SVERIGES GEOLOGISKA UNDERSÖKNING

SERIE C NR 762 AVHANDLINGAR OCH UPPSATSER ÅRSBOK 73 NR 3

VALDAR JAANUSSON, SVEN LAUFELD
AND
ROLAND SKOGLUND, EDITORS

LOWER WENLOCK FAUNAL AND FLORAL DYNAMICS – VATTENFALLET SECTION, GOTLAND

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Preface

It is increasingly evident that in order to understand the complex relationships affecting the distribution and succession of fossil faunas and floras, our knowledge of local distributional patterns at the species level must be considerably expanded. This volume is aimed at assessing data from a single section, some 30 m thick, through the latest Llandovery and early Wenlock (Silurian) in Visby on the Swedish island of Gotland. The section, known as Vattenfallet, was collected bed by bed in the early part of this century by G. Liljevall, who amassed over 10,000 macrofossils that form the main basis of this study: all this material, together with other collections (including countless microfossils) has been incorporated in an analysis of faunal dynamics and general biotic relationships to a degree that has not previously been attempted. In order to achieve the necessary precision at the species level a team of 32 specialists from throughout the world has investigated the material to give a reasonably complete coverage of the whole fauna and flora. Their contributions are presented separately for each fossil group, and the results are then integrated in an overall analysis of the material.

In editing the manuscripts for this volume a great degree of uniformity has had to be imposed on various contributions in order to relate the results in a meaningful way. The space available for presentation of the vast amounts of data has been limited and this has therefore placed some restrictions on the scope of individual contributions. Most manuscripts have had to be cut from their original size, some of them considerably. Documentation of many of the species by photographs would have been most desirable, but this would have been unrealistic with regard to the total space available for publication. Only a limited number of new taxa are described and illustrated, mostly those which are important quantitatively and are frequently mentioned in the text.

Dr. Michael G. Bassett has undertaken the time-consuming task of linguistically checking all manuscripts apart from those written by native English-speaking authors. We are also very much indebted to him for useful editorial suggestions.

We thank Mr. Stig Lindbom (Section of Palaeozoology, Riksmuseum) for obtaining samples from Vattenfallet below the base of Liljevall's section, Mr. Arne Philip (Visby) for aerial photographs of the Vattenfallet area, Dr. Barrie Rickards (Sedgwick Museum, Cambridge) for examining specimens of *Thallograptus* from Högklint *d,* Dr. Lembit Sarv (Geoloogia Instituut, Tallinn) for topotype specimens of various Silurian ostracodes from the East Baltic area, and Dr. Gunnar Svahnström, *Landsantikvarie* and Head of the Gotland Museum, for the loan of old photographs of Vattenfallet.

Most of the illustrations have been drafted by the artists of the Geological Survey of Sweden (SGU), namely Greta Hellström, Ingemar Kjellberg, Inga

Palmaer, and Elin Pulkkinen. A minor part has been prepared at the Section of Palaeozoology, Swedish Museum of Natural History (Naturhistoriska Riksmuseet) by Bo Bergman, Bertil Blücher and Celso Salgueiro.

VALDAR JAANUSSON, SVEN LAUFELD and
ROLAND SKOGLUND

Introduction

VALDAR JAANUSSON

The section at Vattenfallet in the southern outskirts of Visby on Gotland (Vattenfallsprofilen 1, Laufeld 1974b) has received particular fame through the discovery of the scorpion *Palaeophonus nuncius* (Thorell & Lindström 1885) in the so-called *Pterygotus* Beds (uppermost 40 cm of the Högklint Limestone). To obtain additional specimens of the scorpion, as well as eurypterids, these beds were literally quarried over a period of several years at the end of the 19th century. The rich collections assembled, including also many other invertebrates, are housed in the Section of Palaeozoology, Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm.

In connection with mapping the bedrock of Gotland the Geological Survey of Sweden intended to establish several biostratigraphical reference sections through parts of the Silurian sequence. One of the exposures selected for that purpose was the Vattenfallet section, where continuous strata were exposed from the base of the Upper Visby Marl to the top of the Högklint Limestone. The total thickness of the beds exposed was 29 m.

For systematic collecting from Vattenfallet the Geological Survey temporarily employed G. Liljevall, who in the summer of 1908 assembled a large collection of fossils from the section. Collecting was done with great stratigraphical precision, mostly bed by bed. According to his diary, in 1908 Liljevall spent altogether 32 days working on the section, each day from 7 a.m. to 7 p.m. with a two hour rest for lunch. For 21 days he was assisted by Edvin Håkansson, a local quarry-man, who brought with him a great assortment of tools for prizing slabs of limestone from the bed-rock and for crushing the rock. Liljevall's work was very systematic. Normally he spent a whole day collecting and extracting fossils bed by bed from about a single metre of the section, moved next day to the next highest metre, and continued to do so, day by day, up to the top of the section. At suitable intervals limestone and marl samples were also collected. In Stockholm Liljevall himself sorted the material and labelled it with detailed information on the horizons within the section, given in metres above sea-level and based on levelling of the exposure with a theodolite carried out by the Survey a year before. Liljevall's 1908 collections are deposited at the Geological Survey. Subsequently, he also collected some additional material from the section and much of that is deposited at the Riksmuseum.

Georg Gideon Liljevall (1848–1928) was an artist and he worked as such for most of his adult life at the Riksmuseum. He prepared illustrations for most of the papers and monographs issued from the Department of Palaeozoology between 1885 and 1925, not least for those on Gotland fossils written by Gustav Lindström, head of the Department between 1876 and 1901. Incidentally, one of his very first assignments was to illustrate Thorell & Lindström's (1885) monograph on the scorpion from Vattenfallet. Liljevall was also an outstanding collector of fossils and it was in this capacity that he was employed during the summers by the Geological Survey in the course of their mapping of Gotland (Hedström 1929).

A preliminary report on the Vattenfallet section, based on Liljevall's collections, was published by Hedström (1910). However, an exhaustive description of the section promised by him was never completed. Some of Liljevall's material from Vattenfallet was included in the monographic description of calcareous algae (Rothpletz 1913) and rugose corals (Wedekind 1927) from Gotland, but subsequently most of the collection was stored away and access to it was difficult for many years.

In connection with the examination of cores from Gotland for ostracodes, Sethi assembled and unpacked the Vattenfallet material, and the importance of Liljevall's collections was soon realised. The upper third of Liljevall's section, above 20.5 m, is now covered and the only documentation is in Liljevall's material. Lindström's old scorpion-locality in the "*Pterygotus*" Beds was already built on before 1908. Only traces of it remained and Liljevall succeeded in tieing it into his section 30 m to the northwest. All this material offers a unique opportunity to study the fossil succession in detail through a substantial portion of the lower Wenlockian sequence of Gotland.

Initial plans were to present studies of the fauna of the section in a series of separate papers, and several such studies were started (Sethi on beyrichiacean ostracodes, Klaamann on tabulate corals (see Klaamann 1977a), Brood on bryozoans, and Neuman on rugose corals). At that time Kjellesvig-Waering had also started his study of the eurypterids from the "*Pterygotus*" Beds of Vattenfallet, based on the collections at the Riksmuseum. As a result of discussions in May 1975, between Bassett, Jaanusson, Klaamann, Sethi, and Skoglund, it was found that splitting of the description of the Vattenfallet material between many individual papers, published separately and at irregular intervals, would make it difficult to summarise the results within a reasonable time. Furthermore, without centralised coordination of the project there was a danger that many groups would not be properly covered. It was thus decided that an attempt should be made to cover the whole fauna and flora of the section and to present the results in a single publication. Jaanusson undertook the task of acting as general coordinator of what was now termed "Project Vattenfallet".

The fauna and flora from the section proved to be far more diverse than at first realised. Cooperation of many specialists was needed. Ultimately a team of 32 specialists from eight different countries was assembled, and virtually the whole fauna and flora from the section could be covered, in the first ever attempt to elucidate the succession of all fossil organisms during an interval of time and to analyse biotic changes based on practically all preserved taxa.

In the lower half of the section the density of Liljevall's rock samples is low. For this reason a series of additional samples was collected by Jaanusson and Skoglund in 1975 throughout the exposed portion of the section, assisted by Bengtson with a theodolite for determining the level of horizons. These samples were used for lithological analyses, for isolating acritarchs, chitinozoans, and foraminifers, and for qualitative and quantitative work on bryozoans based on thin sections and peels. The field party in 1975 also included Franzén, Jeppsson, and Sethi. In 1970 Jeppsson had collected a series of limestone samples from the section, and these were processed for conodonts and scolecodonts, and yielded remains of various other fossils. For the upper part of the section, above 20.5 m above sea-level, Liljevall's samples were used for lithological studies as well as for isolating acid-resistant microfossils. From Högklint *d* ("*Pterygotus*" Beds) a large number of samples were available in the Riksmuseum collections. When it became apparent that in parts of the section the density of Liljevall's marl samples is low, some additional samples were collected by Brood in 1976. These, as well as Liljevall's washed marl samples, were picked for various fossils by some authors themselves and also by Mrs. Meit Lindell at the Department of Palaeobiology, Uppsala University.

In June 1978 Stig Lindbom, who is currently studying the hard-bottom boring endofauna in the Upper Visby Marl, succeeded in obtaining rock samples down to the 0.5 m level at Vattenfallet. Examination of these samples revealed that the section below 1.1 m belongs to the Lower Visby Marl, that the lowermost bed (1.1–1.3 m) accessible to Liljevall was actually the very base of the Upper Visby Marl, and that the lowermost rock sample (1.0 m) collected by Jaanusson and Skoglund was the uppermost bed of the Lower Visby Marl. Despite the shortage of time, various contributors managed to identify the shelly fauna recovered from the Lower Visby samples and the new data have been incorporated in the logs. The only group which has not been covered because of lack of time is the "non-palaeocope" ostracodes.

Sorting of the extensive material presented unexpected problems, not least because of the frequent occurrence of individuals of several groups on a single specimen or slab. The patience of many contributors was sorely tested because of repeated receipt of additional specimens up to the dead-line or even after their manuscript had been submitted.

The main results are presented in the form of logs showing the levels from which a species has been recorded in the section. In Liljevall's collection the precision of data on the level varies from one centimetre to several metres, although cases in which the precision is less than 20 cm are infrequent. For an analysis of faunal changes in general and faunal dynamics in particular it is important that the entries into the logs are systematic and that differences in the precision of base data are clearly indicated. For the Vattenfallet section the minimum vertical interval entered into the logs was chosen to be 20 cm; that is, irrespective of whether the level was originally given with a precision of one, five or ten centimetres, the occurrence is entered into the logs as an interval of 20 cm. A minimum interval of ten centimetres would have been more satisfactory, but in view of the average precision of the collecting the increase in precision would have been largely illusory. Occurrences recorded with a precision of equal to or greater than 20 cm are marked on the logs as black quadrangles. If the precision is between 20 and 100 centimetres, the corresponding interval is drafted as an open rectangle. With a few exceptions, records with a precision of less than a metre are not used; however, if these data contribute to the vertical range of the species in the section, they are recorded in the annotated faunal or floral list.

Final drafts of all logs were compiled by Jaanusson based on lists of taxa and levels submitted by the contributors or, in a few cases, on the logs prepared by authors themselves. That the entries of all data into the logs should be made centrally proved necessary, since otherwise a uniform presentation would have been difficult to accomplish.

For several groups of organisms in the Wenlockian of Gotland modern monographic descriptions were either available or in an advanced state of preparation. For some additional groups there existed reliable old monographic studies which could be easily updated. The rest of the Wenlockian fauna and flora of Gotland has never been properly described, or even in some cases never recorded. For such groups, as well as in cases where the state of preservation was sufficient for recognising differences between species but insufficient for identifying described species, an extensive use of open nomenclature was necessary. For taxa of species category which could not be named the letters *a, b, c,* etc. are used to designate the species. This is done in order to facilitate the recognition of the species when subsequent monographic studies might provide a formal name. The designation sp. indet. *a, b,* etc. implies that although the specimen is not identifiable at the species level, it cannot possibly be identical with any of the other species recorded in the log. The abbreviation sp. without a letter is normally used if there is some doubt as to whether or not several different species might be involved in the material. Conditional identifications with a confer (cf.) are recorded in the logs with a question mark.

In the logs, an arrow indicates that a species is known above or below the sequence of the section. However, for many species the range is still poorly known and the lack of an arrow does not necessarily imply that a species does not occur in adjacent beds. For supraspecific categories (recorded as sp. or spp.) such information is normally omitted.

For references in this chapter see the list of references at the end of this volume.

Stratigraphical and environmental background

VALDAR JAANUSSON

General stratigraphical relationships

The location of the Vattenfallet section is best described in Lindström's words (in Thorell & Lindström 1885:3): "Just beyond the mediaeval walls of the town of Visby, on its southern side, there is a public park extending along the shores of the Baltic. It is called "Palisaderna" (=the palisades) from some part of the fortifications of the now vanished castle of Visborg, which formerly stood close to this locality. A natural ravine, excavated by the action of water, traverses this park from east to west. It bears the name of Gammelå (=the old brook) or more commonly "Vattenfallet" (=the Waterfall)."

The rock exposed at Vattenfallet on the steep slopes of a series of diminutive canyons belongs to the uppermost Lower Visby Marl, the Upper Visby Marl and the Högklint Group as defined by Hede (1921). In descending order the section is briefly as follows (levels refer to height above sea-level).

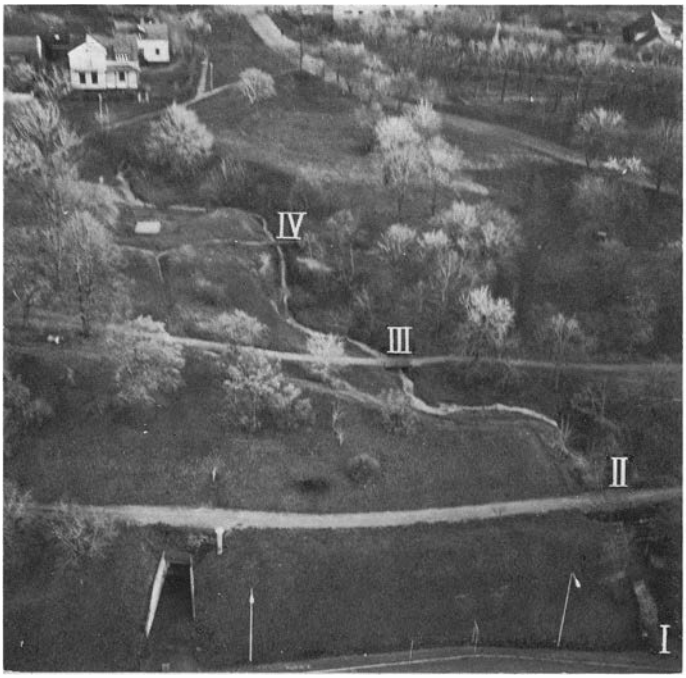

Fig. 1. Aerial photograph of the Vattenfallet area taken by Arne Philip in November, 1977. The numbers of bridges over the brook correspond to those in Fig. 2.

Högklint Limestone 20.0 m

29.6–30.0 m. Högklint *d* (so-called *Pterygotus* Beds). Soft pelletal marl and calcareous mudstone with some thin intercalations of pelletal limestone (for detailed section, see Hedström 1904 and below).

24.2–29.6 m. Högklint *c*. Regularly bedded limestones (sparitic pelletal calcisiltites to sparitic pelletiferous calcarenites) virtually without argillaceous intercalations. In the upper 80 cm the rock consists of sparitic calcirudites to conglomerate.

12.65–24.2 m. Högklint *b*. Somewhat nodular to regularly bedded limestones with argillaceous intercalations of varying thickness. In the lower 3.5 m the limestone consists predominantly of calcilutites; limestone beds of the remainder of the division are formed of micritic to sparitic pelletiferous calcarenites.

10.02–12.65 m. Högklint *a*. Thick-bedded, coarse-grained limestones (sparitic calcarenites) with thin argillaceous intercalations.

Upper Visby Marl 8.9 m

3.8–10.02 m. Irregularly bedded to nodular limestones with argillaceous intercalations of varying thickness. The composition of limestone beds varies from calcilutites to micritic and sparitic calcarenites.

1.1–3.8 m. Nodular to irregularly bedded argillaceous limestones with argillaceous intercalations that mostly exceed the thickness of the limestone beds. The limestone is mainly calcilutite.

Lower Visby Marl 0.7 m +

0.4–1.1 m. Lithologically indistinguishable from the lowermost Upper Visby Marl.

The boundary between the Lower and Upper Visby Marl cannot be defined lithologically but it is sharp faunally. The Lower Visby Marl is not easily accessible at Vattenfallet and the available small samples did not contain large

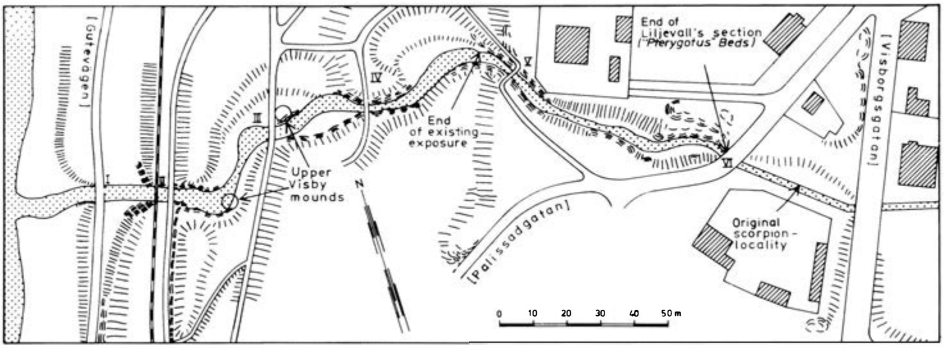

Fig. 2. A copy of Liljevall's map of the Vattenfallet area. The successive bridges over the brook are numbered. In order to facilitate orientation, the modern names of streets are given in brackets.

macrofossils. The boundary is particularly well defined by palaeocope ostracodes, not only qualitatively (Fig. 41) but also quantitatively (Fig. 44). Among small macro-organisms the brachiopod *Eoplectodonta transversalis* and the tentaculitoid *Gotlandellites visbyensis* have never been found above the Lower Visby Marl. Every sample from the Lower Visby Marl also contained several specimens of the distinctive rugose coral *Palaeocyclus porpita,* which is common on Gotland only in this topoformation, although it also occurs rarely in the Upper Visby Marl (Lindström 1861:340; Mori 1969:20; Sheehan 1977).

