard-bottom and one for soft-bottom.

The frequencies obtained through sample-frequency analysis agree remarkably well with individual-based relative frequencies (for articulate brachiopods see Fig. 61) and relative volumetric data (for bryozoans see Fig. 56), which strongly supports the assumption that sample-frequency data provide a satisfactory approximation to average abundance of various species.

Fig. 78. Distribution pattern of macro-organism species included in the Average Macro-organism Assemblage Nuclei (AMAN) of analysed intervals. Crosses refer to hard-bottom epifauna, black triangles and circles to rhizosessile and recumbent soft-bottom epifauna, respectively, and black quadrangles to vagile organisms. Circles together with crosses designate ambitopic species of corals and stromatoporoids. Only those data are included for which the precision of the level is within 20 cm.

The composition of the AMAN assemblages agrees far more closely with that of the skeletal sand in the same beds than do the individual-based quantitative data. This is a clear indication that these assemblages are far closer to the original composition of the communities than the assemblages based mainly on data on recognisable individuals. On average, the species distinguished as AMAN formed important constituents, in terms of production, in the composition of the benthic faunal communities, though not necessarily always. At times one or several other species may have been more important either numerically or by volume. It is even possible that, through representing a kind of average over a period, the composition of AMAN does not reflect the actual quantitative relations within any standing crop that existed during that period. The quantitative composition of skeletal species of a standing crop tends ot be poorly reflected in the composition of death assemblages (Johnson 1965).

In the Upper Visby Marl the AMAN of the soft-bottom epifauna does not contain any recumbent articulate brachiopods. Hurst's (1975b) individual-based quantitative data from a bed of the Upper Visby Marl (Buske 1) shows a strong dominance of *Eoplectodonta duvalii,* but in the Upper Visby Marl the distribution of this species is demonstrably very patchy, except possibly in the uppermost beds. In the samples from Vattenfallet the species has not been recorded at all below 7 m, but it does not appear to be rare in the uppermost metre of the Upper Visby Marl. Sowerbyellids are also known elsewhere to have a patchy distribution. This also shows that quantitative data from a single bed, probably selected because of its relative abundance of macrofossils, may not be at all characteristic for a division as a whole (see also Bassett, this volume).

The sponge *Atractosella* is tentatively regarded here as rhizosessile and thus probably a member of the soft-bottom epifauna. That it forms one of the dominant components of AMAN in the Upper Visby Marl was unexpected. Of particular interest is the similarly unexpected strong representation of echinoids in the AMAN of the vagile epifauna of the Upper Visby Marl. A soft-bottom epifaunal community in which dominant constituents include echinoids, sponges and probably also polychaetes has a fairly modern appearance.

Some of the recorded specimens of the ambitopic species *Clathrodictyon simplex, Heliolites decipiens* and *Catenipora quadrata* were encrusting and belonged to hard-bottom fauna, other specimens were probably recumbent. The skeletons of these species as well as other corals and stromatoporoids formed patches of hard-bottom substrate for attached hard-bottom organisms.

The hard-bottom epifauna of the Upper Visby Marl was diverse. The AMAN includes encrusting bryozoans *(Fistulipora pusilla, Ceramoporella lindstroemi),* forms with encrusting holdfasts (the rest of the bryozoans), and pedunculate articulate brachiopods.

Data from Högklint *a* and the lower, calcilutitic part of Högklint *b* are insufficient for sample-frequency studies. Moreover, much of the material in Högklint *a* was transported and sorted, and the AMAN data may not be meaningful.

In upper Högklint *b* the importance of echinoids and especially *Atractosella* declines and recumbent brachiopods form an important constituent of the soft-bottom epifauna. Trilobites form a far more important component of the soft-bottom AMAN than in the Upper Visby Marl. The absolute frequency of polychaete jaw elements is higher than in the Upper Visby Marl (Fig. 27). The rarity of colonial corals and stromatoporoids suggests that the hard-bottom epifauna attached mostly to pebble- or gravel-sized skeletal grains. In the AMAN for the hard-bottom epifauna *Eocoelia angelini* forms a dominant component, associated with some other pedunculate brachiopods and several bryozoans which all attached with a holdfast. The mode of attachment of the crinoid *"Cyclopagoda"* is unknown.

In general the soft-bottom AMAN of Högklint *c* resembles that of the upper part of Högklint *b,* but with notable shifts at the species level. In particular, *Valdaria testudo* enters the composition of AMAN and *Calymene blumenbachii* n. subsp. *a* (frequency number 80) is somewhat more important in the vagile benthos than *Encrinurus punctatus* (50) and *Acernaspis* sp. *a* (40). In the AMAN of the hard-bottom epifauna *Eocoelia angelini* is still the dominant pendunculate brachiopod, but *Microsphaeridiorhynchus* sp. also has a high frequency number. Bryozoans are represented only by *Helopora lindstroemi* but this may be due to inadequate sampling. In some beds *Coenites juniperinus* forms the major source of skeletal material, but much of it may be transported.

The presence of leperditiids as accessory elements in Högklint *c*, associated with numerous calcareous algae, indicates some resemblance to the shallow-water macro-organism assemblages in the Ordovician Black River Series and Devonian Manlius Limestone (Walker & Laporte 1970). However, on Gotland leperditiids have an intricate distribution pattern. No leperditiids have been recorded from the Upper Visby Marl, but in the Lower Visby Marl, which most evidence suggests was deposited in low energy, relatively deep water environment, *Herrmannina hisingeri* is a common species. Thus on Gotland this group is represented in shallow water environments but is by no means restricted to them.