The top of the section has been assumed to correspond to the boundary between the Högklint and Tofta Limestones. However, Liljevall's observations indicate that the main break in the sequence is at the base and not at the top of the "*Pterygotus*" Beds. Because of the lack of existing continuous exposures in this part of the sequence in the Vattenfallet area, the stratigraphical significance of the break is difficult to determine. The overlying beds (31.0–31.8 m), which are discontinuously exposed, contain oncolites ("*Spongiostroma*") and lithologically resemble parts of the Tofta Limestone.

The index letters for the lithostratigraphical subdivisions of the Högklint Limestone are here used in the same sense as by Laufeld (1974a:8). The boundaries of the subdivisions are not necessarily synchronous over the whole outcrop area in which these lithological units can be distinguished.

Several authors have suggested that the Tofta Limestone is only a facies of the upper part of the Högklint Limestone (Hadding 1956; Jux 1957; Mori 1969; Manten 1971), but from a stratonomic point of view this is hardly possible. In places where the contact relationships between the Högklint reefs and the Tofta Limestone can be observed or deduced the oncolitic ("*Spongiostroma*") Tofta Beds always overlie the Högklint reefs (Martinsson 1967:362). If the Högklint reef mounds continued to grow during deposition of the Tofta Beds, this must have taken place outside the present outcrop area.

For stratigraphical orientation along the brook the following notes may be useful. The stream is crossed by a number of bridges, numbered originally by Liljevall in ascending order from I to VI (Figs. 1,2). The first bridge (Fig. 3) has now been replaced by the broad road, named Gutevägen, alongside the harbour, so from that point to the west the brook runs underground to the sea. Immediately east of Gutevägen is the first waterfall and a canyon cut into the lower part of the Upper Visby Marl (Fig. 3). East of the second bridge is the second waterfall (Hedström 1910, Fig. 60b; 1912, Fig. 10), where the top of the section is formed by thick-bedded limestones of Högklint *a,* the base of which (10.02 m) forms one of the easily recognizable index horizons in the section. Below the fourth bridge is the third waterfall (Hedström 1910, Fig. 60a; 1912, Fig. 11) with a canyon cut into the limestones of Högklint *b.* The thick bentonitic bed (17.0 m) close to the summit of the waterfall is a further

Fig. 3. Vattenfallet, photograph of the first bridge (now Gutevägen) from the west, with the second bridge in the background. In the left background the steep wall is formed by the lower part of the Upper Visby Marl (about 3–6 m above sea-level). Photograph by K.J.A. Gardsten, probably around 1900; by courtesy of the Gotland Museum, Visby.

important index horizon. The existing exposure, still in Högklint *b*, extends eastwards almost to the point where, in Liljevall's time, the fifth bridge crossed the brook. Southeast of that point the brook now runs underground in a drain and bedrock is no longer exposed. The nearest outcrop of Högklint *c* is a low road-cut (with a section of c. 0.5 m) at Palisadvägen, about 50 m southwest of the brook. Högklint *d* ("*Pterygotus*" Beds) was accessible to Liljevall just north of the sixth bridge at what now is Palisadgatan. Lindström's scorpion-locality was located 30 m farther southeast along the brook (Fig. 2). For the location of pegs used for topographic fixed points, see Laufeld (1974b, Fig. 26; note that in that figure the numbers of the scale should be reduced by a factor of ten).

A stratigraphical correlation of the Vattenfallet section with conodont and graptolite zonations is given in Table 1. For details see Jeppsson (this volume) and Skoglund (this volume).

The boundary between the Lower and Upper Visby Marls appears to correspond to the boundary between the Llandovery and Wenlock Series (Bassett & Cocks 1974:4–5). The Upper Visby Marl and Högklint Limestone belong to the lower part of the Sheinwoodian Stage.

Series	VATTENFALLET		Conodonts	Graptolites
Wenlock	Tofta		*Hindeodella sagitta*	?
	Högklint Limestone	d		
		c	[*Kockelella patula*]	
		b		*Monograptus riccartonensis*
		a		[*Cyrtograptus murchisoni*] [*Cyrtograptus centrifugus*]
	Upper Visby Marl		*Pterospathodus amorphognathoides*	
Llandovery	Lower Visby Marl			[*Monoclimacis crenulata*]

TABLE 1. Correlation of the Vattenfallet sequence with the graptolite and conodont zones.

General lithofacies relations

Much of present knowledge of the distribution of various Silurian lithofacies in the Balto–Scandian region is based on gross macroscopic characteristics and not on rock composition derived from quantitative data. For this reason definition of lithofacies belts is often vague, and the location of boundaries between the belts is uncertain in places.

The Upper Visby Marl belongs to a lithofacies belt in which the rock can be characterized as an alternation of thin beds or nodules of limestone and friable calcareous mudstone ("marl"). The limestone mostly has a high terrigenous clay content. For brevity, this belt is here termed the marl belt. It can be followed eastwards into the lower Jaani Marl of Saaremaa and the eastern mainland of Estonia (Kaljo 1970, Fig. 84; Kaljo & Jürgenson 1977, Fig. 4). Southwards the terrigenous clay content increases and the marl belt merges into a belt formed mainly of mudstone and shale. Whether the boundary between these belts is within southern Gotland or south of the island cannot be determined before cores have been studied lithologically. Northwards the marl belt was probably bordered by a belt consisting of bedded limestone in which argillaceous intercalations have a subordinate importance. There is a good possibility that this belt also included patches of reef-like stromatoporoid mounds. On the assumption that this belt did exist at all, it has now been completely removed by erosion.

Distribution of the main lithofacies belts during the period of deposition of the Högklint Beds is shown in Fig. 4. During this time skeletal sand, pelletal silt, and argillaceous carbonate mud was deposited on northwestern Gotland, now forming various bedded limestones of the outcrop area. Rock with a similar lithology probably extends also east of northern Gotland below the sea-floor. This is all that remains of a lithofacies belt which possibly extended along much of the northern margin of the Balto-Scandian epicontinental basin. In Estonia rocks of Högklint age (represented by a part of the Jaani Stage) are formed of marlstones belonging to the marl belt (Kaljo 1970, Fig. 84). The bedded Högklint limestones of northwestern Gotland merge to the south and southwest into similar marl deposits, but details are unclear. The mudstone and shale belt is located farther to the south and southwest.

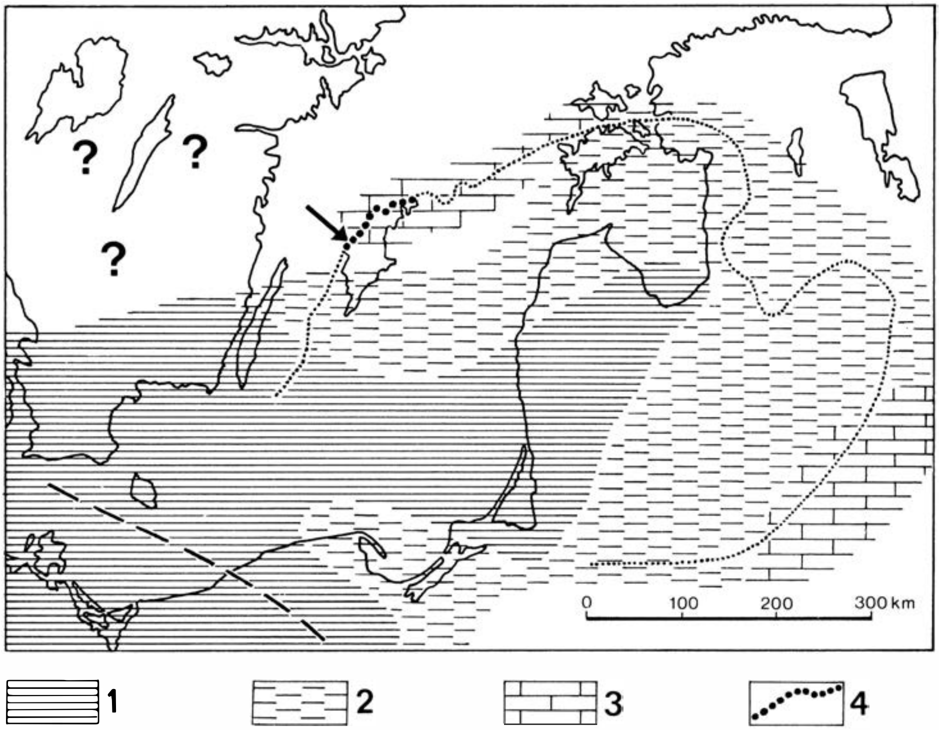

Fig. 4. Distribution of the main lithofacies in southern Balto-Scandia during early Wenlockian times when the Högklint Limestone was deposited. East Baltic area after Kaljo & Jürgenson (1977, Fig. 4); various highly argillaceous limestones with mostly friable "marly" intercalations are grouped together as "marl". Dotted line, the boundary of the preserved subsurface and submarine Wenlockian deposits of the Russian Platform, including the outcrop areas; thick dashed line, the approximate boundary between the epicontinental sea of the Russian Platform and the Wendean Basin. The position of the Vattenfallet area is indicated by an arrow. 1, shale and mudstone; 2, "marl"; 3, bedded, predominantly calcarenitic limestones; 4, reefs of the outcrop area.

In its outcrop area the Högklint Limestone contains a great number of separate lenses of massive limestone of varying size (Eriksson & Laufeld 1978, Figs. 4–6), some up to two kilometres in cross-section and up to 30 m thick. These unstratified, mainly flat lenses abound in stromatoporoids and are generally regarded as representing a type of reef with accompanying flank deposits (Hede 1933, 1940; Hadding 1941, 1950; Rutten 1958; Manten 1962, 1971). Despite of numerous studies, the construction of the reef-like mounds still is poorly understood. The distribution of the reefs along the outcrop area gives the impression that they form a well-defined individual belt, which has been compared with a barrier reef (Wedekind & Tripp 1930; Jux 1957). However, the original spatial extent of the Högklint reefs is difficult to reconstruct and they may well have been developed also to the north of the outcrop area, where the equivalent sequence is now eroded away. That they had been developed immediately outside the present coast has been inferred from the distribution of so-called Philip structures (Eriksson & Laufeld 1978). The outcrop area of the reef belt appears to be at least slightly oblique to the original axis of the belt (see also Fig. 4), and may represent the southern margin of an originally wide belt with numerous patch reefs. In any case, the comparison with a modern ocean-facing barrier reef is misleading in several respects.

The Vattenfallet section is in bedded limestones between the reefs, and to understand depositional conditions it is important to know how much the reefs controlled sedimentation around them. In this respect widely divergent opinions have been expressed. According to Jux (1957) much of the coarse-grained bedded limestone sequence on Gotland consists of material derived from the reefs. On the other hand, Rutten (1958) found almost no influence of the Högklint reefs on sedimentation in the immediate reef-surroundings. Manten (1971:217–219) traced the distribution of reef-derived debris and found that even within a relatively short distance from the reef the proportion of coarse reef debris in the sediment is fairly low.

The sediment now forming bedded limestones around the reefs was deposited at almost the same rate as the reefs (Hadding 1941, 1950). According to Hadding (1941) the surface of a reef cannot have protruded more than a few metres above the level surface of the surrounding sea-floor. Thus during the growth of a reef, its surface formed a low mound of varying dimensions, normally flanked by a belt of reef talus mixed with autochthonous skeletal remains. Only a short distance from a reef, pelletal silt and skeletal sand was deposited. Pellets could not possibly have been derived from the reef. The relative importance of reef-derived skeletal material in the inter-reef deposits varied with the distance from, and the size of the reef and is now difficult to estimate. However, the general impression is that, in terms of the source of sedimentary particles, the reefs seem to have exerted only a limited control on sedimentation between reefs. The sea-floor between reefs supported a varied fauna and flora which probably produced much of the carbonate sediment in that environment.

Limestone lithologies

Remarks on methodology and terminology

The principal method of quantitatively studying microlithology of the limestone is point counting of thin sections. Application of this method to limestones has been discussed recently by Jaanusson (1972) and the recommendations outlined there are followed here. The main pertinent points are as follows. (1) Skeletal sand is defined as those skeletal particles of 0.1 mm or greater length in thin section (Jaanusson 1952; Martna 1955). (2) Sparry calcite comprises inter- and intragranular cement, rim cement, and frequently also some neomorphic calcite formed by assimilation (recrystallization) of skeletal grains and other carbonate particles into sparry calcite mosaic. (3) The matrix, that is most of the remainder of the rock, consists of material of various origins, such as skeletal grains smaller than 0.1 mm in thin section, carbonate mud, terrigenous mud, and considerable amounts of calcium carbonate cement incorporated into micrite. (4) The grain-solid definition of the skeletal grain (Dunham 1962) is applied.

Discrete micritic particles are here classified as peloids (McKee & Gutschick 1969). They mostly represent true indurated pellets, but also include completely micritized skeletal grains, fragments of such grains or of micritic envelopes, and micritic envelopes cut by the thin section so that skeletal core is not visible. The predominant size range of peloids in the Vattenfallet section is between 0.03 and 0.07 mm, but some attain larger size, particularly in beds in which micritic envelopes are abundant. In order to show the importance of peloids as a constituent of the rock, it is advantageous to distinguish here between peloids and the matrix proper. As the true indurated pellets represent the majority of peloids and in many beds appear to form the only type of peloids, the term pellet is often used instead of peloid. It should be stressed that, because the size of peloids is mostly less than or close to the thickness of the thin section, their amount is systematically overestimated (Jaanusson 1972). In some cases the values obtained for peloids represent fairly rough estimates. This is particularly the case when minute pellets are embedded in a micritic martrix in which individual pellet grains are difficult to distinguish from the surrounding micrite (particularly at 13.3, 14.3 and 15.9 m). The same problem arises when such pellets are very densely packed.

In some beds many skeletal grains have a distinct micritic envelope (Fig. 12 B), and the micritized portion of the grain forms a substantial part of the rock volume. For the latter reason micritic envelopes were distinguished as a separate constituent in point counts.

Classification of limestones is an intricate problem because a limestone is normally composed of a mixture of many constituents (skeletal grains, peloids, sparry calcite, micrite, terrigenous mud, etc.) and the proportions between the constituents vary within wide limits. Based on arbitrary sets of proportions a great number of different rock types can be distinguished. Classification can

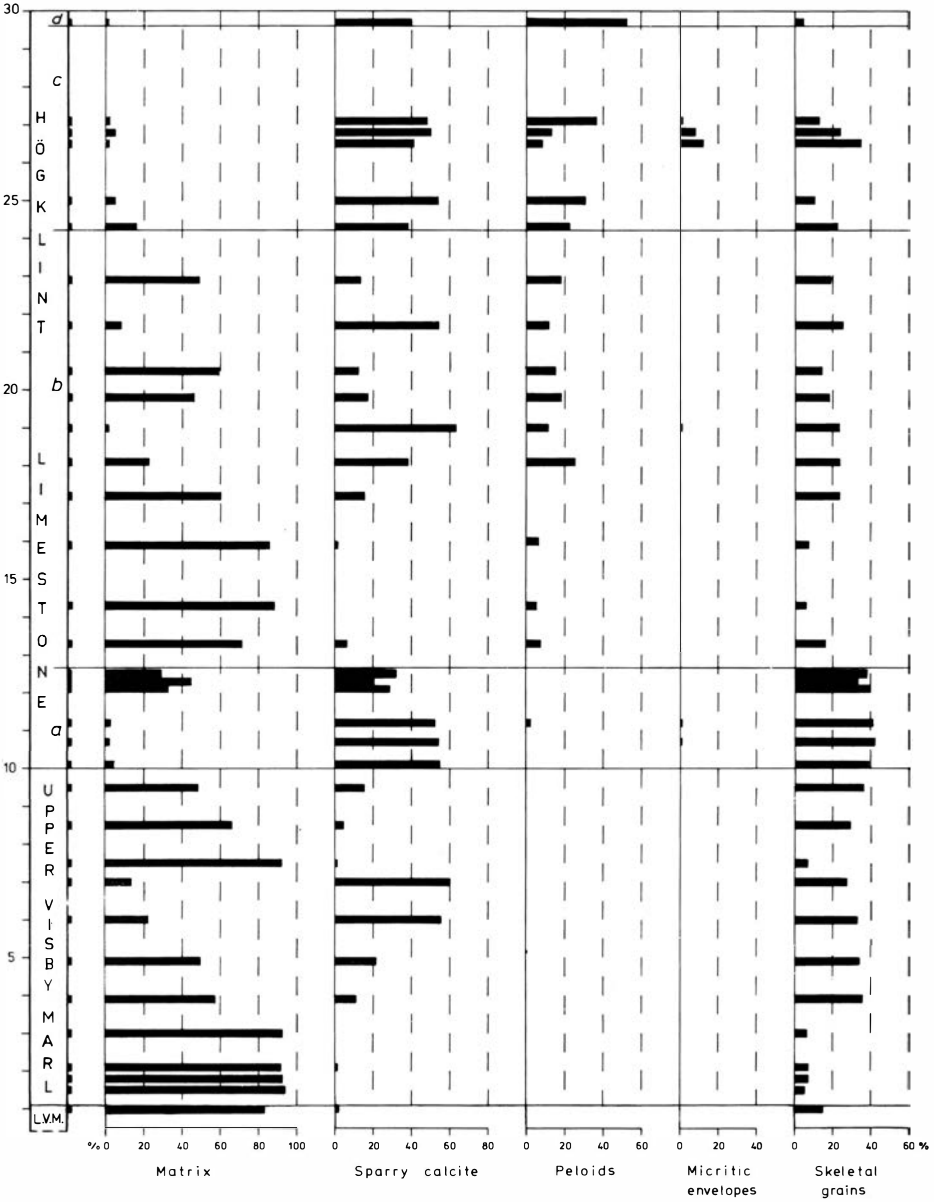

Fig. 5. Main microscopic constituents of the limestone based on point counting of thin sections.

also be based on other characteristics such as grain size or depositional texture. Irrespective of which classification is followed, reasonably representative data on the volumetric proportions of various constituents are of primary importance for characterizing a limestone and comparing it with other limestones. For the limestones of Vattenfallet such data are given in Fig. 5. For a study in which ecological background is involved, an emphasis on grain size is normally preferable.

Based on these premises the following simple classification is adopted here. Calcilutites contain less, and calcarenites more, than about 20 per cent of sand grains (Jaanusson 1952). If sand grains in a calcarenite are embedded in a micritic matrix, the rock is termed micritic calcarenite; if the content of presumably intergranular sparry calcite exceeds about 20 per cent, the limestone is called sparitic calcarenite. The content of peloids is recorded by adding "pelletiferous" or ("peloidiferous") to the term, except when they form more than 20 per cent of the rock and dominate by volume over sand grains. In the latter case the rock is termed pelletal (or peloidal) calcisiltite (provided that, as at Vattenfallet, the overwhelming majority of peloids falls into the size range of silt) which, like calcarenites, can be either micritic or sparitic. If the dominant grain size falls within the range of gravel, the rock is termed a calcirudite.

Compared with the original soft sediment, it should be noted that an originally early lithified limestone normally contains at least 50 per cent additional calcium carbonate precipitated as cement. This amount of calcium carbonate corresponds roughly to the pore volume in the soft sediment when lithification started. When determining the grain size of a soft sediment by weighing different grain size fractions, the pore volume is not considered, whereas when determining the grain size volumetrically, the pore volume, or the cement filling the original pores, forms a part of the volume of the sediment or rock. Thus, if the pore volume of the soft sediment was, say 50 per cent when lithification started, then the content of 50 per cent sand grains by weight would correspond to about 25 per cent sand grains by volume (Jaanusson 1972:226–227).

In the argillaceous beds of the Upper Visby Marl and Högklint *b*, aragonitic shells (gastropods, pelecypods, etc.) are mostly preserved as internal moulds, provided that they did not possess a thin, outer calcitic layer. This indicates that aragonite was mostly dissolved before the sediment became lithified, and that thus lithification started relatively late. In Högklint *c* many such fossils preserve the original shell volume, indicating that there lithification was earlier than the change in composition of the shell from aragonite to calcite. This suggests that prior to lithification the sediment of the argillaceous beds in the Upper Visby Marl and Högklint *b* became reduced in volume by compression to a greater degree than sediment now forming the limestone beds in Högklint *c*. In the friable marl the effect of compression is particularly noticeable through deformation of the shape of many large, thin-walled fossils. No special study of the diagenesis of the rock at Vattenfallet has been made, and it is also possible that some limestone beds in the Upper Visby Marl and Högklint *b* were lithified early. The effect of reduction of sediment volume on the grain size of the sediment or rock is shown by Martna (1955, Fig. 2). It should be noted that compaction also affects the content of terrigenous material. With decreasing pore volume less calcium carbonate can be precipitated in the voids and the relative proportion of terrigenous material in the rock increases. Thus, with respect to the content of terrigenous material the contrast between limestone beds and argillaceous beds is now greater than it was prior to lithification.

In parts of the Vattenfallet section the limestone is relatively inhomogeneous. This is particularly true in the Upper Visby Marl and Högklint *b,* Within a single thin section there occur patches of sparitic and micritic calcarenite, or calcarenitic and calcilutitic limestone. Much of the heterogeneity is demonstrably due to uneven bioturbation. In the upper part of the Upper Visby Marl as well as in parts of Högklint *b,* calcarenitic and calcilutitic beds frequently alternate. The surface of a thin section is too small to display correct proportion between different rock types within a bed, and the number of samples is too small to illustrate all vertical variations in lithology. Despite this, the series of thin sections that have been analysed microlithologically (Fig. 5) appear to provide a satisfactory basis for characterizing the rock. The lithological study is admittedly incomplete because only calcium carbonate constituents have been analyzed in some detail, whereas the terrigenous component has not been studied.

Lower Visby Marl (0.4–1.1 m)

No lithological change at the boundary between the Lower and Upper Visby Marl could be observed in the field. Only the uppermost bed of the Lower Visby Marl was studied microlithologically and no differences from the lowermost Upper Visby Marl could be noted.

Upper Visby Marl (1.1–10.02 m)

Up to about 3.6 m above sea-level the Upper Visby Marl consists of bluish-grey marl with nodules and irregular nodular beds, mostly one to three cm thick, of fine-grained argillaceous limestone. The limestone is a calcilutite, mostly with a low content of skeletal sand (Figs. 5, 6A) and normally with a high admixture of terrigenous clay. The sediment was a mixed carbonate and terrigenous mud.

In the main upper part of the Upper Visby Marl limestone predominates, forming irregular beds or nodules, mostly 2 to 4 cm thick, intercalated with soft

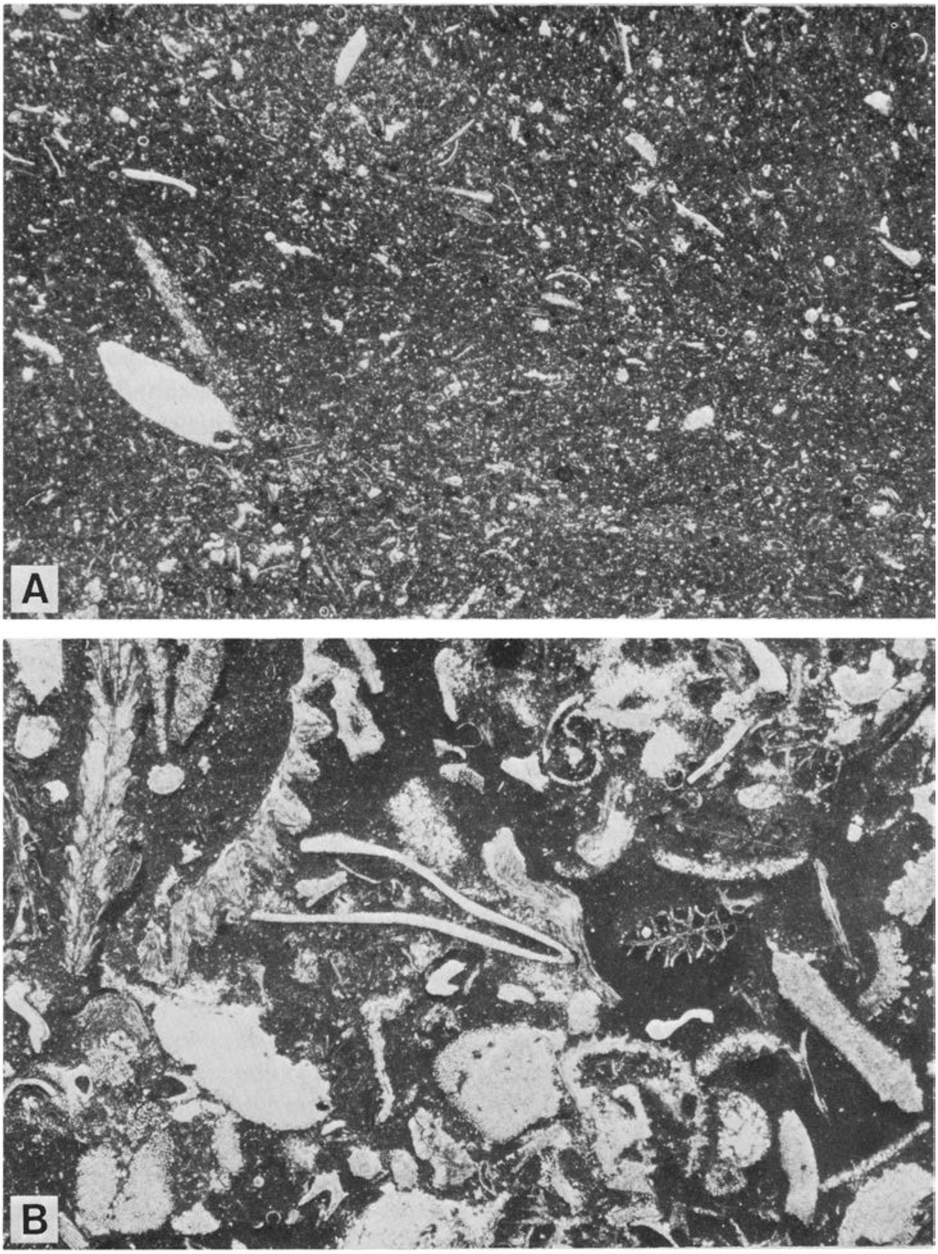

Fig. 6. A. Calcilutite, Upper Visby Marl at Vattenfallet, 3.0 m. The large skeletal grain to the left is an oblique cross-section of an *Atractosella* spicule. B. Micritic calcarenite, Upper Visby Marl at Vattenfallet, 9.6 m. Thin sections, ×15.

marl (Fig. 7). The grain size of the limestone varies (Fig. 5). Some beds (7.5 m) are as fine-grained as in the lowermost part of the section and originally formed the same kind of sediment. In some other beds (4.9, 8.5, 9.5 m) the rock is a micritic calcarenite (Fig. 6B). The sediment was a mud-supported skeletal sand. The limestone also includes beds (6.0, 7.0 m) with a high content of sparry calcite, most of which was originally precipitated as intergranular cement. In these beds the content of skeletal sand is also high (Fig. 5). The rock can be classified as sparitic calcarenite and the sediment was a largely grain-supported skeletal sand. In order to determine the proportion of the different types of limestone within this part of the section a far denser series of samples is needed.

In the micritic portions of the rock the micrite is fairly homogeneous in thin sections. In only a few cases could faint traces of flocculation be observed but it is uncertain whether these indicate pelletal structures. Much of the sequence shows traces of bioturbation.

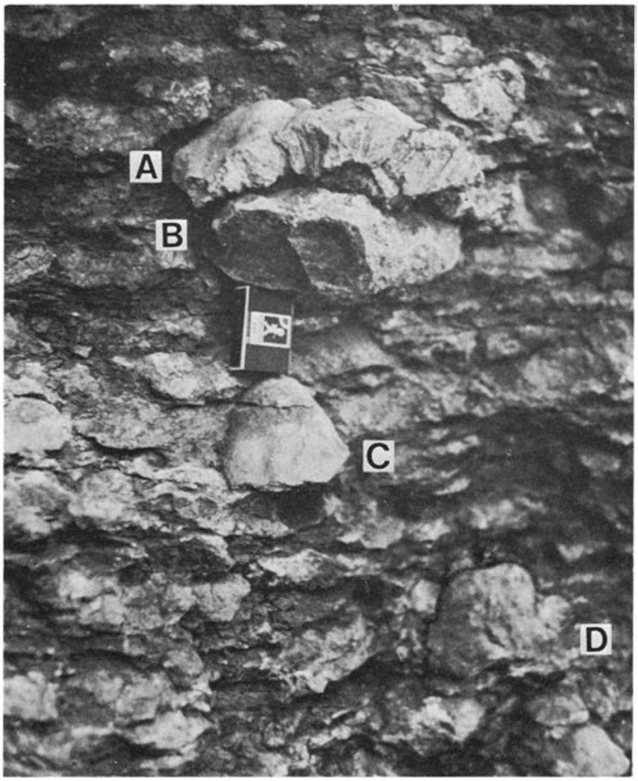

Fig. 7. Upper Visby Marl at Vattenfallet, 9.1–9.65 m. A. Colony of *Catenipora quadrata* encrusting *Densastroma pexisum* (B). Other colonies of the stromatoporoid *D. pexisum* are below the match-box (C) and in the lower right corner (D). All colonies are in original growth position and all stromatoporoids were resting on the sediment. Length of match-box 5 cm. Photograph Ulf Borgen, 1976.

The mound of unstratified limestone in the Upper Visby Marl

At the second waterfall a massive carbonate mound is developed in the upper part of the Upper Visby Marl (Fig. 8; Hedström 1910, Pl. 60:b). The visible height of the mound is about 3.5 m but the base is not exposed. Its top extends to the level of the lowermost beds of Högklint *a*. There the contact relationships between the stratified limestone and the mound are not quite clear but appear to indicate an abrupt change in lithology between the thick-bedded calcarenites and the mound rock. The change from the bedded Upper Visby Marl to the unstratified limestone of the mound is also fairly abrupt, but some marly intercalations can be followed into the mound almost horizontally, indicating that it did not protrude very much above the level sea-floor. The rock of the mound includes thin discontinuous argillaceous intercalations and pockets of soft argillaceous limestone.

The mound is one of numerous similar structures in the upper part of the Upper Visby Marl of northwestern Gotland (see Manten 1971:79–114), generally referred to as reefs. It is less well exposed than many others and does not form a satisfactory basis for a detailed study.

In order to examine the structure of the mound, a surface, measuring about one square metre and located about 2.2 to 3.3 m below its top, was cleaned with a steel brush, etched with hydrochloric acid, and stained with blue ink (Brood and Jaanusson,

Fig. 8. Etched surface of the unstratified Upper Visby mound at Vattenfallet, about 2.2–3.3 m below its top (about 7–8 m above sea-level). Light areas (A) at the base are favositid colonies (mostly *Angopora hisingeri*), in part displaced from the original growth position. Length of match-box 5 cm. Photograph Ulf Borgen, 1976.

assisted by Ulf Borgen, in June 1976). Although the best surface was chosen for etching, it is irregularly rough and with a varying slope that is mostly not perpendicular to the depositional surface (Fig. 8). After etching and staining the surface revealed the main compositional features of the mound but it was unsuitable for illustrating the structures. The tabulate and heliolitid corals were identified by Klaamann and the stromatoporoids by Nestor.

The massive limestone has no organic skeletal frame. It contains scattered colonies of tabulate corals and small stromatoporoids embedded in a mostly fine-grained, calcilutitic to calcarenitic limestone. The volume of colonial skeletons probably comprises 10 to 15 per cent of the total rock volume. Favositids dominate, mainly as *Angopora hisingeri.* Other tabulates and heliolitids include *Planalveolites fougti, Heliolites decipiens* and *Stelliporella* sp. Stromatoporoids, *Stromatopora impexa* and *Clathrodictyon delicatulum,* are represented by very small colonies. On the very top of the mound, at the level of the lowermost part of Högklint *a,* is a large colony (at least 0.5 m wide) of *Catenipora* n.sp. *a.* At the same level another halysitid colony was found, belonging to *Catenipora gotlandica* (Yabe) (RM Cn59638), encrusted by *Planalveolites* sp. Both halysitid species are rare but they are known elsewhere only from the Högklint Beds (Einar Klaamann, personal communication). The specimens from the mound were not entered in the logs because the levels in the mound do not correspond exactly to those of the adjacent bedded limestone.

The mound probably never projected above the seafloor more than 0.5 m, and it did not appear to have controlled deposition in its immediate vicinity. Nor could any influence from the mound be observed in the composition of the fauna of the adjacent bedded limestone.

A second, similar Upper Visby mound is probably located about 25 m ENE of that described above. The mound itself is not exposed at that point but the uppermost beds of Högklint *a* there form a distinct dome (Liljevall's *stuphäll*) the height of which was estimated by Liljevall to about a metre. The dome is reflected also in the lowermost beds of Högklint *b.*

Högklint a *(10.02–12.65 m)*

Högklint *a* consists of coarse-grained, mainly thick-bedded calcarenites with thin argillaceous intercalations. The change in lithology from the underlying Upper Visby Marl is fairly abrupt (Fig. 9). The microlithology of the limestone is uniform throughout the division, with a high content of both skeletal sand and sparry calcite (Fig. 5). Skeletal sand particles are frequently somewhat rounded. The sparry calcite was precipitated as intergranular cement although subsequently some neomorphic recrystallization has also taken place. The rock is a sparitic calcarenite (Fig. 10A) and the sediment was a well winnowed, grain-supported skeletal sand. Rare particles have been observed which might represent peloids (0.2 to 1.9 per cent of the rock volume). Coatings around skeletal grains also occur (0.2 to 1.7 per cent of the rock volume) but most of these represent algal structures.

Högklint b *(12.65–24.2 m)*

In its main lower part (12.65 to c. 20.2 m), Högklint *b* consists of thin (mostly 3

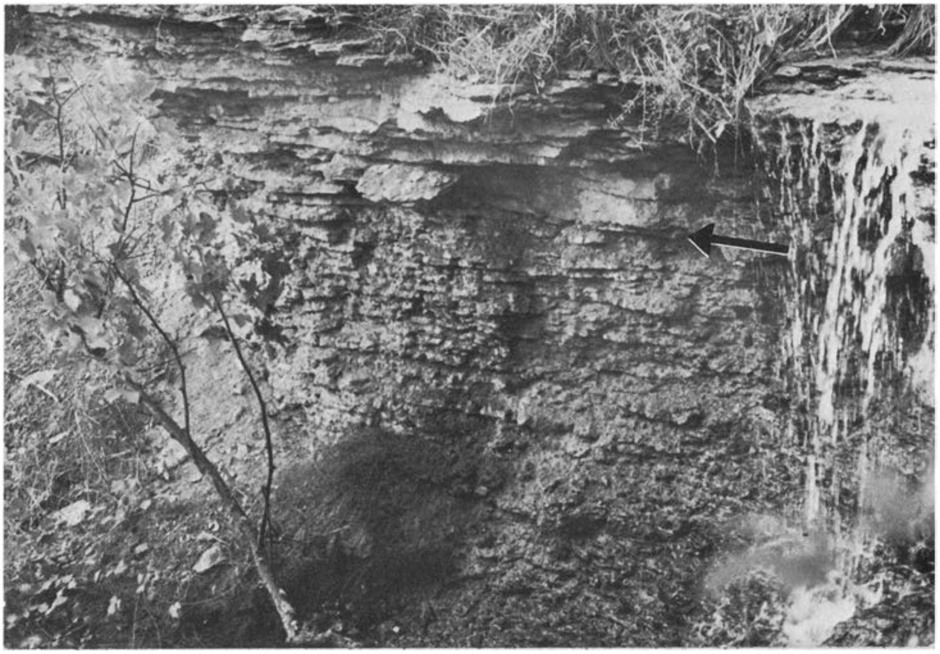

Fig. 9. The arrow points to the boundary between thin-bedded Upper Visby Marl and the overlying coarse-grained, thick-bedded limestones of Högklint *a*. Second waterfall at Vattenfallet. Photograph Stig Lindbom, 1977.

to 6 cm thick) predominantly irregular to nodular beds of grey fine-grained limestone intercalated with irregular argillaceous beds, up to 5 cm thick (Fig. 11). Many limestone beds show evidence of intensive bioturbation. In the upper part of Högklint *b* (c. 20.2 to 24.2 m) the bedding tends to be regular and some of the argillaceous beds are up to 10 cm thick. The top of the division is formed by a bed crowded with *Atrypa* sp. which Liljevall could follow over a distance of 10 m.