Throughout the section there are thus several distinct shifts in the composition of AMAN as a response to changing environments. The intervals which were not analysed because of inadequate sampling (Högklint *a*, 12.65–16.9 m, and 20.5–24.2 m) do not appear to include additional distinctive high-frequency species. In most respects the fauna in the 20.5–24.2 m interval is transitional between the assemblages in adjacent beds. The shifts in the composition of AMAN assemblages portray the changes in the dominant elements of the fossilised fauna and this, in turn, reflects some of the main changes in the composition of the communities. To carry the analysis further to the level of separate communities comparable to those in modern benthic fauna is difficult and requires comparative studies not only of additional sections elsewhere but also of the relationships between modern death assemblages and the standing crops from which they are derived. The need for more comparative data of the latter type should be particularly stressed.

The difficulties of recognising original trophic relationships in assemblages of fossils has been discussed recently by Stanton (1976), who found that the trophic composition of shell-bearing organisms in a modern community differs significantly from that of the total community from which they are derived. Compared with an assemblage of fossils the differences would be still greater because such an assemblage reflects the total production of preserved individuals during a succession of standing crops. For this reason no serious attempt is made here to reconstruct trophic relationships within various assemblages.

The AMAN assemblages comprise species which have a high average density in a selected interval, but in each interval the density and relative frequency of various species can fluctuate within wide limits. Such fluctuations occur among articulate brachiopods in particular (Fig. 61; Bassett, this volume). In several beds a single species occurs in very high densities without clear indications of sorting, mostly crowding the rock. An illustrative example is the superdominance of *Eoplectodonta duvalii* at 12.35–12.40 m (Fig. 61; Bassett, this volume). There are two explanations which may be applicable to mass-occurrence of skeletons of a single species. (1) It may be due to resurgent populations. Such populations develop when a combination of a number of favourable factors occurs by chance: a large spawning population, suitable conditions during the period of pelagic larval life, favourable currents and settling conditions for the larvae, and adequate opportunities for continued growth (Coe 1953). The net result of this combination of favourable conditions is an enormous increase in population size. (2) Many modern pedunculate brachiopods tend to have a patchy distribution, each patch being crowded by individuals of a single species or two species. In either case the development of the mass-occurrence is largely due to chance and it cannot be treated in terms of a normal community structure.

No quantitative faunal data based on the sample-frequency approach are available for comparison with those from Vattenfallet. However, there is some information on individual-based frequencies of macrofossils in contemporaneous beds which may be of some interest.

Marl pockets in Högklint reefs are commonly rich in fossils, not least in articulate brachiopods and bryozoans. In 1968 I sampled five different marl pockets for macrofossils in the lower and middle part of the Högklint reefs of the Visby area, roughly corresponding to Högklint *b* in the bedded limestone sequence. From these samples semi-quantitative individual-based data are available, but as the samples were not collected and examined with the purpose of quantitative studies, only some general remarks are possible. *Dicoelosia verneuiliana* is abundant and dominates in four samples. Another common species is *Stegerhynchus* sp. *a,* which even appears to dominate in one sample. *Eocoelia angelini* is rare and trilobites appear to be much less frequent than in the corresponding beds at Vattenfallet. No specimens of *Eoplectodonta* or *Strophochonetes* were recorded, and other recumbent brachiopods, such as *Coolinia pecten,* are exceedingly rare. Soft-bottom epifauna is thus very poorly represented in such pockets of the reefs and the macrofauna consists almost exclusively of representatives of hard-bottom epifauna. With regard to dominant brachiopod species, the pockets in the Högklint reefs far more closely resemble the middle part of the Upper Visby Marl at Vattenfallet than the contemporaneous bedded Högklint limestone. Among bryozoans, fenestellids are conspicuously more common in the Högklint reef pockets than at Vattenfallet, especially *Isotrypa gotlandica* (K. Brood, personal communication). The marly pockets in Högklint reefs are also characterized by a different assemblage of palaeocope ostracodes (*Craspedobolbina ornulata* fauna, Martinsson 1967) than in the contemporaneous bedded limestones (*Apatobolbina gutnica* assemblage, see Fig. 44).

Contributors responsible for both the stromatoporoids (Nestor, this volume) and colonial rugose corals (Hanken in Neuman & Hanken, this volume) have observed that in the Högklint Limestone at Vattenfallet many specimens are worn and thus probably transported. The probability of transportation of skeletal material from reefs is also suggested for some Vattenfallet bryozoans (Brood, this volume) and crinoids (Franzén, this volume). Thus the skeletal material at Vattenfallet certainly includes a transported and probably reef-derived component. However, in view of the widely different brachiopod and ostracode assemblages in reef pockets and the bedded limestone at Vattenfallet, the reef-derived material does not appear to have significantly changed the general quantitative composition of the fauna.

Analysis of faunal dynamics

The fauna from Vattenfallet by no means represents the total fauna of the Upper Visby and Högklint Beds known from northwestern Gotland. Some groups, such as cephalopods, crinoids and gastropods are particularly underrepresented in terms of species frequency, and in almost every other group species are known that are not uncommon in these beds elsewhere on Gotland but have not been found at Vattenfallet. Thus the material from Vattenfallet forms a sample from the fauna of the Upper Visby and the inter-reef Högklint

Beds, although the size of the sample is comprehensive. Because of the relatively low sample density in the Upper Visby Beds, their fauna at Vattenfallet represents a smaller sample of the total Upper Visby fauna than the material from the Högklint Beds relative to the total fauna of the inter-reef Högklint Limestone.

The flora of the beds under consideration is poorly studied outside Vattenfallet. The species frequency of the calcareous algae is low and the majority of acritarchs range from the underlying to the overlying beds. For this reason the following discussion will be restricted almost entirely to the fauna.

The Upper Visby Marl and Högklint Limestone are rich in fossils, giving an impression that life on and in the sea-floor was luxurious during their deposition. However, this impression may easily be misleading. The average net rate of deposition (Jaanusson 1973:25) for the Wenlockian of Gotland can be calculated to have been in the order of 5 to 10 mm per 1000 years, and with such a slow accumulation of sediments a succession of even very poor standing crops could have produced enough shells to form a sediment rich in fossils. On the other hand, the rate of sedimentation has certainly fluctuated within wide limits and there is no reliable measure of it.

It is difficult to analyse faunal dynamics based on data from a single section. Without the possibility of comparing contemporaneous faunal successions in different parts of a depositional basin, it is not always clear which aspects of faunal changes were controlled by local environmental factors (faunal shifts, Jaanusson 1976), and which were affected by extra-regional factors (immigrations, Jaanusson 1976). Furthermore, without a three-dimensional framework the environmental background as reconstructed from a single section may be somewhat out of focus. When other Balto-Scandian lower Wenlockian carbonate sections have been studied with the same approach, additional conclusions on the faunal succession at Vattenfallet should be possible. The presentation of material in this publication was made with this in mind.

Attempts have been made to assess the great quantity of data presented in the faunal logs statistically. However, the poor control of sample size, selective collecting, varying sample density, and the difficulty in integrating data based on different sampling methods made the results dubious. For an advanced statistical treatment such data must be assembled from the beginning in a strictly systematic way and with due consideration to integration of different sampling methods.

The samples obtained at Vattenfallet from the uppermost beds of the Lower Visby Marl are small and have yielded only a limited number of species. An analysis of the faunal change at the boundary between the Lower and Upper Visby Marl is also hampered by uncertainties as to the range across the boundary of a number of species. The uncertainties depend firstly on the doubtful reliability of reports of several species from the Lower Visby Marl, particularly if they are based on old collections. For example, the only record of *Plectatrypa lamellosa* from the Lower Visby Marl is based on a single specimen from the old locality at Visby Norderstrand (Bassett & Cocks 1974:30) which is now built over, and should be considered as doubtful until additional specimens have been found. Secondly, because the boundary cannot be recognised lithologically the correct stratigraphical reference of specimens found in the boundary region is frequently uncertain.

At Vattenfallet the boundary appears to be surprisingly well defined in ostracode, brachiopod, tentaculitid, and rugose coral faunas. Palaeocope ostracodes, in particular, show a sharp change, both qualitatively (Fig. 41) as well as quantitatively (Fig. 44). The bryozoan fauna, on the other hand, does not appear to show any distinct change at this level (Fig. 54), and a similar condition was claimed by Mori (1969) for stromatoporoids. Many species, belonging to almost all groups, cross the boundary. Because of insufficient taxonomic knowledge of many groups in the Lower Visby fauna, many more species probably continue downwards into the Lower Visby Marl than indicated in the faunal logs.

The faunal change at the Lower/Upper Visby boundary as it appears in the Vattenfallet faunal logs is characterized by the extinction of a number of high-density species rather than the appearance of new species. Very few of the Upper Visby species which are not known in the Lower Visby Marl have high densities. It is notable that, with a single exception or possibly two, the species forming the Upper Visby AMAN assemblage continue upwards from the Lower Visby Marl (Fig. 78). The exceptions are *Encrinurus laevis* (probably not conspecific with the common *Encrinurus* species from the Lower Visby Marl; Christian Magnus, personal communication) and possibly *Dicoelosia verneuiliana* (identification of the Lower Visby *Dicoelosia* is uncertain; Bassett, this volume). A causal interpretation of the faunal change is difficult at present. The change appears to have taken place approximately contemporaneously over wide areas of northern Europe and the British Isles, and possibly also elsewhere. The change in the physical environment that caused the faunal change, not reflected in lithology at Vattenfallet, was probably of inter-regional importance. Change in sea-water temperature is one of the factors that may cause such inter-regional faunal changes.

Most faunal logs from Vattenfallet show a step-wise temporal apperance of species in the Upper Visby Marl. Most of this pattern is due to what here is termed the *stochastic staircase effect,* as analysed by Jaanusson (1976) on simulated models. Almost all species which appear in the Upper Visby Marl occur in that division with relatively low frequencies, and the effect is caused by this factor in combination with low sample density and a relatively small sample size in many beds. The effect is exaggerated by the low overall densities of macrofossils in the lowermost, calcilutitic portion of the Upper Visby

Marl. That the level in the logs at which a species appears in this interval, possibly with the exclusion of the uppermost metre, is largely controlled by chance can be illustrated by comparing the step-wise appearance in the Upper Visby Marl of species which are known to continue from the Lower Visby Marl; the successive appearance of these species too is due to a stochastic staircase effect.