Thin section analysis shows that limestone in the lowermost 3.5 m of the division consists of a calcilutite with a low skeletal sand content (Figs. 5, 10B). Small pellets enter as an important constituent of the limestone. They are not always easy to distinguish from the micritic matrix and their relative proportion as given in the log (Fig. 5) is therefore approximate. In small sparitic patches within the calcilutite the pellets form distinct discrete particles suggesting that they were indurated grains. The predominant sediment was a pelletiferous carbonate mud intercalated with calcareous terrigenous mud. Adjacent to the dome above the probable second Upper Visby unstratified mound, a few sparitic beds (up to 11 cm thick) occur intercalated in the lowermost part of the calcilutitic portion of Högklint *b*. In these beds (studied from Liljevall's sam-

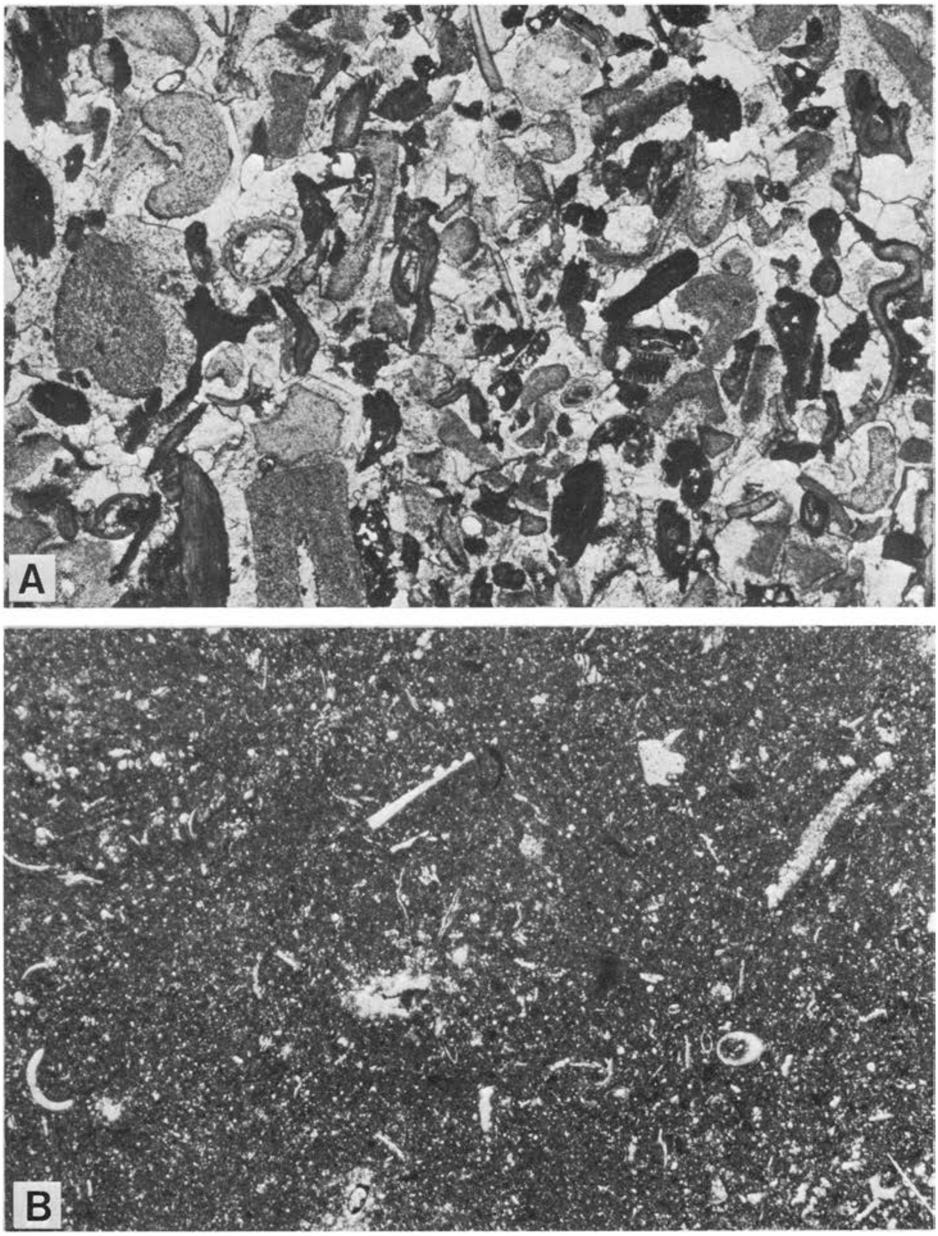

Fig. 10. A. Sparitic calcarenite, Högklint *a* at Vattenfallet, 10.7 m. The interspaces between skeletal grains are filled with sparry calcite. B. Calcilutite, lower Högklint *b* at Vattenfallet, 15.0 m. Thin sections, ×15.

Fig. 11. Stratification in the lower part of Högklint *b* at Vattenfallet, 14.5–15.0 m. Length of matchbox 5 cm. Photograph Krister Brood, 1976.

ples and not entered in the lithological log), pellets form an important constituent and the rock can be classified as sparitic pelletal calcisiltite to sparitic calcarenite. The intragranular cavities of skeletal particles are mostly filled with micrite, suggesting that some of the sediment may have been a residue formed by winnowing carbonate mud. In Liljevall's collections the calcarenitic beds are represented at 13.0–13.1 (at these levels large surfaces were available for collecting), 13.55 and 14.05 m.

In the main upper part of Högklint *b* (about 16.7 to 24.2 m) calcarenites predominate, in part micritic and in part sparitic. At several levels both types of rock have a patchy distribution within a single thin section due to uneven burrowing activities by organisms. The sand fraction is formed by skeletal particles whereas the silt fraction is dominated by pellets. Sparry calcite was originally precipitated mainly as intergranular cement. The carbonate sediment was a pelletiferous skeletal sand, in part mud-supported and in part grain-supported. Micritization phenomena are common, mainly in sparitic limestones, but micritic envelopes are quantitatively unimportant.

A bentonite bed at 17.0 m, 3 to 4 cm thick, forms an easily recognizable index horizon (Hedström 1910, Pl. 60:a). Additional bentonite layers occur at 18.05, 16.10, 15.33, 14.78 (a very thin layer), and 14.33 m (Laufeld & Jeppsson 1976). From about 15 m upwards fossils are partially silicified in places.

At the base of Högklint *b* (12.65–13.05 m) dwelling burrows or resting trails of varying size, belonging to the trace fossil *Conichnus* (Männil 1966), are not uncommon. Otherwise trace fossils are rare.

Högklint c *(24.2–29.6 m)*

Högklint *c* is formed of regularly bedded mainly light grey limestone with virtually no argillaceous intercalations. Many of the beds with a high pellet content show a lamination on polished surfaces and lack traces of bioturbation. Distinct cross-bedding was observed by Liljevall in the bed 26.45–26.55 m above sea-level. Indistinct ripple-marks occur at 27.65 m. From 26.2 m upwards, scattered, rounded, water-worn fossils of varying size occur in many beds. Much of the sequence above 28.8 m is calciruditic to conglomeratic.

Below about 28.8 m the limestone is alternatingly sparitic pelletal calcisiltite and sparitic pelletiferous calcarenite. The sand fraction is formed mostly of skeletal particles whereas the silt fraction is dominated by peloids (mostly pellets) (Fig. 12A). This rock has previously been referred to as oolitic but not a single ooid has been observed in thin sections or peels. As in other sparitic limestones of the section, most of the sparry calcite was originally precipitated as intergranular cement but neomorphic assimilation of skeletal grains has also taken place. Micritization phenomena (Fig. 12B) occur in all thin sections studied. Micritic envelopes are quantitatively unimportant except at some levels where they form up to 13 per cent of the rock volume (Fig. 5). At these levels part of the sand fraction is formed by peloids of various shape and size (Fig. 12B), many possibly representing completely micritized skeletal grains. Such grains also occur rarely at other levels. In this part of the section much of the sediment was originally a grain-supported pelletal silt to grain-supported skeletal sand.

In the uppermost part of Högklint *c,* above c. 28.8 m, the grain size increases and much of the rock is a sparitic calcirudite. Many gravel grains, 2 to 5 mm long, are rounded. They are in part skeletal (*Coenites,* echinoderms, *Solenopora,* stromatoporoids, corals, etc.) and in part pieces of pelletal limestone, lithified, eroded and rounded. Algal coatings around the grains are not uncommon. The interspaces between the gravel grains are filled either by sparry calcite or pelletal silt. Much of the original sediment was a grain-supported skeletal gravel.

Högklint d ("Pterygotus" *Beds; 29.6–30.0 m)*

This subdivision, although only 40 cm thick, has received wide attention

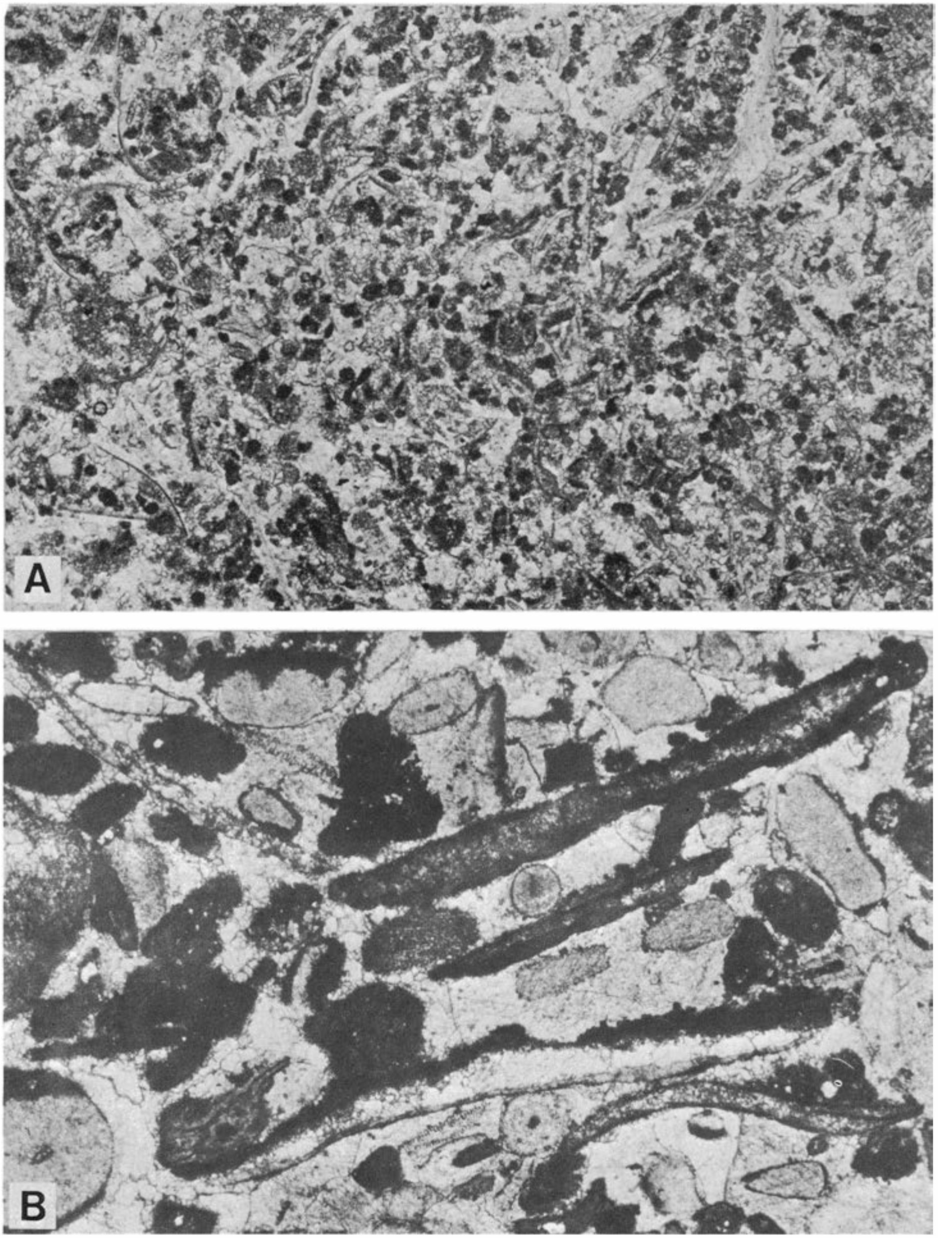

Fig. 12. A. Sparitic calcisiltite, Högklint *c* at Vattenfallet, 24.2–24.3 m. B. Sparitic calcarenite with numerous micritic envelopes, Högklint *c* at Vattenfallet, 26.45–26.55 m. Thin sections, ×15.

because of its remarkable fauna. It has commonly been called the "*Pterygotus* Beds", named after the eurypterid *Truncatiramus serricaudatus* (Kjellesvig-Waering, this volume) which was previously erroneously identified as *Pterygotus osiliensis* Schmidt (Lindström 1885; Thorell & Lindström 1885:4).

A detailed section of Högklint *d* measured in 1894, and situated at or close to Lindström's original scorpion-locality, was published by Hedström (1904; see also Hede 1940:29). A translation of Hedström's description is given below, in ascending order of the beds. The original numbers of the beds are retained, the text is somewhat abbreviated and terminology brought up to date.

8. 0.02 m. Dark grey "marlstone", wedging out laterally and replaced by grey, bituminous limestone containing beyrichiacean ostracodes.
7. 0.12–0.16 m. Grey bituminous limestone, intercalated by paper-thin layers of greyish "marlstone".
6. 0.08 m. Hard grey, dark grey to black "marlstone".
5. 0.06 m. Grey bituminous limestone with *Strophomena* (= probably *Valdaria*) and leperditiids (= *Herrmannina phaseolus catarractensis*).
4. 0.05–0.06 m. Soft, reddish, in places dark grey "marlstone", with very thin layers of limestone in the lower part.
3. 0.02–0.03 m. A thin, characteristic bed of reddish limestone or "marlstone", particularly rich in *Strophomena* sp. (= *Valdaria testudo*).
2. 0.02–0.03 m. Soft, reddish, in the lower part grey "marlstone" with very thin discontinuous layers of grey limestone. The bed is rich in scolecodonts, pieces of *Pterygotus* (= *Truncatiramus* and other eurypterids), *Eatonia* (= probably mainly *Septatrypa subaequalis*), etc. This is probably the bed in which *Palaeophonus nuncius* (Thorell and Lindström) was found. The boundary with the underlying bed of limestone (top of Högklint *c*) is uneven.

Högklint *d* thus includes several different lithologies, most of which are represented in the large collection of rock samples, labelled as "*Pterygotus*-lager" or "*Pterygotus*-märgel", excavated from the original scorpion-locality by Lindström, Liljevall, and others. The material includes three main lithologies: (1) a soft, greyish marl with abundant scolecodonts and remains of eurypterids; (2) a bed of grey limestone abounding in *Valdaria testudo;* and (3) grey limestone rich in and often crowded with *Herrmannina*. It is possible that these rock samples came from beds 2,3 and 5, rexpectively. On the other hand, there was obviously some rapid lateral variation in the lithology, and in places where some of the material was collected the sequence may not have conformed exactly to the section described by Hedström.