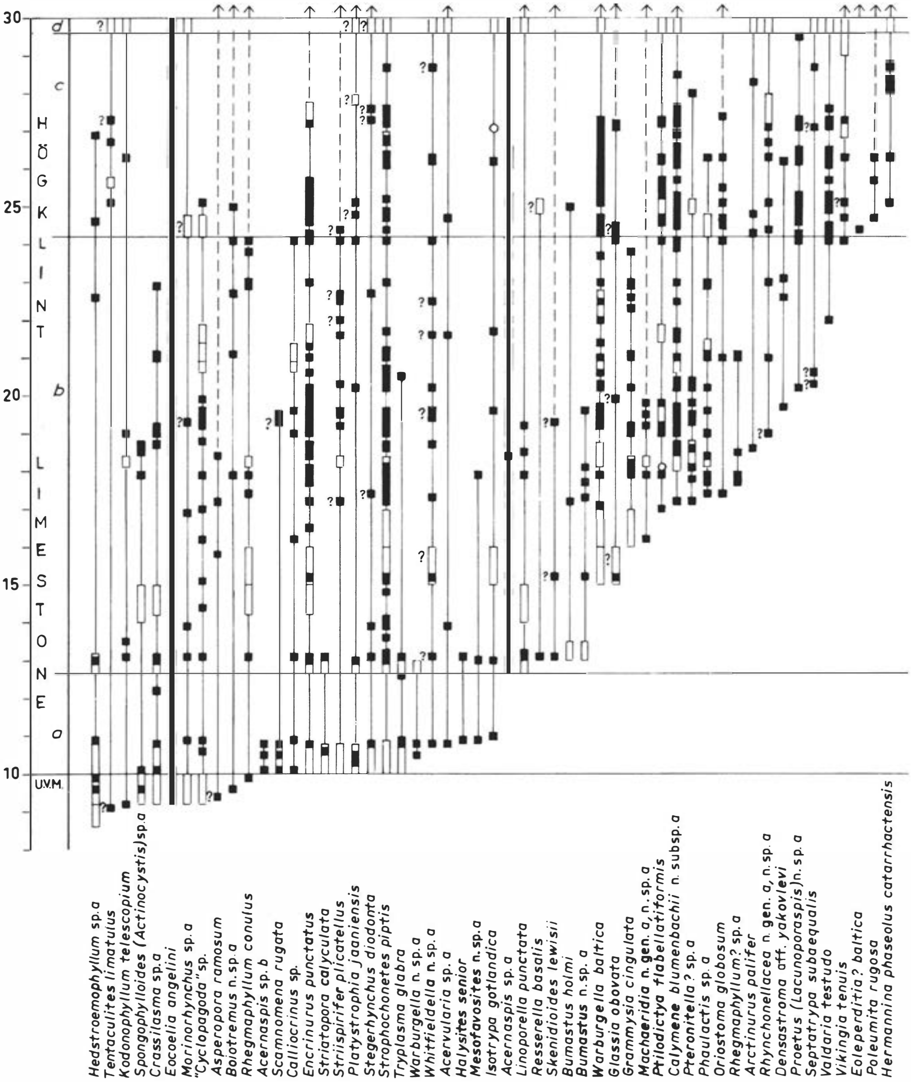


Fig. 79. Species appearing in the uppermost Upper Visby Marl or in the Högklint Limestone. For full explanation see text.

The available material does not appear to indicate any clear difference in the fauna between the lower, calcilutitic portion and the remaining parts of the Upper Visby Marl, which consist of alternating calcilutites and calcarenites. The difference may be obscured by the "noise" of the stochastic staircase effect in the faunal logs, and further studies may show that not all species which appear in the Upper Visby Marl enter at the base of the division. It is therefore difficult to prove whether or not the probable shallowing of the water towards the top of the Upper Visby Marl is reflected in the fauna. In any case, the faunal change, if it exists, is not conspicuous.

The appearance of macro-organism species in the Högklint Limestone at Vattenfallet is illustrated in Fig. 79. Species which are very rare (recorded only from one or two levels) are excluded, except for two which are common in the Högklint Beds elsewhere. The pattern of appearance of very rare species is controlled to a very high degree by chance and such species do not contribute essentially to the understanding of faunal dynamics in the sequence. Further excluded species are Cornulitidae gen. *b,* sp. *a, Lepidocoleus* cf. *britannicus,* and *Conularia cancellata,* because elsewhere they occur demonstrably in the Upper Visby Beds (K. Larsson, S. Bengtson and K. Brood, personal communications). *Coolinia pecten* is recorded at Vattenfallet at 6–8 m (Bassett, this volume). Scolecodonts are not considered because their sampling was different from that of the other macro-organisms.

Many species continue from the Upper Visby Marl into the Högklint Limestone. However, there is a notable faunal change at the base of the Högklint Beds, involving the appearance of a number of species, some occurring almost immediately with high densities. The faunal change coincides roughly with the spectacular lithological change at the base of Högklint *a*, but it is initiated in the uppermost beds of the Upper Visby Marl, at a level where no lithological change can be observed. A number of easily recognisable species involved in the faunal change have never been recorded previously from the Upper Visby Beds, despite collecting over many generations. Such species are *Eocoelia angelini, Rhegmaphyllum conulus, Halysites senior, Striatopora calyculata, Platystrophia jaaniensis, Stegerhynchus diodonta, Acernaspis* sp. *a* and *b, Linoporella punctata,* and *Resserella basalis*. Some of these can now be shown to enter the sequence close to the top of the Upper Visby Beds. It is possible that some of the species which appear at Vattenfallet in the boundary beds between the Upper Visby Marl and the Högklint Limestone occur with very low densities lower in the Upper Visby Marl but have not yet been found there. In Liljevall's material the lowermost level recorded for the rugose coral *Spongophylloides (Actinocystis)* sp. *a* is 9.2 m, but after the drafting of all logs had been completed, a specimen was found at 3.0 m (B. Neuman, personal communication; the level is not entered in the logs Figs. 25, 79). However, it is unlikely that the majority of these species range downwards.

Indications of a faunal change at the base of the Högklint Limestone are also shown by ostracodes (Figs. 41, 53) and jawed polychaetes (Fig. 26). Thus the basal Högklint faunal change involves the appearance of numerous species which are not known in the Balto-Scandian region in earlier beds.

The faunal change also involves changes in the relative frequencies of some species which continue from the Upper Visby Marl. For example, *Coolinia pecten*, which is very rare in the Upper Visby Marl at Vattenfallet, becomes a moderate to high density species from Högklint *a* upwards (Fig. 59). *Dicoelosia verneuiliana* is dominant up to the middle of Högklint *a* and is then replaced by other species (Fig. 61). In the reef environment it retains its dominance higher up in the sequence. *Apatobolbina gutnica* increases in frequency in Högklint *a* and is a dominant species in Högklint *b* (Fig. 44).

The close link of a faunal change with a marked change in lithology normally indicates a faunal shift, that is, the drastically changed environmental conditions reflected in lithology caused a shift of the habitat and an invasion of species which inhabited the habitat. Habitats close to those of the Högklint Limestone at Vattenfallet may have existed during the deposition of the Upper Visby Marl in a belt to the north and northwest of the outcrop area, but this part of the sequence is now removed by erosion. The species characteristic of the faunal change at the base of the Högklint Limestone may have lived there or in some other marginal area of the Balto-Scandian region during Upper Visby times. However, it is possible that in addition to a faunal shift immigration is also involved, that is, invasion of taxa which did not previously live in the region. This problem is difficult to analyse before more information is available on ranges of various taxa in different parts of Balto-Scandia. If the faunal change was almost exclusively a faunal shift, then this has important biostratigraphical consequences. Faunal shifts tend to be metachronous and are rarely traceable outside the distribution of the associated habitats. Hence the basal Högklint faunal change may not be recognisable outside the distribution of the particular lithofacies. There is some support to this assumption in the difficulties of recognising the level corresponding to the base of the Högklint in the nearby Estonian sequence.

The change in lithology from Högklint *a* to *b* is fairly drastic although not as sharp as at the base of Högklint *a*. In terms of sediment, well winnowed skeletal sand was replaced by carbonate mud with some intercalations of skeletal sand. In contrast to the lowermost Upper Visby Marl the carbonate mud bottom in lower Högklint *b* was obviously unsuitable for large colonial organisms, such as tabulate corals and stromatoporoids. The tabulate corals that do occur belong to an assemblage (*Favosites jaaniensis* assemblage, Klaamann 1977b), different from that in Högklint *a* and the lowermost calcarenitic intercalations of Högklint *b*, which also occurs in a similar fine-grained rock on Saaremaa. Otherwise the fauna which enters at the base of the

Högklint Limestone continues into the calcilutites of Högklint *b* with no distinct qualitative or quantitative differences. The details are unclear because of the low sample density. The appearance of many species at 13.0–13.1 m is comparable to a "density-dependent immigration" (Jaanusson 1976, Fig. 2B) and is caused by a far larger than average sample size at these levels (Fig. 74). Most of these species are probably also present in Högklint *a*. The small faunal differences, except in tabulate corals, between Högklint *a* and the calcilutites of the lower Högklint *b*, raise the question as to whether the fauna in the coarse and probably unstable skeletal sand of Högklint *a* was specific for that substrate or consists largely of specimens transported and redeposited from other environments.

The step-wise appearance of species in the middle part of Högklint *b* suggests a stochastic staircase effect, accentuated by larger than average sample size at several levels and relatively small sample size combined with low sample density in the lower, calcilutitic Högklint *b*. The entry of some moderate to high density species, such as *Ptilodictya flabellatiformis, Calymene blumenbachii* n. subsp. *a, Pteronitella?* sp. *a,* and *Phaulactis* sp. *a,* coincides roughly with the lithological change from a predominantly calcilutitic rock to pelletal calcarenites in the middle and upper Högklint *b*. This probably indicates a faunal shift in response to the changed environment. However, the change in lithology otherwise appears to be poorly reflected in the fauna, and also with respect to the quantitative composition of articulate brachiopods (Fig. 61) and palaeocope ostracodes (Fig. 44).

The lithological change from Högklint *b* to the pelletal calcisiltites and winnowed calcarenites of Högklint *c* does not appear to be sharp, and also the faunal change in response to changed environment is gradual. This faunal change, associated with decreased water depth, is basically a faunal shift and is reflected in the AMAN assemblage as well as in the quantitative composition of articulate brachiopods (Fig. 61). It is particularly strongly expressed in palaeocope faunas (Figs. 42–43) and is also characterized by the appearance of leperditiids. Again, the assumption that the faunal change is basically a faunal shift demands that a similar environment with a largely similar fauna had existed earlier in some marginal area of the Balto-Scandian basin. This assumption also implies that the faunal change was metachronous and is probably not recognisable outside the limits of the particular environment.

The fossil material collected from the calcirudites of uppermost Högklint *c* (28.8–29.6 m) is limited and does not give much information on the composition of the fauna. The uppermost beds are formed by a gravel which consists almost exclusively of worn fragments of *Coenites juniperinus* (Fig. 56) that appear to have been transported before being accumulated in these beds.

The fauna in Högklint *d*, in the sediment deposited in depressions on an eroded surface, has an unusual composition. Despite the thinness of the unit, it is not faunally homogenous. In a thin bed of soft indistinctly laminated pelletal marl, obviously Bed 2 in Hedström's section (1904) in which the scorpion *Palaeophonus nuncius* was found, the most common macro-organisms are polychaetes, eurypterids, the thin-walled conulariid *Metaconularia aspera,* the crinoid Melocrinitidae n.gen. *a,* n.sp. *a,* the articulate brachiopod *Septatrypa subaequalis,* the inarticulate brachiopod Discinacea n.gen. *a,* n.sp. *a,* and the dendroid graptolite *Thallograptus* sp. *a*. Eurypterid remains are disarticulated and probably represented by exuvia (see discussion in Kjellesvig-Waering, this volume). Several delicate skeletons of other groups are articulated and excellently preserved, such as the celebrated scorpion (Thorell & Lindström 1885, Plate), several crinoids, an ophiurid, an asteroid (Fig. 68A), and the type specimen of *Hercolepas signata* (see Bengtson, this volume). The rock is finely laminated and such lamination is normally preserved in the sediment only when no burrowing endofauna inhabits the substrate. The lack of a burrowing endofauna is normally associated with environmental conditions unfavourable for life, which suggests that the unusual fossil assemblage in this bed may not represent just the remains of an *in situ* community but includes a substantial component that was transported to the locality by water movement. The transported specimens were then embedded into the layer of pelletal silt that lined the depression in the rocky surface, and they were preserved mainly because of the lack of destructive activity by organisms. It should also be remembered that tiny eurypterid fragments are common throughout upper Högklint *b* and Högklint *c* (Fig. 66), but in that high energy depositional environment the fragile skeletons have been broken down into small pieces.