Bed 2 is formed of an argillaceous, fine-grained, fairly soft rock abounding in densely packed small carbonate pellets. The somewhat flattened condition of thin-walled skeletons embedded in the rock indicates that the sediment has undergone some compression, although the degree of volumetric decrease is difficult to estimate. This suggests that the lithification was late relative to the limestone beds, in which, as a rule, similar fossils retain their original convex-

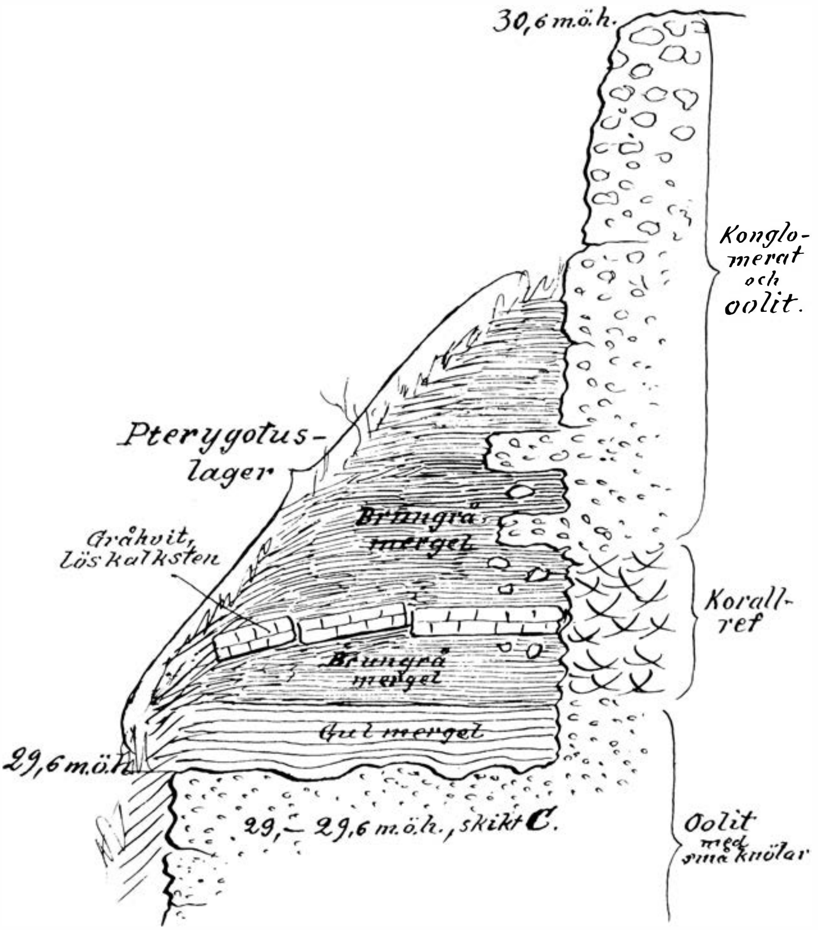

Fig. 13. Liljevall's original, "somewhat schematic" drawing of the depositional relationships between the "*Pterygotus*" Beds (Högklint *d*) and adjacent beds of mainly conglomeratic limestone. Vattenfallet, just north of the sixth bridge (see Fig. 2).

ity. In fact, the rock is still not well lithified and can be easily disaggregated. Thin sections show an indistinct fine lamination and a distinct preferential orientation of elongate skeletal grains (mostly ostracode valves) parallel to the lamination. No traces of bioturbation could be observed. The rock is difficult to classify but pelletal marl may be an appropriate term. The sediment was a kind of mud-supported pelletal silt.

For the composition of a limestone bed, see the log (Fig. 5). The rock is a sparitic pelletal calcisiltite. In places the pellets are densely packed, in other places intergranular sparry calcite is common. No lamination or preferential orientation of elongate skeletal grains can be observed. The sediment was a grain- to mud-supported pelletal silt.

The general concept of stratigraphical relationships of the "*Pterygotus*" Beds (Thorell & Lindström 1885; Hedström 1904, 1910; Hede 1940, and others) has been one in which the division conformably overlies bedded Högklint limestones and is overlain by beds now classified as the Tofta Limestone. According to Hedström (1910) the underlying beds (Högklint *c*) "become gradually coarser and at the same time nodulous and conglomerate-like towards the top". The "*Pterygotus*" Beds, in turn, are "covered by a conglomerate with water-worn gastropoda" which "reminds us in certain respects of the discordance-layer in Lindström's old quarry to the south of Gustavsvik", that is, the base of the Tofta Limestone. However, according to the description and drawings of the relevant portions of the Vattenfallet section in Liljevall's diary of 1908, the depositional relationships of the "*Pterygotus*" Beds differ essentially from those generally assumed.

Liljevall's section through the "*Pterygotus*" Beds was excavated on the slope of the eastern bank of the brook, just north of the so-called sixth bridge (Fig. 2) and about 30 m northeast of Lindström's scorpion-locality. There, remains of the "*Pterygotus*" Beds, somewhat disturbed by solifluction and transected by roots, were found resting discordantly against a natural vertical "wall" (Fig. 13) of limestone beds which were continuous downwards with, and similar to, the top of Högklint *c*. These limestone beds were overlain by a reef-like accumulation of dome-shaped corals and stromatoporoids (29.7–29.9 m), and a conglomerate with upwards-increasing pebble size (29.9–30.6 m). Some beds of the "wall" projected somewhat into the "*Pterygotus*" Beds (Fig. 13), and pebbles derived from the rock of the wall were found embedded in the "*Pterygotus*" Marl. Liljevall's conclusion was that the sediment forming the wall must be older than the "*Pterygotus*" Beds, and that it was not only lithified prior to the deposition of the "*Pterygotus*" Beds but also deeply eroded. "*Pterygotus*" Beds were then deposited in depressions on the eroded surface.

At Lindström's original scorpion-locality some remains of the "*Pterygotus*" Marl were still accessible to Liljevall on the bottom of a shallow pit which represented the last remains of the once extensive excavation. Here too, bedded limestone of the same general type as that forming the steep "wall" farther to the north was found by Liljevall to occur at the level of the "*Pterygotus*" Marl, but the contact relationships could not be observed in detail. This indicates, according to Liljevall, that at that locality the "*Pterygotus*" Marl was also deposited in a depression formed in "semi-lithified" and eroded beds of older limestone. It should also be noted that samples of the "*Pterygotus*" Marl from the scorpion-locality contain occasional pebbles of rounded stromatoporoids and corals.

Tofta Limestone?

No exposure available to Liljevall showed the contact between the "*Pterygotus*" Beds and the overlying beds. According to Hedström (1904) the "*Pterygotus*" Beds were overlain by a conglomeratic limestone which was almost brecciated in the lowermost part. He noted that the "pebbles" consisted of a finely crystalline limestone embedded in a yellowish matrix of fairly soft limestone. The stratigraphical attribution of these beds is not clear. Some samples obtained by Liljevall at Vattenfallet from beds above 30 m contain *Thecia podolica* (c. 31 m; identified by Klaamann), *Vikingia* cf. *nestori* (31.8 m; identified by Nestor), and the algae *Hedstroemia halimedoidea* and fenestral non-skeletal oncolites (31.5 m; identified by Riding).

Depositional environments

It is difficult to reconstruct depositional environment based on data from a single section, particularly within an area where topography of the nearby sea-floor was variable. Ideally, this report should have been complemented by a regional lithological study of the Upper Visby Marl and Högklint Beds at least in the immediate vicinity of Vattenfallet, but this was far beyond the scope of the project.

When interpreting depositional environments of ancient limestones, absolute depth can rarely be determined, and in general the relative depth can only be roughly reconstructed in terms of whether water during deposition at any one time was deeper or shallower than it was when underlying or overlying beds were deposited (Bathurst 1967). For interpretation of relative depth, data on the relative level of water energy may yield useful information. In a sea, water energy has some relationship to depth, in that there is an overall probability that with increasing depth water energy decreases rather than increases. However, this is true only in general terms, and even in very shallow water a wide amplitude of water energies, from very high to very low, can be represented. The factors that control water energy, such as slope of the sea-floor, exposure, current velocity, etc., are very difficult to reconstruct. Moreover, in shallow-water carbonate sediments the trapping and binding action of plants and the possible occurrence of gelatinous mats on the sediment surface may effect the grain-size distribution so that it does not reflect the real water energy level.

The presence of algae throughout the Vattenfallet section (Fig. 20) indicates that deposition took place entirely within the depth range of the photic zone. The lower, calcilutitic part of the Upper Visby Marl was deposited in a fairly constant low-energy environment, whereas during deposition of the upper part of the division the water energy fluctuated, at times reaching moderately high levels. Depth of the sea is difficult to estimate, but the presence of a probable dasycladacean alga almost down to the base of the section indicates that it was less than 100 m even in the lowermost Upper Visby Marl (Riding, this volume). That water depth decreased successively during deposition of the Upper Visby Marl has been repeatedly suggested (Hadding 1941, Manten 1962, etc.).

In the Upper Visby Marl exposed in the cliff along the beach north of Kneippbyn the orientation of 38 tabulate and heliolitid colonies was recorded in two calcarenitic and adjacent marly beds. About 75 per cent of the these colonies are in their original growth position, and 20 per cent are tilted relative to the horizontal (of which a part might be in original growth position). Two of the colonies were lying upside down, indicating that at times water energy was sufficiently high to move small coral colonies. In this context it should be remembered that the weight of a living or dead tabulate or stromatoporoid colony, prior to the voids in the skeleton becoming filled with sediment or cement, was but a fraction of its present weight. Displacement of coral colonies also indicates that skeletons of other groups may have been moved around or transported, particularly small and light shells. That this has happened is evident from the disorderly accumulations of skeletons of various macrofossils in some beds of sparitic calcarenites.

The origin of small, unstratified mounds in the upper part of the Upper Visby Marl is not yet understood. Mounds similar to that at Vattenfallet are not uncommon and a few of them, at Kneippbyn and Snäckgärdsbaden 1, were briefly examined during a postgraduate student field course in June 1967.

Some reasonably smooth surfaces, approximately normal to the depositional plane, were etched with hydrochloric acid, stained with potassium ferrous cyanide as well as blue ink, and point counted in the field. No coherent organic frame has been observed in any of the mounds. Favositids, in particular *Angopora hisingeri,* dominate among colonial organisms. Scattered favositid colonies were found to form 8 to 13 per cent of the total area of the surfaces studied, and other colonial corals (heliolitids, halysitids and rugose corals) one to three per cent. Stromatoporoids are relatively rare and mostly represented by small colonies. If the growth of the mounds was controlled by organisms, the skeletal colonial organisms must have been supplemented by soft-bodied forms that have perished without trace. On the other hand, although skeletal colonial organisms do not appear to have been the main cause of the growth of the mounds, the content of tabulate corals in the mounds is significantly higher than in the adjacent contemporaneous bedded sequence.

The "anatomy" of the Upper Visby mounds differs from that of the upper part of the Högklint reefs where the core in places abounds in colonial skeletal organisms, almost all stromatoporoids, and where a skeletal frame might have been developed. The top of some Upper Visby mounds is at the level of the lowermost Högklint *a,* but after that their growth appears to have ceased in the Visby area. No continuity between the Upper Visby mounds and the Högklint reefs has been observed in that area.

The pronouncedly sparitic calcarenites of Högklint *a* indicate a further increase in water energy. This division has a fairly uniform lithology throughout its extent in northwestern Gotland. At Vattenfallet it is relatively thin whereas elsewhere the thickness reaches up to 15 m (Hede 1940). The distribution of Högklint *a* along the outcrop area is discontinuous, which indicates that the sediment accumulated as a series of skeletal sand banks, of varying size and unknown shape. Hede (1933, 1940) has stressed that even within a short distance from the Högklint reefs the lithology of the division begins to change, in that the thickness of the individual beds decreases and the sequence becomes increasingly more argillaceous. At a greater distance from the reefs the equivalent beds are formed of a thin–bedded dense to fine-grained limestone with thin intercalations of marl. Hede (1933, 1940) also pointed out that Högklint *a* forms the base of the Högklint reefs, and surrounds the basal portion of the reefs in many cases. Only in a few instances are the Högklint reefs known to rest on the Upper Visby Marl without intervening coarse calcarenitic beds (Hede 1933; Manten 1971). In some other cases the Högklint reefs start to grow higher upp in the sequence, but then it is not always clear whether the exposed section of the reef is cut along the periphery of the reef complex or is located centrally. The close association of Högklint *a* banks with overlying reefs suggests shat the skeletal sand banks formed a suitable substratum upon which many of the reefs were founded.

Some authors (Jux 1959; Manten 1971) have emphasized the importance of supply of crinoidal remains for development of "crinoidal limestones", including those in Högklint *a*. According to them the accumulation of "crinoidal limestones" is mainly the result of luxurious growth of crinoids on flanks of the reefs. This may be true for same reef flank deposits in the strict sense, but at Vattenfallet the accumulation of skeletal sand in Högklint *a* cannot possibly have been merely supply-dependent. Quantitative data (Fig. 77) show that in Högklint *a* about half of the skeletal sand grains belong to echinoderms, which is only some ten to fifteen per cent more than in beds below and above. The relatively high content of echinoderm sand grains in these beds is more probably associated with the general tendency of increased relative frequency of echinoderm grains when the grain size increases (Jaanusson 1972, Fig. 11). This, in turn, is dependent on the natural grain-size distribution of disintegrated echinoderm particles and the hydrodynamic properties of these particles. In Högklint *a* the sand fraction also includes, on average, more articulate brachiopods than in other parts of the section (Fig. 77), and many of these show rounded contours (in echinoderm grains the degree of secondary rounding is difficult to estimate because of their commonly original rounded shape). This, the winnowed character of the grain-supported sediment, and other characteristics show that Högklint *a* was deposited in an environment with a conspicuously higher level of water energy than in beds above and below. The most distinctive features in the lithology of Högklint *a* were a product of this high energy level.

The lithological change from the Upper Visby Marl to Högklint *a* is pronounced (Figs. 5,9), indicating that relative to the rate of deposition the change in water energy level was fairly sudden. A possible explanation for the relatively sudden change is that the sea-floor came within wave-base through a further decrease in water depth. However, other explanations are also possible and without knowledge of the geometry of the banks no safe conclusions can be made.

The calcilutites of the lower part of Högklint *b* at Vattenfallet indicate a considerable drop in water energy level, resulting in the deposition of carbonate and terrigenous mud. During that time low reef-like mounds and possibly also some low Högklint *a* banks were forming in the vicinity. The decrease in water energy might have been associated with a sheltered position of the Vattenfallet area behind moundlike elevations on the sea-floor. On the other hand, the change from sparitic calcarenites of Högklint *a* to argillaceous calcilutites of Högklint *b* seems to be a wide-spread phenomenon in the outcrop area of northwestern Gotland. This suggests that the decrease of energy may have been caused by factors which controlled deposition at least on a regional scale, such as increase in water depth. Without a detailed regional survey of the lithology of the equivalent sequence throughout northwestern Gotland, meaningful conclusions are difficult.

Higher up in Högklint *b* the water energy fluctuated, reaching moderately high levels during deposition of beds which now are sparitic calcarenites. The abundance of pellets indicates deposition in an environment in which water could be warmed up and calcium carbonate (possibly aragonite) precipitated to transform soft pellets into indurated grains. The size range of the pellets (0.4 to 0.7 mm) is close to that on the Great Bahama Bank (0.3 to 0.5 mm; Purdy 1963:342). The general depositional environment was probably in relatively sheltered, warm shallow water.

During deposition of the main lower part of Högklint *c* the same general environment prevailed, except that fluctuations in water energy level appear to have been smaller than during deposition of the upper Högklint *b*, reflected among other things by the almost complete lack of deposition of terrigenous mud. Beds with current bedding and the occurrence of water-worn skeletal pebbles indicate higher maximum levels of water energy than in Högklint *b*. Beds in which the skeletal grains are intensely micritized (Fig. 12B), have almost exact counterparts in the sediment of the Great Bahama Bank, for example in Bimini lagoon (Bathurst 1966). The relative increase of the average water energy was probably associated with decrease in water depth.

In uppermost Högklint *c* the sparitic calcirudites, with water-worn pebbles and gravel, in places apparently well sorted, suggest deposition close to or at a beach, and in any case within reach of wave abrasion. Thus during the deposition of the middle and upper part of the Högklint Beds the water became successively more shallow.

Liljevall's observation show convincingly that prior to the deposition of the "*Pterygotus*" Beds (Högklint *d*) the sediments of Högklint *c* were lithified to a certain degree and fairly deeply eroded. This suggests emersion and subaerial exposure, although submarine lithification and channeling may produce somewhat similar effects. In the depressions of the eroded surface the distinctive "*Pterygotus*" Marl was deposited, a laminated, fine-grained, pelletal calcareous mud. The lack of bioturbation is probably the main reason why delicate exoskeletons of the scorpion and eurypterids were preserved. The intercalated beds of limestone were probably bioturbated to some extent and may have been deposited in somewhat more agitated water than the marl. The general depositional environment of Högklint *d* was in very shallow, warm, and tranquil water in a sheltered position.

For references see the list of references at the end of this volume.

Acritarchs

FRITZ H. CRAMER, MARÍA DEL CARMEN R. DÍEZ and GÖRAN KJELLSTRÖM

Acritarchs are a heterogeneous, unicellular microfossil group with probable phytoplanktic affinities. Research into this polyphyletic group was initiated by Alfred Eisenack, whose extensive studies were based originally on Lower Palaeozoic glacial erratics (Eisenack 1931, etc.), but subsequently included some material from Gotland (Eisenack 1954, 1959, 1974). As yet there has been no systematic study of acritarchs from the Silurian of Gotland, either taxonomically or biostratigraphically, and this contribution is thus the first attempt to determine the composition of assemblages through a substantial portion of the sequence.

From the Vattenfallet section 24 samples have been investigated, of which 14 were processed and analyzed by the Instituto de Investigaciones Palinológicas in Leòn, Spain; the remainder (15.95 m and above 20 m) were processed and analyzed at the Geological Survey of Sweden. The samples came from the standard series of rock samples (see Jaanusson, this volume); the level of the samples is indicated by a black rectangle along the rock column (Fig. 14).

Since variation in the flotation constants may alter the reproducibility of results, the essential steps are listed here.

(1) Except in the centrifugal flotation, constant temperature is not essential; however, to obtain constancy in settling rates, flotation – including breaking the centrifuge – must be carried out at 4° C (± 1° C) because, although both viscosity and density of the heavy liquid vary quite considerably in the interval 6 to 25° C, around 4 to 6 degrees they do not vary practically. The heavy liquid is aqueous zincbromide, not stabilized with acid, measured density = 2.0 at 20° C.

(2) Two flotations: the first for thirty minutes at 6500 G, distance between meniscus and bottom of tube 7.5 cm, diameter of tube 16 cm; the second in pointed, heavy duty 12 ml tubes, volume of liquid 10 ml, thirty minutes at 2500 G.

Acritarchs are abundant and preservation is good, although many specimens show the three-dimensional deformation typical for a calcareous matrix. They are colourless to light yellowish or greenish–brown. Apart from most specimens of the *Multiplicisphaeridium piriferum*-group – most of whose thickwalled, mostly cystbearing, central stages are still globular in form – almost all others forms are compressed.

Each sample was processed at least twice and counts were made with two preparations from separate processing runs. The counts thus obtained are very similar and show that neither detectable operator nor laboratory errors were introduced.