Higher in Högklint *d* a thin limestone bed (possibly Hedström's Bed 3) abounds in *Valdaria testudo,* and in another limestone bed *Septatrypa subaequalis* and Rhynchonellacea n.gen. *a,* n.sp. *a* are subequally dominant (Bassett, this volume). A further limestone bed (possibly Hedström's Bed 5) is crowded with valves of the leperditiacean ostracode *Herrmannina phaseolus catarractensis.* The valves exhibit a considerable size range (Fig. 40) and no clear indications of sorting can be observed. Thus within this thin interval there are several conspicuous changes in dominant species, and there is also crowding of beds by a single species. Some of these features suggest resurgent populations rather than normal communities, and this impression is strengthened by the poorly fossiliferous condition of the intervening shaly beds.

At Vattenfallet the level of graptolite zone boundaries cannot be determined precisely and the approximate levels indicated in Table 1 are tentative. For conodont zones the approximate levels of boundaries are reasonably well defined (Jeppsson, this volume). The upper boundary of the *amorphognathoides* Zone is somewhere within an interval of the Upper Visby Marl (2.0–3 m) where no changes in the benthic fauna can be recognized. The lower boundary of the *sagitta* Zone is within Högklint *c* (26–27.6 m) and again at a level where no clear change in the benthic fauna can be observed. Thus the environmental events that were responsible for changes in the conodont and benthic faunas appear to have been largely different.

REFERENCES

GFF = Geologiska Föreningens i Stockholm Förhandlingar
SGU = Sveriges Geologiska Undersökning

AGER, D.V., 1963: Principles of Palaeoecology. 371 pp. – Mc Graw-Hill Co.

ALLEN, J.A., 1953: Observations on the epifauna of the deep-water muds of the Clyde Sea Area, with special reference to *Chlamys septemradiata* (Müller). – J. Anim. Ecol. 22:240–260.

BASSETT, M.G., & COCKS, L.R.M., 1974: A review of Silurian brachiopods from Gotland. – Fossils and Strata 3: 1–56.

BATHURST, R.G.C., 1966: Boring algae, micritic envelopes and lithification of molluscan biosparites. – Geol. J. 5: 15–32.

– 1967: Depth indicators in sedimentary carbonates. – Mar. Geol. 5:447–471.

BERGSTRÖM, J., 1973a: Organization, life, and systematics of trilobites. – Fossils and Strata 2. 69 pp.

– 1973b: Palaeoecologic aspects of an Ordovician *Tretaspis* fauna. – Acta Geol. Pol. 23.

CALEF, C.E., & HANCOCK, N.J., 1974: Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. – Palaeontology 17:779–810.

CARRIKER, M.R., & SMITH, E.H., 1969: Comparative calciobiocavitology: summary and conclusions. – Am. Zool. 9:1011–1020.

COCKS, L.R.M., 1970: Silurian brachiopods of the superfamily Plectambonitacea. – Bull. Br. Mus. Nat. Hist. (Geol.) 19:141–203.

COE, W.R., 1953: Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. – Ecology 34:225–229.

CRAIG, G.Y., & JONES, N.S., 1966: Marine benthos, substrate and palaeoecology. – Palaeontology 9:30–38.

CRICKMAY, C.H., 1966: The external apical cavity of strophomenacean brachiopods. – Can. J. Earth Sci. 3:499–508.

DELL, R.K., 1951: Some animal communities of sea bottom from Queen Charlotte Sound, New Zealand. – New Zealand J. Sci. Techn. 33B:19–29.

DRISCOLL, G.E., GIBSON, J.W., & MITCHELL, S.W., 1971: Larval selection of substrate by the Bryozoa Discoporella and Cupulandria. – Hydrobiologia 37:347–359.

DUNHAM, R.J., 1962: Classification of carbonate rocks according to depositional texture. In W.E. HAM, (Ed.): Classification of carbonate rocks. – Am. Assoc. Pet. Geol. Mem. 1:108–121.

ELTON, C., 1927: Animal ecology. – Macmillan Co., New York.

ERIKSSON, C.-O., & LAUFELD, S., 1978: Philip structures in the submarine Silurian of northwest Gotland. – SGU C 736. 30 pp.

FISHER, R.A., CORBET, A.S., & WILLIAMS, C.B., 1943: The relation between the number of species and the number of individuals in a random sample of an animal population. – J. Anim. Ecol. 12:42–58.

FÜRSICH, F.T., & WENDT, J., 1977: Biostratinomy and palaeoecology of the Cassian Formation (Triassic) of the southern Alps. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 22:257–323.

GISLÉN, T., 1930: Epibioses of the Gullmar Fjord, I–II. – Kristinebergs Zool. Stat. 1877–1927. 123 and 360 pp.

GOREAU, T.F., & YONGE, C.M., 1968: Coral community on muddy sand. – Nature 217:421–423.

HADDING, A., 1941: The pre-Quaternary sedimentary rocks of Sweden, 6. Reef limestones. – Lunds Univ. Årsskr., N.F., Avd. 2, (10):1–137.

– 1950: Silurian reefs of Gotland. – J. Geol. 58:402–409.

– 1956: The lithological character of marine shallow water limestones. – K. Fysiogr. Sällsk. Lund Förh. 26:1–18.

HECKER, R.F., 1928: Paleobiologicheskie nablyudeniya nad nizhnesiluriyskimi bespozvonochnymi, 1. German summary: Paläobiologische Betrachtungen an untersilurischen Invertebraten, 1. – Ezhegodnik Russkogo Paleontol. Obshchestva 7:47–86.

HEDE, J.E., 1921: Gottlands silurstratigrafi. – SGU C 305. 100 pp.