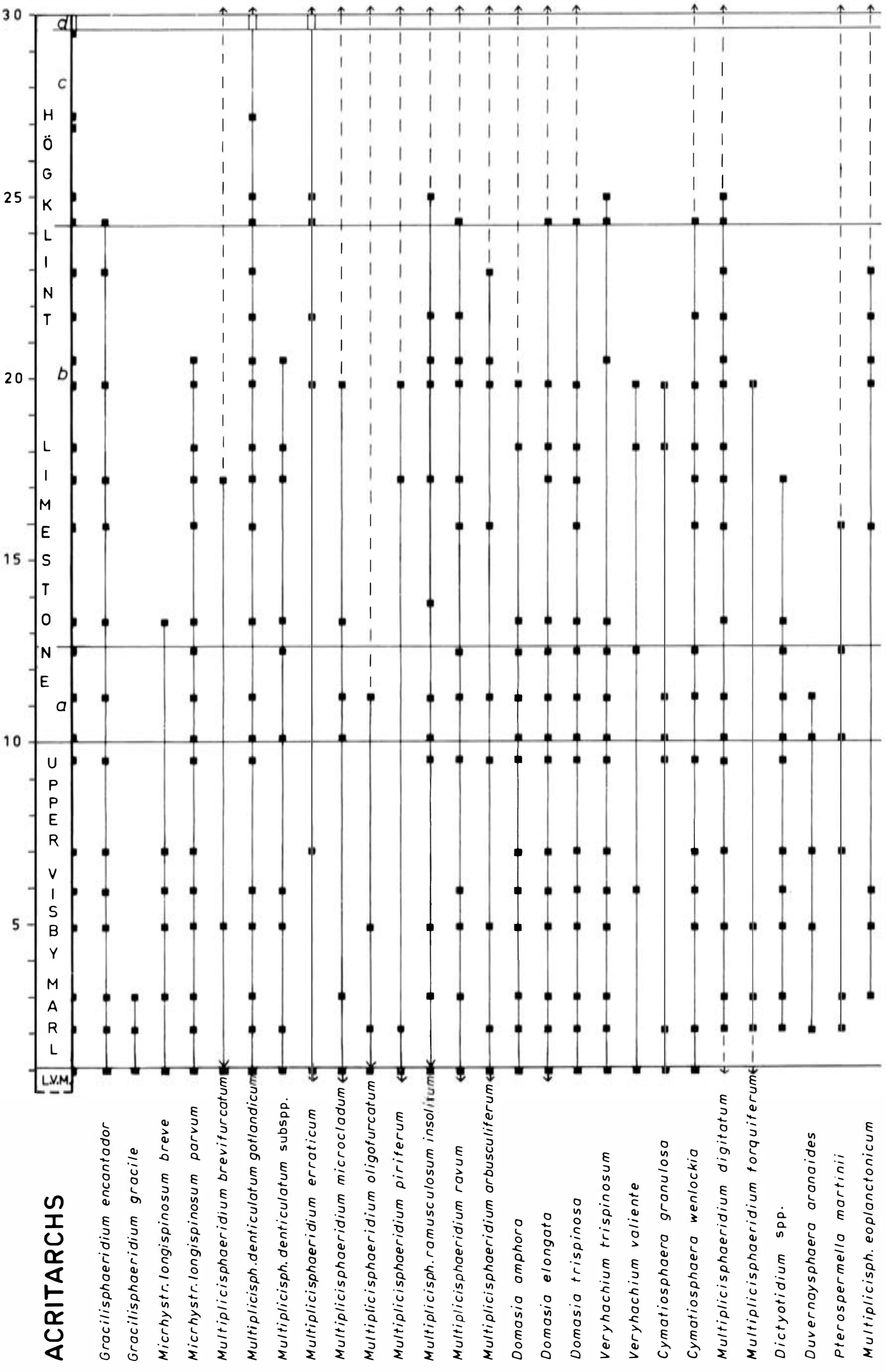
30
25
20
15
10
5
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
a
b
c
d
ACRITARCHS
Gracilisphaeridium encantador
Gracilisphaeridium gracile
Micrhystr. longispinosum breve
Micrhystr. longispinosum parvum
Multiplicisphaeridium brevifurcatum
Multiplicisph. denticulatum gotlandicum
Multiplicisph. denticulatum subspp.
Multiplicisphaeridium erraticum
Multiplicisphaeridium microcladum
Multiplicisphaeridium oligofurcatum
Multiplicisphaeridium piriferum
Multiplicisph. ramusculosum insolitum
Multiplicisphaeridium ravum
Multiplicisphaeridium arbusculiferum
Domasia amphora
Domasia elongata
Domasia trispinosa
Veryhachium trispinosum
Veryhachium valiente
Cymatiosphaera granulosa
Cymatiosphaera wenlockia
Multiplicisphaeridium digitatum
Multiplicisphaeridium forquiferum
Dictyotidium spp.
Duvernaysphaera aranaides
Pterospermella martinii
Multiplicisph. eoplanctonicum

Fig. 14.

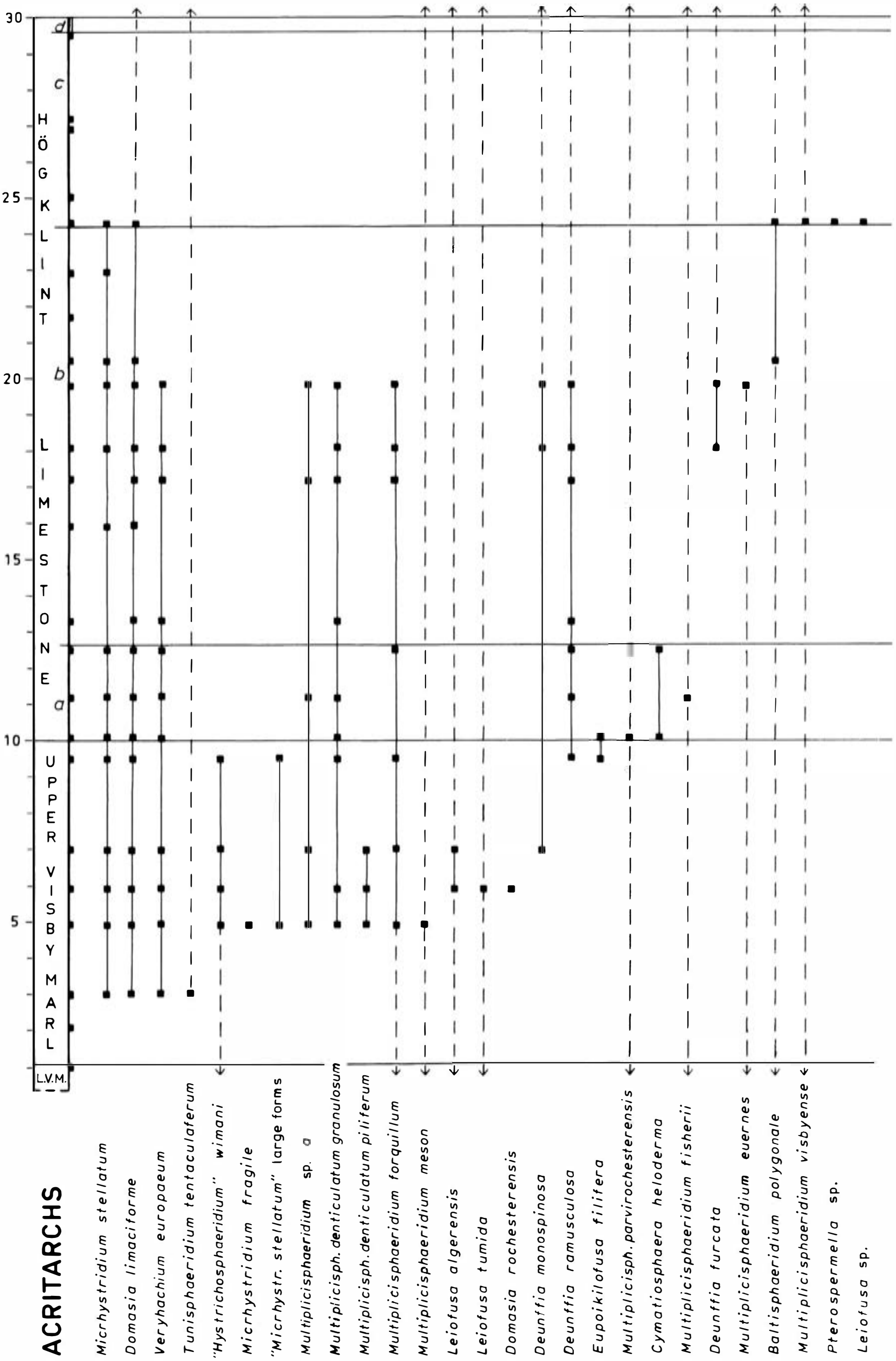
30
25
20
15
10
5
d
c
b
a
HÖGKLINT
LIMESTONE
UPPER VISBY MARL
L.V.M.
ACRITARCHS
Micrhystridium stellatum
Domasia limaciforme
Veryhachium europaeum
Tunisphaeridium tentaculaferum
"Hystrichosphaeridium" wimani
Micrhystridium fragile
"Micrhystr. stellatum" large forms
Multiplicisphaeridium sp. a
Multiplicisph. denticulatum granulosum
Multiplicisph. denticulatum piliferum
Multiplicisphaeridium forquillum
Multiplicisphaeridium meson
Leiofusa algerensis
Leiofusa tumida
Domasia rochesterensis
Deunffia monospinosa
Deunffia ramusculosa
Eupoikilofusa filifera
Multiplicisph. parvirochesterensis
Cymatiosphaera heloderma
Multiplicisphaeridium fisherii
Deunffia furcata
Multiplicisphaeridium euernes
Baltisphaeridium polygonale
Multiplicisphaeridium visbyense
Pterospermella sp.
Leiofusa sp.

Fig. 15.

Annotated floral list

Apart from the new species described in the taxonomic section of this paper, there are illustrations of all taxa in published literature. The illustrations referred to in the taxonomic discussion below are those which best identify the forms from Gotland. Acritarchs are rather variable in morphology, and different variants often display a patchy distribution pattern in their geographical and chronological provinces. Therefore, the illustrations listed hereafter are not necessarily those of the holotypes of the species.

Group Acritarcha Evitt, 1963

Subgroup Acanthomorphitae Downie, Evitt & Sarjeant, 1963

Baltisphaeridium polygonale (Eisenack, 1931) Eisenack, 1959: cf. Cramer, 1970, Pl. 23:328.

Gracilisphaeridium encantador (Cramer, 1970): Variants with long processes (Fig. 16A); variants with short processes (Fig. 16B).

G. gracile, new species (variants with spatulate to awlshaped processes): See taxonomic section.

"*Hystrichosphaeridium*" *wimani* Eisenack, 1968: See Fig. 16C.

Micrhystridium fragile Deflandre, 1947: As *M. stellatum,* but with processes shorter than the body diameter.

M. longispinosum breve (Downie, 1963) Cramer et al. (herein): This group is morphologically similar to *M. longispinosum parvum,* but is distinguished by the length and greater number of its processes (generally slightly shorter than the body diameter and most commonly fifteen or more), and the thinner, often wrinkled vesicle walls, which are generally finely scabrate (Fig. 16D).

M. longispinosum parvum (Downie, 1963) Cramer et al. n. comb. (herein): cf. Downie, 1963, Pl. 91:2 (Gotland forms generally have a more spherical body than Downie's illustration). Most commonly, the processes number eight to twelve, and are about twice as long as the body diameter. The vesicle wall is smooth to scabrate and relatively stiff.

M. stellatum Deflandre, 1945: This group comprises single-walled forms, of which the body form is determined by the number of processes. These are up to twice as long as the body diameter and are never trabeculate. There are six or more processes. – "*Micrhystridium stellatum*" (large forms), see Fig. 17A.

Multiplicisphaeridium arbusculiferum (Downie, 1963): cf. Downie 1963, Pl. 91:5.

M. brevifurcatum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:2; Eisenack et al. 1973, figure on p. 547.

"*M.*" sp. *a*: These forms are similar to but definitely not conspecific with the Ordovician species *Baltisphaeridium brevispinosum* (Eisenack, 1931)

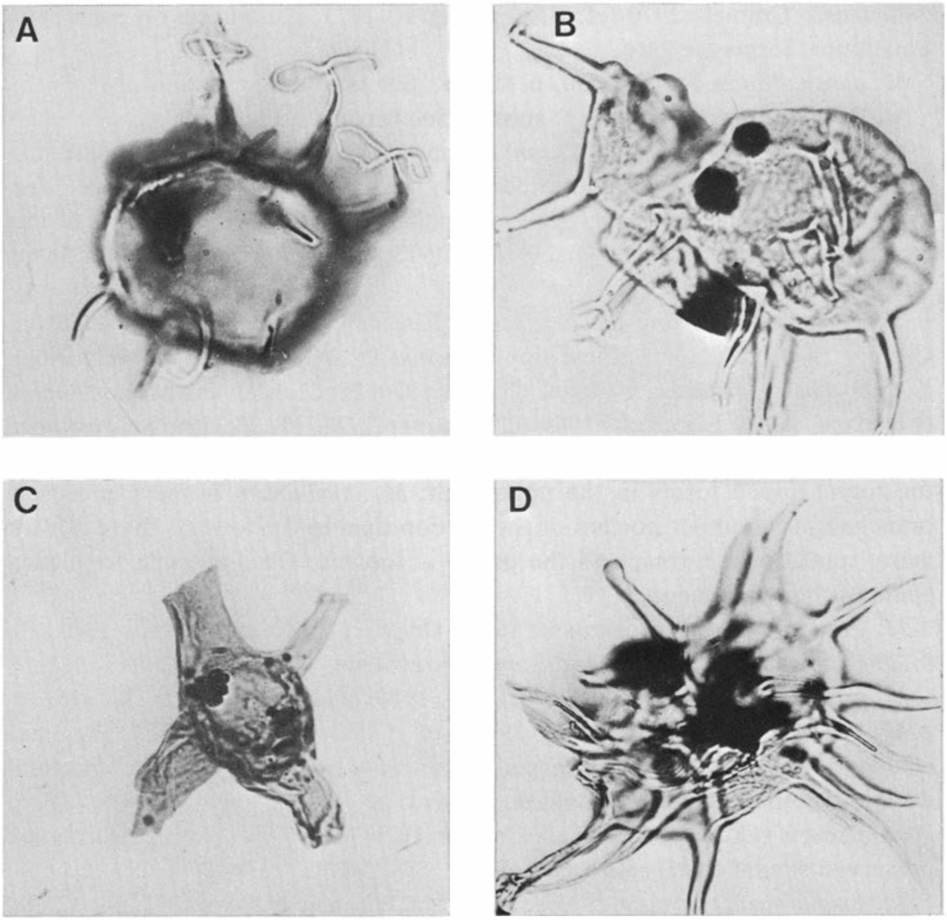

Fig. 16. A. *Gracilisphaeridium encantador* (Cramer, 1970) Eisenack et al., 1973, long forms. Vattenfallet, Lower Visby Marl, 1.1 m, grid number 760001 A03, Axiomat 85.6×24.5, ×1000. B. *Gracilisphaeridium encantador* (Cramer, 1970) Eisenack et al., 1973, short forms. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 90.8×28.1, ×1000. C. *"Hystrichosphaeridium" wimanii* Eisenack, 1968. Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760004 A02, Axiomat 92.1×31.4, ×1000. D. *Micrhystridium longispinosum breve* (Downie, 1963) Cramer et al. (herein). Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 79.8×13.6, ×1000.

Eisenack, 1958, illustrated in Eisenack et al. 1973, figure on p. 73 (for taxonomic considerations, see Kjellström 1971). For a typical form of *M.* sp. *a*, see Fig. 19A; it differs from *B. brevispinosum* in its clearly palmate and relatively shorter processes.

M. denticulatum gotlandicum Cramer, 1970: cf. Eisenack et al. 1973, illustration on page 595; this group also includes forms (about 20 % in total) of *M. d.*

ontariensis Cramer, 1970 (cf. Eisenack et al. 1973, illustration on page 599); transitional forms are rare.

M. denticulatum granulosum, n. subsp.: See taxonomic section.

M. denticulatum piliferum, n. subsp.: See taxonomic section.

Other forms of *M. denticulatum:* Forms characterized by denticulate processes, smooth to microsculptured body and a habitus similar to *M. denticulatum,* without however, being attributable to any of the variants of this group yet described (cf. Eisenack et al. 1973; *M. denticulatum* and following pages).

The group comprising *M. digitatum* (Eisenack, 1938) Eisenack, 1958 (cf. Cramer 1970, Pl. 22:320, round-tipped forms; Pl. 23:321, sharp-tipped forms), *M. cylindricum* Cramer, 1970 (cf. Cramer 1970, Pl. 21:309), and *M. corallinum* (Eisenack, 1959) Eisenack, 1969 (cf. Cramer 1970, Pl. 22:319): Sharp-tipped variants of *M. digitatum* are more abundant in the lower half of the section and the round-tipped forms in the upper half; *M. corallinum* is more profusely branched in the upper portion of the section than in the lower. There are too many transitional forms, and the group is too rare for a reliable frequency count of the components.

M. eoplanctonicum (Eisenack, 1955) Cramer, 1970: cf. Cramer 1970, Pl. 8:129 (illustrated as *Baltisphaeridium monterrosae – B. eoplanctonicum*).

M. erraticum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1955, Pl. 315.

M. euernes (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:12 (Gotland forms are entirely transparent, showing neither colour nor structural differentiation between body and processes).

M. fisherii (Cramer, 1968): cf. Cramer 1970, Pl. 7:118 (Gotland forms are preserved similar to *M. euernes*).

M. forquiferum (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:20.

M. forquillum (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:15.

M. meson (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:3 (illustrated as: *Hystrichosphaeridium intermedium*) & cf. Eisenack et al. 1973, figure on p. 681.

M. microcladum (Downie, 1963): cf. Downie 1963, Pl. 91:3.

M. parvirochesterensis (Cramer & Díez, 1972): cf. Eisenack et al. 1973, illustrations b and c on page 719 (Gotland forms are about 50 % larger than the dimensions given in Eisenack et al. 1973).