– 1933: Berggrunden (Silursystemet). In MUNTHE, H., HEDE, J.E., & LUNDQVIST, G., 1933: Beskrivning till kartbladet Kappelshamn. – SGU Aa 171. 129 pp.

– 1940: Berggrunden. In LUNDQVIST, G., HEDE, J.E., & SUNDIUS, N., 1940: Beskrivning till kartbladen Visby och Lummelunda. – SGU Aa 183. 167 pp.

HEDSTRÖM, H., 1904: Detaljprofil från skorpionfyndorten – Pterygotus-lagret – i siluren strax S om Visby. – GFF 26:93–96.

– 1910: The stratigraphy of the Silurian strata of the Visby district. – GFF 32:1455–1484.

– 1912: Om grundvattensförhållandena i trakten af Visby. – SGU C 239. 70 pp.

– 1929: Nekrolog över Georg Liljevall. – GFF 51:116–120.

HUBBARD, J.A.E.B., 1972: *Diaseris distorta,* an "acrobatic" coral. – Nature 236:457–459.

HURST, J.M., 1975a: Wenlock carbonate, level-bottom brachiopod-dominated communities from Wales and the Welsh Borderland. – Palaeogeogr. Palaeoclimatol. Palaeoecol. 717:227–255.

– 1975b: Some observations on brachiopods and the level-bottom community ecology of Gotland. – GFF 97:250–264.

IMBRIE, J., 1955: Quantitative lithofacies and biofacies study of Florena Shale (Permian) of Kansas. – Bull. Am. Assoc. Pet. Geol. 39:649–670.

INGHAM, J.K., 1968: British and Swedish Ordovician species of *Cybeloides* (Trilobita). – Scottish J. Geol. 4:300–316.

JAANUSSON, V., 1952: Untersuchungen über die Korngrösse der ordovizischen Kalksteine. – GFF 74:121–130.

– 1971: Evolution of the brachiopod hinge. – Smithson. Contr. Paleobiol. 3:33–46.

– 1972: Constituent analysis of an Ordovician limestone from Sweden. – Lethaia 5:217–237.

– 1973: Aspects of carbonate sedimentation in the Ordovician of Baltoscandia. – Lethaia 6:11–34.

– 1976: Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia. In BASSETT, M.G., (Ed.): The Ordovician System: proceedings of a Palaeontol. Assoc. Symp., pp. 301–326.

JOHNSON, R.G., 1964: The community approach to paleoecology. In J. IMBRIE & N.D. NEWELL, (Eds.): Approaches to paleoecology, pp. 107–134.

– 1965: Pelecypod death assemblages in Tomales Bay, California. – J. Paleontol. 39:80–85.

JUX, U., 1957: Die Riffe Gotlands und ihre angrenzenden Sedimentationsräume. – Stockholm Contr. Geol. 1:41–90.

KAESLER, R.L., & PETERSON, R.M., 1977: Environmental control of patterns of hierarchical diversity among Late Paleozoic ostracoda. – Geol. Soc. Am. Abstr. Programs 9 (7): 1042.

KALJO, D., (Ed.) 1970: Silur Estonii. English summary: The Silurian of Estonia. – Eesti NSV Teaduste Akad. Geol. Inst. 343 pp. Tallinn.

– & JÜRGENSON, ERIKA, 1977: Fatsial'naya zonal'nost' silura Pribaltiki. English summary: Sedimentary facies of the East Baltic Silurian. In KALJO, D., (Ed.): Facies and fauna of the Baltic Silurian. – Acad. Sci. Estonian SSR Inst. Geol. 122–148. Tallinn.

KLAAMANN, E., 1977a: K korrelyatsii razrezov Visbyuskogo vodopada (o. Gotland) i glinta severnovo Saaremaa (Estoniya) po korallam. German summary: Zur Korrelation des Wasserfallprofils von Visby (Gotland) und des Glints vom nördlichen Saaremaa (Estland) nach Korallen. – Eesti NSV Teaduste Akad. Toimetised, Keemia Geol. 26:33–37. Tallinn.

– 1977b: Uber die silurischen Tabulatensukzessionen Estlands und der Insel Gotland. – Ibid. 26:203–210. Tallinn.

LAUFELD, S., 1974a: Silurian Chitinozoa from Gotland. – Fossils and Strata 5. 130 pp.

– 1974b: Reference localities for palaeontology and geology in the Silurian of Gotland. – SGU C 705. 172 pp.

– & JEPPSSON, L., 1976: Silicification and bentonites in the Silurian of Gotland. – GFF 98:31–44.

LAWRENCE, D.R., 1968: Taphonomy and information losses in fossil communities. – Bull. Geol. Soc. Am. 79:1315–1330.

LINDSTRÖM, G., 1861: Bidrag till kännedomen om Gotlands brachiopoder. – Öfvers. K. Sven. Vetensk. Akad. Förh. 17 (for 1860):337–382.

– 1885: List of the fossils of the Upper Silurian Formation of Gotland. 20 pp. Stockholm.

LOWENSTAM, H.A., 1950: Niagaran reefs of the Great Lakes area. – J. Geol. 58:430–487.

– 1957: Niagaran reefs in the Great Lakes area. In M.S. LADD, (Ed.): Treatise in marine ecology and paleoecology 2. – Geol. Soc. Am. Mem. 67:215–248.

MÄNNIL, R., 1961: K morfologii polusfericheskikh mshanok otryada Trepostomata. English summary: On the morphology of the hemisphaeric zoaria of Trepostomata (Bryozoa). – Eesti NSV Teaduste Akad. Geol. Inst. Uurimused 6:113–140. Tallinn.

– 1966: O vertikal'nykh norkakh zaryvaniya v ordovikskikh izvestnyakakh Pribaltiki. – In Organizm i sreda v geologicheskom proshlom, pp. 200–207. Akad. Nauk SSSR. (In Russian.)