M. oligofurcatum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:4; Eisenack et al. 1973, figure on p. 703.

Complex of *M. piriferum* (Eisenack, 1954) Cramer, 1970: The most common variants of this complex are similar to those illustrated by Eisenack 1954, Pl. 1:1; 1965, Pl. 21:1 (these have a smooth body). In addition are found, in about 1 out of 10 specimens, forms with slender smooth processes and with a scabrate body (cf. *M. p. gotlandicum* (Cramer, 1970) in Eisenack et al. 1973, figure on p.

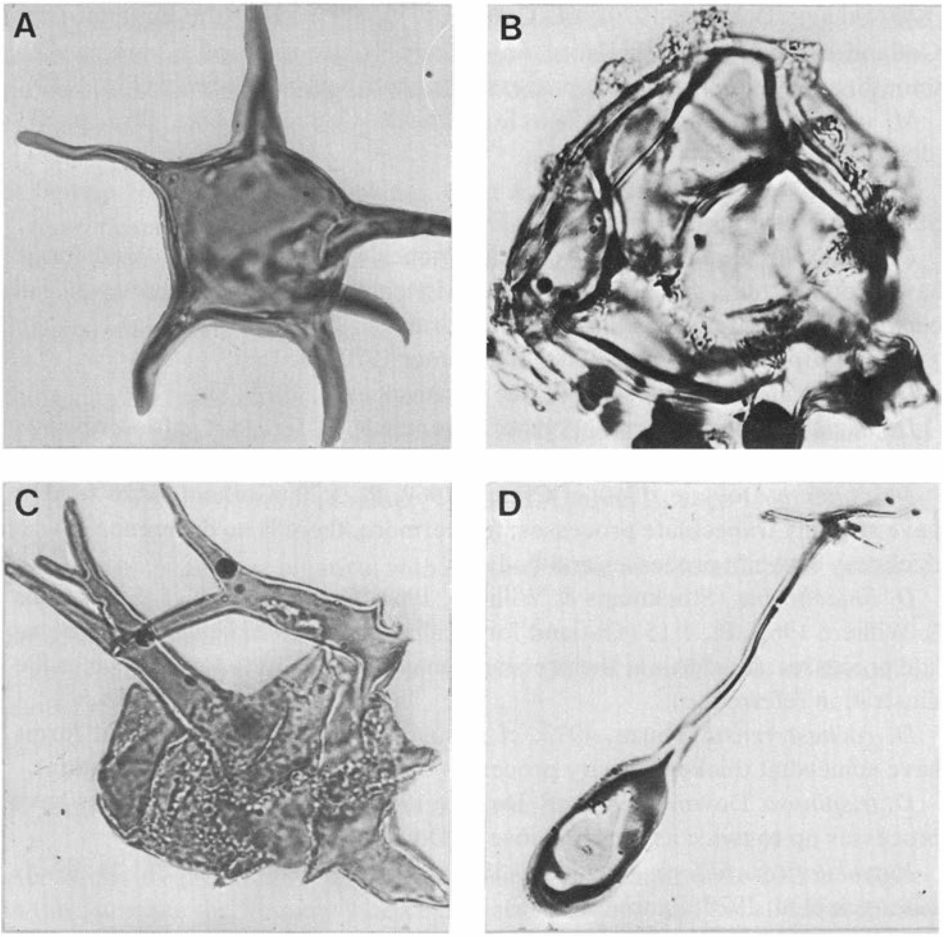

Fig. 17. A. *"Micrhystridium stellatum"* Cramer et al. (herein). Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760004 A03, Axiomat 78.5×27.9, ×1000. B. *Multiplicisphaeridium piriferum* (Eisenack, 1954) Cramer, 1970. Vattenfallet, Upper Visby Marl, 5.95 m, grid number 760005 A02, Axiomat 91.8×27.0, ×1000. C. *Multiplicisphaeridium ravum* (Downie, 1970), cf. Cramer, 1970. Vattenfallet, Upper Visby Marl, 9.5 m, grid number 760007 A01, Axiomat 102.3×26.0, ×1000. D. *Deunffia ramusculosa* Downie, 1960. Vattenfallet, Högklint *b*, 18.10 m, grid number 7600013 A02, Axiomat 83.7×21.0, ×1000.

733). In practically all specimens of either variant the processes are distributed without apparent topological preference; however, half a dozen specimens of fragments were found in which the processes appear to be distributed similar to the arrangement in *Cymatiogalea*, that is, in rows, bordering some kind of polygons, see Fig. 17B.

M. ramusculosum insolitum (Cramer & Díez, 1972): cf. Eisenack et al. 1973, figure on p. 757.

M. ravum (Downie, 1970): cf. Cramer 1970, Pl. 10:150 (the material from Gotland comprises two variants; an entirely psilate one and a variant with smooth, or essentially smooth, processes but with a granulate body (Fig. 17C).

M. visbyense (Eisenack, 1959): cf. Eisenack, Cramer & Díez 1973, p. 831 (drawing).

Subgroup Netromorphitae Downie, Evitt & Sarjeant, 1963.

Deunffia furcata Downie, 1960: cf. Cramer 1970, Pl. 1:5 (Gotland forms have process-stems that are quite variable in length; the majority, however, fall between such extremes as illustrated by Cramer 1970, Pl. 1:5 & 1:15).

D. monospinosa Downie, 1960: cf. Cramer 1970, Pl. 1:15.

D. ramusculosa Downie, 1960: See Eisenack et al. 1973 (Fig. 17D).

Domasia amphora Martin, 1969: cf. Cramer 1970, fig. 18:q, r (described as *Domasia hermosa*).

D. elongata Downie, 1960: cf Cramer 1969, Pl. 1:20 (Gotland forms tend to have strongly trabeculate processes; furthermore, there is no difference in wall thickness between processes and body).

D. limaciforme (Stockmans & Willière, 1963) Cramer, 1970: cf. Stockmans & Willière 1963, Pl. 1:15 (Gotland forms almost always have clearly trabeculate processes; in addition, the processes may be up to 50 % longer than in the illustration referred to).

D. rochesterensis Thusu, 1973: cf. Thusu 1973, Pl. 104:2 (Gotland forms have somewhat thicker primary processes than those in Thusu's illustration).

D. trispinosa Downie, 1960: cf. Downie 1960, Pl. 1:17 (Gotland forms have processes up to twice as long as those in Downie's illustration).

Eupoikilofusa filifera (Downie, 1959): cf. Downie 1959, Pl. 11:6; cf. Eisenack et al. 1970, figure on p. 361.

Leiofusa algerensis Cramer, 1970, Pl. 11:5.

L. sp. *a*: A species that does not belong to either of the above *Leiofusa* species, but cannot be identified more closely.

L. tumida Downie, 1959: cf. Downie 1959, Pl. 11:5.

Subgroup Polygonomorphitae Downie, Evitt & Sarjeant, 1963.

Veryhachium europaeum Stockmans & Willière, 1960: This group comprises single-walled forms with a tetragonal body and a process at each corner. The processes are about as long as the short edge of the body. The ectoderm is entirely sculptureless and the processes are never trabeculate.

V. trispinosum (Eisenack, 1938) Deunff, 1954: This morphological group comprises smooth forms with a convex, straight or concavely triangular body, and with processes of a length that varies from approximately 50 to 200 % of that of a body edge. In contrast to *Domasia* spp., the processes are never trabeculate.

Veryhachium valiente Cramer, 1964: This group comprises single-walled forms with a square to rectangular body and with a process at each corner. The processes are about as long as the short edge of the body. The ectoderm is entirely sculptureless and the processes are never trabeculate.

Subgroup Herkomorphitae Downie, Evitt & Sarjeant, 1963.
Cymatiosphaera granulosa, n. sp.: See taxonomic section.
C. heloderma Cramer & Díez, 1972: cf. Cramer & Díez 1972, Pl. 32:22.
C. wenlockia Downie, 1959: cf. Downie 1959, Pl. 11:4.
Dictyotidium spp.: See Fig. 18A.

Subgroup Pteromorphitae Downie, Evitt & Sarjeant, 1963.
Duvernaysphaera aranaides (Cramer, 1964) Cramer, 1970 b: cf. Eisenack et al. 1976, figure on p. 239.
Pterospermella martinii (Cramer, 1967): cf. Cramer & Díez 1968, Pl. 21:82–87.
P. sp.: A species not identical with *P. martinii* but not identifiable at present.

Subgroup Uncertain
Tunisphaeridium tentaculaferum (Martin, 1966) Cramer, 1970: cf. Deunff & Evitt 1968, Pl. 1:1–12.

Remarks on frequency of the acritarchs

Acritarchs are present in great abundance in every sample up to 20.5 m. Higher in the sequence the frequency decreases considerably, and the slides prepared from the uppermost samples contain only a few specimens (27.0–27.1 m and Högklint *d*) or are barren (26.8–26.9 m). The decrease in frequency is also reflected in taxonomic diversity, which is high in the main lower part of the section but low in the upper part of Högklint *b* and in Högklint *c*.

Some common species (forming at least 10 per cent of the acritarchs in several samples) show proportionally small fluctuations in frequency throughout most of the section (*Domasia elongata, Micrhystridium longispinum parvum* and *Multiplicisphaeridium denticulatum gotlandicum*) whereas the relative frequency of some other common species (*Domnasia trispinosa, Veryhachium trispinosum*) fluctuates greatly from sample to sample. Short forms of *Gracilisphaeridium encantador* (up to 42 per cent) and *Multiplicisphaeridium ramusculosum* (up to 11 per cent) show high frequencies in the lower, calcilutitic part of the Upper Visby Marl and *Domasia limaciformes* (up to 26 per cent) together with *Veryhachium europaeum* (up to 19 per cent) in the Högklint Limestone. In Högklint *b Multiplicisphaeridium corallinum* (up to 16 per cent) and the round-tipped forms of *M. digitatum* (up to 17 per cent) are abundant in some beds. No other species forms 10 per cent or more of acritarchs in any sample.

Description of selected taxa

Gracilisphaeridium encantador (Cramer, 1970) Eisenack et al., 1973

Fig. 16A–B

1970 *Baltisphaeridium encantador* – Cramer, pp. 189–190, Pl. 19:296–299, fig. 61.
1972 *Baltisphaeridium encantador* – Cramer & Díez, p. 147.
1973 *Gracilisphaeridium encantador* – Eisenack et al., pp. 513–514, Pl. 4:A–C.

Discussion. – This species shows two morphological maxima within an array of transitional forms. We have called these: "*G. encantador*, long forms" (Fig. 16A), and "*G. encantador*, short forms" (Fig. 16B). As long forms we have classed all specimens whose process length exceeds the body diameter. These have, in general, long, well developed loops, three or four per process. Furthermore, the number of processes is lower than in the short forms. The short forms have processes of a length equal to, or shorter than, the body diameter. The loops are quite small. (It appears logical to us that the unlooped specimens – that is, specimens whose processes show an even number, six or eight, of short simple palmate pinnae – represent forms of which the loops are broken). In fact, all kinds of combinations of loops and palmate pinnae may occur on the same specimen. Both long and short forms always have a sculptured body. This feature distinguishes fragments of *G. encantador* from *Micrhystridium longispinosum breve* (Fig. 16D).

Distribution. – In addition to Vattenfallet, long forms of *G. encantador* are known from the very latest Llandoverian Alger Shale and equivalents of Ohio and Kentucky (Cramer & Díez 1972); from the early Wenlockian Rochester Shale of Ontario and New York; from the Wenlockian portion of the Ekwan Formation (both in outcrop and subsurface material) around the southern part of the Hudson Bay, Canada.

Gracilisphaeridium gracile n. sp.

Fig. 18B

Holotype. – Specimen figured as Fig. 18B, Vattenfallet, Upper Visby Marl, 2.1 m.

Diagnosis. – Central portion of vesicle spherical, clearly differentiated from the processes. Process distribution regular and without apparent topological preference. Approximately fifteen heteromorphic processes visible in optical section. The morphology of the processes is rather variable: some have three or four loops (as in *G. encantador*), some have an even or uneven number of slender, whiplike palmate pinnae (the uneven number suggests that these pinnae are not – or not all – fragments of damaged loops), and some of the processes have one single long whiplike pinna. The latter processes are awl-shaped, invertedly club-shaped, or have an elongated, inverted bulbous form. The final whiplike pinna is situated on the extreme tip of these processes.

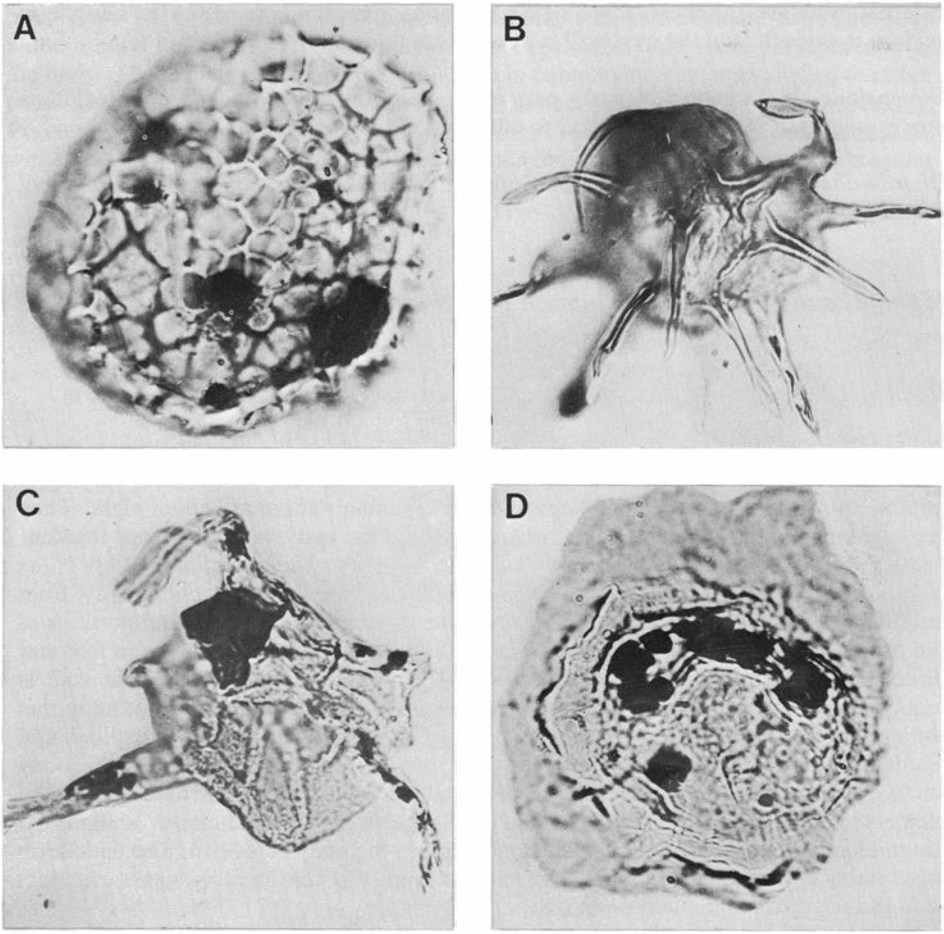

Fig. 18. A. *Dictyotidium* sp. Vattenfallet, Upper Visby Marl, 21.0 m, grid number 760002 A03, Axiomat 89.1×24,8 ×1000. B. *Gracilisphaeridium gracile* n. sp., holotype. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 84.5×26.5, ×1000. C. *Multiplicisphaeridium denticulatum granulosum* n. subsp., holotype. Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760004 A02, Axiomat 89.7×31.3, ×1000. D. *Cymatiosphaera granulosa* n. sp., holotype. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 88.6×18.1, ×1000.

The processes which bear loops and whiplike pinnae, or which bear solely whiplike pinnae, are normally slenderly columnar, but some are awl-shaped, or even bulbous. The process stems are hollow, and the process cavities are in free and direct communication with the central vesicle cavity, or – in forms which bear a cyst – may be separated from the vesicle cavity by the continuation of the endoderm, but apparently without a union structure. In forms without a cyst, the vesicle wall is unilayered and of uniform thickness (about 0.5 μm). The sculpture distribution on the ectoderm surface is subregular: the processes are psilate, but the body portion of the vesicle is ornamented by a variable sculpture of elements ranging from microscabrate to scabrate. (The sculpture is identical to that of *G. encantador* illustrated in Eisenack et al. 1973: Pl. 4.)

Internal cysts are spherical, more rigid and darker than the ectoderm. The endoderm surface is smooth, and the cyst wall is about 1 µm thick.

Dimensions. – Diameter of body part of vesicle, up to 40 µm; diameter including processes, up to 75 µm (generally 50 to 60 µm).

Distribution. – Early Wenlockian of Gotland; Wenlock portion of Ekwan Formation, Hudson Bay area, Canada.

Multiplicisphaeridium denticulatum granulosum n. subsp.

Fig. 18C

Holotype. – Specimen figured as Fig. 18C, Vattenfallet, Upper Visby Marl, 3.0 m.

Diagnosis. – Central portion of the vesicle spherical, rigid, clearly differentiated from the processes. Processes essentially homogeneous and regularly distributed, varying in number from three to more than twenty; most commonly there are about eight. They are long, slender, and quite flexible, originating from the body without a basal thickening or expansion, and standing perpendicular to the body. The branching pattern is, as in all variants of *M. denticulatum,* simply manate, but varies in complexity from unbranched to slightly branched. All pinnae are concentrated at the distal portions of the processes. Processes and large pinnae are hollow and their cavities are in free and direct communication with the body cavity. In simple stages, the vesicle wall is unilayered, and the ectoderm surface shows a subregular sculpture distribution in that the processes are psilate or bear a sparse cover of widely spaced microdenticules of similar denticulate elements whose elevation does not exceed 0.3 µm, but the body surface is covered by a dense pattern of roundedly granulate to verrucate sculptural elements. (These elements are not of the denticulate kind.) The ectoderm is about 0.5 µm thick. Cysts are spherical, closely concentric to the body ectoderm. The endoderm has a smooth surface, and its thickness is about 1 µm. It is considerably less transparent than the ectoderm and much more rigid.