MANTEN, A.A., 1962: Some Middle Silurian reefs of Gotland. – Sedimentology1:211–234.

– 1971: Silurian reefs of Gotland. – Developments in Sedimentology 13:1–539.

MARCUS, E., & MARCUS, E., 1962: On some lunulitiform Bryozoa. – Bol. Fac. Fil. Cien. Letr. Univ. S. Paulo 261; Zool. 24:281–324.

MARE, MOLLY F., 1942: A study of a marine benthic community with special reference to the microorganisms. – J. Mar. Biol. Assoc. U.K. 25:517–554.

MARTINSSON, A., 1967: The succession and correlation of ostracode faunas in the Silurian of Gotland. – GFF 89:350–386.

MARTNA, J., 1955: Studies on the Macrourus and Slandrom Formations I. Shell fragment frequencies of the Macrourus Formation and adjacent strata at Fjäcka, Gräsgård, and File Haidar. – GFF 77:229–256.

MAY, R.M., 1975: Patterns of species abundance and diversity. In M.L. CODY & J.M. DIAMOND, (Eds.): Ecology and evolution of communities. pp. 81–120.

McKEE, E.D., & GUTSCHIK, R.C., 1969: History of Redwall Limestone of northern Arizona. – Geol. Soc. Am. Mem. 114:1–726.

MODZALEVSKAYA, E.A., 1955: Kolonii mshanok ordovika i zavisimost' ikh formy ot usloviy sushchestvovaniya. – Voprosy Paleontol. 2:125–135.

MOLANDER, A.R., 1930: Animal communities on soft bottom areas in the Gullmar Fjord. – Kristinebergs Zool. Stat. 1877–1927. 90 pp.

MORI, K., 1969: Stromatoporoids from the Silurian of Gotland, 1. – Stockholm Contr. Geol. 19:1–100.

– 1970: Stromatoporoids from the Silurian of Gotland. 2. – Ibid. 22:1–152.

NICOLIĆ, M., 1963: Klasse: Bryozoa (Ectoprocta, Moostiere). In R. RIEDL, (Ed.): Fauna und Flora der Adria, pp. 426–439.

ODUM, E.P., 1959: Fundamentals of ecology, 2nd ed. – W.B. Sanders Co., Philadelphia.

OSGOOD, R.G., 1970: Trace fossils of the Cincinnati area. – Paleontogr. Am. 6:281–444.

PURDY, E.G., 1963: Recent calcium carbonate facies of the Great Bahama Bank. – J. Geol. 71:334–355, 472–497.

RAUNKIAER, C., 1913: Formationsstatistiske Undersøgelser paa Skagens Odde. – Bot. Tidskr. (Copenhagen) 33.

– 1916: Om Valensmetoden. – Ibid. (Copenhagen) 34.

– 1918: Recherches statistiques sur les formations végétales. – K. Dan. Vidensk. Selsk. Biol. Medd. 1.

REMANE, A., 1940: Einführung in die zoologische Ökologie der Nord- und Ostsee. – Die Tierwelt der Nord- und Ostsee Ia. 238 pp. Leipzig.

ROMELL, L.G., 1930: Comments on Raunkiaer's and similar methods of vegetation analysis and the "law of frequency". – Ecology 11:589–596.

ROTHPLETZ, A., 1913: Über die Kalkalgen, Spongiostromen und einige andere Fossilien aus dem Obersilur Gotlands. – SGU Ca 10. 57 pp.

RUDWICK, M.J.S., 1961: The anchorage of articulate brachiopods on soft substrata. – Palaeontology 4:475–476.

RUTTEN, M.G., 1958: Detailuntersuchungen an gotländischen Riffen. – Geol. Rundschau 47:359–384.

SAVILOV, A.J., 1961: Ekologicheskaya kharakteristika donnykh soobshchestv bespozvonochnykh Okhotskogo morya. – Trudy Inst. Okeanol. 46:3–84. (Ecologic characteristics of the bottom communities of invertebrates in the Okhotsk Sea.)

SHEEHAN, P.M., 1977: *Palaeocyclys* in the Upper Visby Marl, Gotland. – GFF 99:74–75.

SLOAN, R.E., 1955: Paleoecology of the Pennsylvanian marine shales of Palo Pinto County, Texas. – J. Geol. 63:412–428.

SPJELDNAES, N., 1975: Silurian bryozoans which grew in the shade. – "Bryozoa 1974." Docum. Lab. Géol. Fac. Sci. Lyon 3(2):415–424.

STANTON, R.J. Jr., 1976: Relationship of fossil communities to original communities of living organisms. In R.W. SCOTT & R.R. WEST (Eds.): Structure and classification of paleocommunities, pp. 107–142. – Dowden, Hutchinson & Ross, Inc.

THORELL, T., & LINDSTRÖM, G. 1885: On a Silurian scorpion from Gotland. – K. Sven. Vetenskapsakad. Handl. 21 (9):1–33.

WALKER, K.R., & LAPORTE, L.F., 1970: Congruent fossil communities from Ordovician and Devonian carbonates of New York. – J. Paleontol. 44:928–944.

WEDEKIND, R., 1927: Die Zoantharia Rugosa von Gotland (bes. Nordgotland). – SGU Ca 19. 95 pp.

– & TRIPP, K., 1930: Die korallenriffe Gotlands. Ein Beitrag zur Lösung des Problems von der Entstehung der Barrierriffe. – Centralbl. Mineral. Geol. B. 1(8):295–304.

WILLIAMS, A., 1953: The classification of strophomenid brachiopods. – J. Washington Acad. Sci. 43:1–13.
ZIEGLER, A.M., 1965: Silurian marine communities and their environmental significance. – Nature 207:270–272.
– & COCKS, L.R.M., & BAMBACH, R.K., 1968: The composition and structure of Lower Silurian marine communities. – Lethaia 1:1–27.