Dimensions. – Overall diameter approximately 120 µm.

Distribution. – Early Wenlockian of Gotland; Wenlockian portion of Ekwan Formation, Hudson Bay area, Canada.

Comparison. – The granulate to verrucate sculpture on the body of *M. d. granulosum* distinguishes it from other variants of *M. denticulatum.*

Multiplicisphaeridium denticulatum piliferum, n. subsp.

Fig. 19B

Holotype. – Specimen figured as Fig. 19B, Vattenfallet, Upper Visby Marl, 3.0 m.

Diagnosis. – Central portion of the vesicle spherical, rigid, clearly differentiated from the processes. Processes homomorphic and distributed regularly. There are about ten processes. They are quite long, slender, and fairly stiff and originate from the body without basal thickenings, union structures, or expansions, and stand perpendicular to the body. The manate branching pattern varies in complexity from unbranched to rather profusely branched. Pinnae are concentrated at the distal portion of the processes. Processes and pinnae are hollow and their cavities are in free and direct communication with the body cavity. The vesicle wall is unilayered, and shows a quite subregular

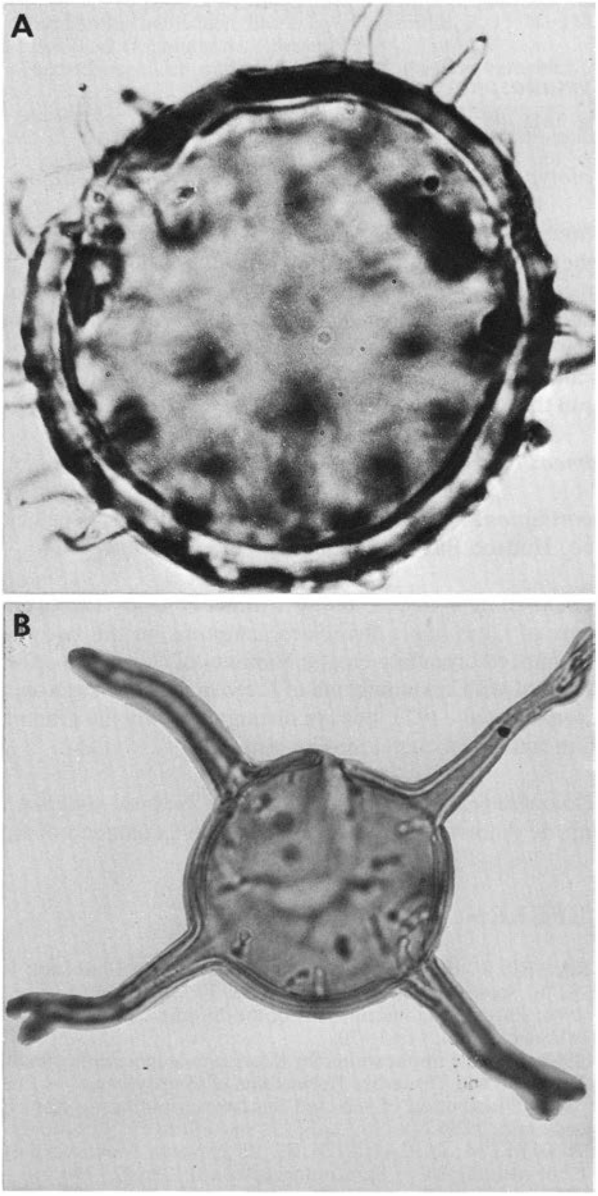

Fig. 19. A. *"Multiplicisphaeridium"* sp. *a*. Vattenfallet, Upper Visby Marl, 9.5 m, grid number 760007 A01, Axiomat 93.3×26.0, ×2000. B. *Multiplicisphaeridium denticulatum piliferum* n. subsp., holotype. Vattenfallet, Upper Visby Marl, 4,9 m, grid number 760004 A03, Axiomat 77.1×24.6, ×1000.

sculpture distribution in that the body wall is psilate to microscabrate (elements less than 0.3 µm in height and width). The processes are smooth. A second sculpture is distributed over the body, consisting of widely spaced elements of the baculate to gemmate kind. These elements seem to be solid and are up to 4 µm high, but usually smaller (about 2 µm). No endoderms, cysts or excystment structures identified.

Dimensions. – Overall diameter approximately 120 µm.

Distribution. – Early Wenlockian of Gotland.

Cymatiosphaera granulosa n. sp.

Fig. 18D

Holotype. – Specimen figured as Fig. 18D, Vattenfallet, Upper Visby Marl, 2.1 m.

Diagnosis. – Central body variable in form: spherical to polygonal, but most commonly spherical. The campi are of variable dimensions and outline, but tend to be subsquare to irregularly pentagonal. The surface of the campi is regularly and densely granulate to (micro)verrucate, thus creating a sunken reticulum. The depressions have a depth of about 1 µm. The muri are normally straight-based and show smooth to slightly crenulate to almenate crests. They are smooth and show no primary folds. The body wall is about 2 µm thick; the muri are less than 0.3 µm thick.

Dimensions. – Body diameter 40 to 60 µm.

Distribution. – Early Wenlockian of Gotland; Wenlockian portion of Ekwan Formation, Hudson Bay area, Canada.

Comparison. – *C. heloderma* Cramer & Díez, 1972 from the latest Llandoverian Alger Shale of Ohio has a foveolate sculpture on the body and often has membranes with pronounced crenulate crests; Variants of *C. granulosa* with a total of two campi may be confused with certain forms of *Pterospermella,* such as, e.g. *P. martinii* (Cramer, 1967) Eisenack et al., 1973, but are distinguished by the granulate body sculpture and absence of an equatorial cingulum-like structure.

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Calcareous algae

ROBERT RIDING

Calcareous algae can be recognised in the field in Gotland as porcelaneous white nodules and masses of *Solenopora* and as laminated balls which have been termed *Sphaerocodium* and *Spongiostroma*. *Solenopora* is usually found in the reefal sediments but the balls form distinctive horizons in several parts of the sequence, notably the Tofta Beds and Eke Beds, and have commonly been mentioned in the descriptions and correlation of various stratigraphic units. Only Rothpletz (1908, 1913) has made a comprehensive study of the systematics of these fossils but several subsequent workers (Hadding 1941, 1950, 1959, and others) have emphasized the sedimentological importance of calcareous algae in both reef and shallow-water, probably restricted, environments throughout the sequence. But many questions remain, especially concerning the volumetric importance and roles of algae in reefal deposits and their systematics.

The material examined comprises 39 thin sections, 102 peels and some 50 hand specimens collected by Liljevall. It includes also thin sections from Vattenfallet of syntype and other material decribed by Rothpletz (1913). The information in the log (Fig. 20) on most algae is based on thin sections and peels made from the standard series of rock samples (the level of these samples is shown by black rectangles along the left column). The data on large algae, such as *Solenopora*, are mostly based on Liljevall's collection.

Annotated floral list

Solenopora gotlandica Rothpletz, S. *compacta* Billings

The diagnosis of *Solenopora* relies primarily upon the poor or irregular development of "tabula-like" cross-partitions in the vertical tubes in order to distinguish it from *Pseudochaetes* and *Parachaetes*. Definition of species has mainly been made on the basis of the dimensions of the resulting "cells". The cross–sectional shape of the tubes has also been used to define species. But all these features: cross-partitions, cell–size, cross–sectional shape, can vary considerably within a single specimen (see also Johnson & Konishi 1959:30). Possibly because of this, numerous species have been erected with characters which overlap, particularly in cell dimensions (see Johnson 1960, table 1). Consequently, the Solenoporaceae require thorough revision. For convenience here, and to prevent further confusion, I have followed Rothpletz and

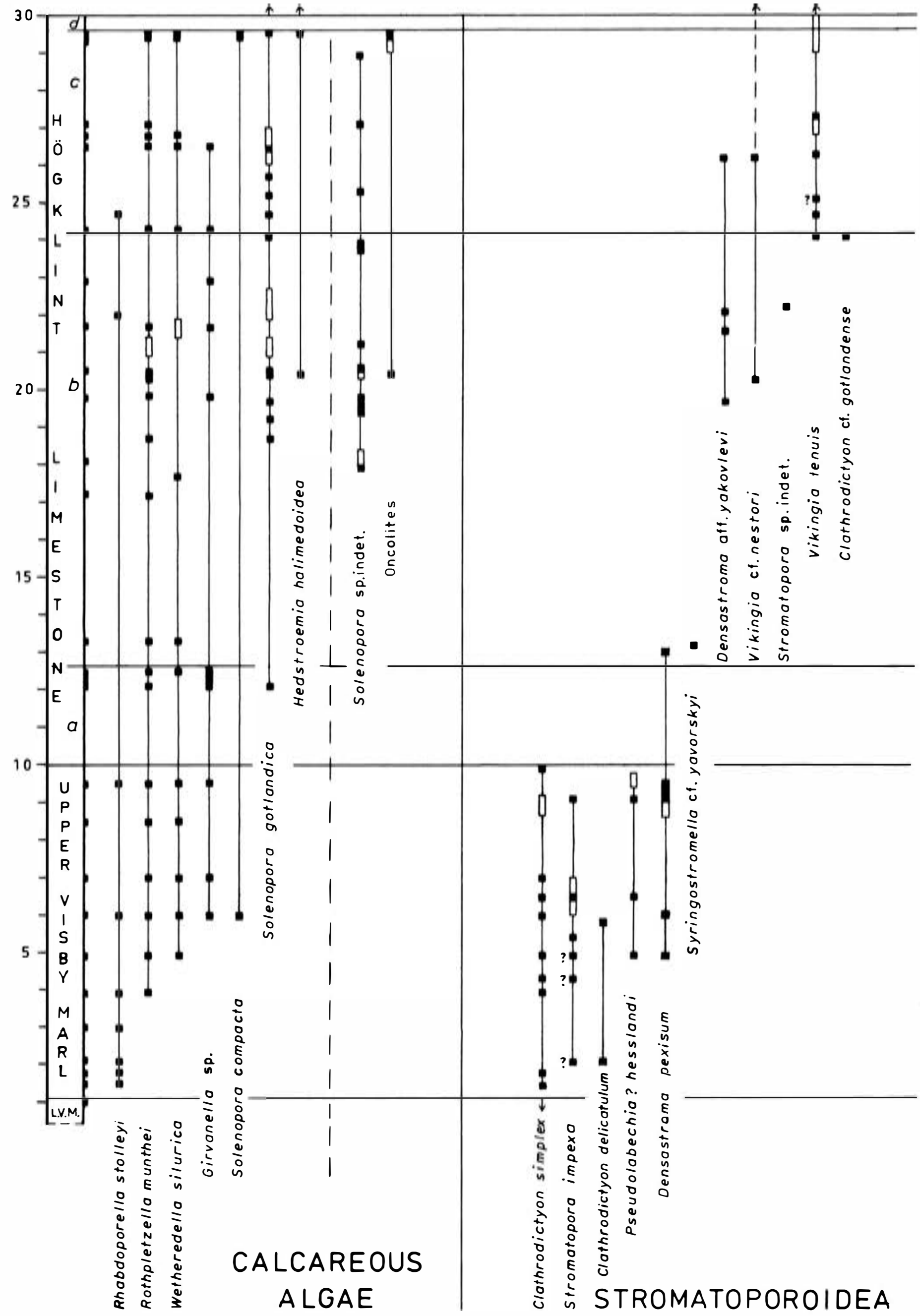
30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
Rhabdoporella stolleyi
Rothpletzella munthei
Wetheredella silurica
Girvanella sp.
Solenopora compacta
Solenopora gotlandica
Hedstroemia halimedoidea
Solenopora sp.indet.
Oncolites
CALCAREOUS ALGAE
Clathrodictyon simplex
Stromatopora impexa
Clathrodictyon delicatulum
Pseudolabechia ? hesslandi
Densastroma pexisum
Syringostromella cf. yavorskyi
Densastroma aff. yakovlevi
Vikingia cf. nestori
Stromatopora sp. indet.
Vikingia tenuis
Clathrodictyon cf. gotlandense
STROMATOPOROIDEA
?
?
?
?

Fig. 20.

have distinguished *S. gotlandica* and *S. compacta*. But it is important to note that Johnson & Konishi (1959:33) placed both these species in *Parachaetes* and also that Sinclair (1956) suggested that *S. compacta* is a stromatoporoid. Nevertheless, the *S. compacta* described from Vattenfallet is not a stromatoporoid and both species can reasonably be retained in *Solenopora* for the present. *S. gotlandica* is readily distinguished in thin section by its very fine "cells" with diameters of approx. 25–30 µm. *S. compacta* has distinctly larger "cells" with diameters of approx. 80–120 µm. Nearly half the specimens of *Solenopora* are so affected by recrystallization that the species is indeterminate. There is some scope for confusion between the coarser species of *Solenopora,* such as *S. compacta,* and *Hedstroemia* (see below), and it is possible that Rothpletz (1913, Pl.2:6) mistakenly referred *S. compacta* to *H. bifilosa*. *Pseudostylodictyon simplex* Mori, 1969, is not a stromatoporoid (Heldur Nestor and Kei Mori, personal communications) and specimens close to the holotype belong to *S. gotlandica*.

Girvanella sp.

This is a very small sinuous tube. Sometimes it forms nodules but without microscopic examination the presence of *Girvanella* cannot be confirmed. There are numerous species of *Girvanella* (see Fournie 1967) primarily characterised by the tube diameter. As in the case of *Solenopora* species the degree of overlap is considerable and confident application of species names is not possible without extensive revision. No specific names have yet, so far as I know, been applied to *Girvanella* from Gotland and I prefer here to leave the species open. The range of the diameter of the tube is 13–20 µm and this is within, although slightly below the average for, the range of variation shown by *G. problematica,* the type species, at the type locality (Wood 1957, text–fig. 1a).

Rothpletzella munthei (Rothpletz)

Rothpletz's error in recognizing *Sphaerocodium* in Gotland was corrected by Wood (1948) who referred Rothpletz's species *S. gotlandicum* and *S. munthei* to a new genus *Rothpletzella*. Wood also distinguished another new genus, *Wetheredella,* in the material which Rothpletz had previously referred to as *Sphaerocodium*. Wood's revision of *Sphaerocodium* was justified but he perhaps did not make it sufficiently clear that the type material of *Sphaerocodium* from the Alps is quite different from the Gotland material described by Rothpletz. Because of this Wray (1967:37) mistakenly assumed that Wood had simply split the genus *Sphaerocodium* and that this name had to be conserved for part of the material from Gotland. Consequently, Wray (1967) emended Wood's revision and replaced *Rothpletzella* by *Sphaerocodium*. But this is not warranted and *Rothpletzella* is valid. Hadding

(1941) used the name *Pilotrix* for laminar or encrusting growths of "*Sphaerocodium*" and *Girvanella* in the Gotland reefs. Consequently, it is possible that *Pilotrix* is a senior synonym of *Rothpletzella* or *Wetheredella*. *Rothpletzella* from Vattenfallet mainly ranges in external tube diameter from 15–25 µm and corresponds approximately to the dimensions of *R. munthei* (20–25 µm) as revised by Wood (1948:19). These are small specimens when compared with the other Gotland species, *R. gotlandicum* (30–35 µm), and Devonian species described by Wray (1967:37–40) are even larger.

Wetheredella silurica Wood
W. silurica has tubes of approx. 100 µm external diameter (Wood 1948:20). Specimens from Vattenfallet are in the range 40–120 µm. Copper (1976:277) has erected *W. tumulus,* on the basis of Ordovician material, which has diameters in the range of 30–140 µm. The validity of this species is questionable and I regard it as a junior synonym of W. *silurica* (Riding 1977d).

Hedstroemia halimedoidea Rothpletz
It can be difficult to separate *Hedstroemia* from some of the larger *Solenopora* species, especially *S. spongioides* (see above, *Solenopora*), and its species are not very well defined. Specimens from Vattenfallet appear to be referable to *H. halimedoidea*.

Rhabdoporella stolleyi Rothpletz
Rothpletz's species *R. pachyderma* and *R. stolleyi* are distinguished mainly by the thickness of the wall. Only the thin-walled form, *R. stolleyi,* has been observed in the Vattenfallet material. The tubes are 60–100 µm in diameter.

Oncolites
Fenestral non-skeletal oncolites, which in the past have been referred to as *Spongiostroma,* occur at Vattenfallet. Rothpletz (1913:36–37) noted *S. holmi* from the Vattenfallet section above 29 m. I prefer not to use Linnean nomenclature for these structures.

Affinity

The systematic position of many Palaeozoic fossils commonly regarded as calcareous algae is uncertain. This is especially true in the Silurian. Only a few of the taxa mentioned here can confidently be regarded as algae, but they cannot, without controversy, be placed in other groups at present. Since they have traditionally been included together it is convenient to consider them here as a group, but their probable heterogeneity places constraints on their environmental significance. Care should be exercised in using these fossils to interpret the Vattenfallet sequence.

General problems regarding the nature of *Solenopora* and *Girvanella* are discussed elsewhere (Riding 1977c). *Solenopora* shows morphological similarities to some bryozoans and tabulate corals. In the past it has also been regarded as a hydrozoan. But because of its resemblance to crustose Corallinaceae it has usually been regarded as a related red alga. The essential problem of its affinity is that it appears to lack positive criteria for placing it in one group rather than another. *Girvanella* represents the calcified sheaths of filamentous cyanophytes (Riding 1977a).

Hedstroemia and *Rothpletzella* consist of densely packed branching tubes. Those of *Hedstroemia* are erect and radiating, with diameters of 50–180 µm. The tubes of *Rothpletzella* are smaller (20–40 µm in Gotland species) and prostrate. Both genera have been placed in the Porostromata by Pia (1927:38–39, *Rothpletzella* being called *Sphaerocodium*) and both cyanophyte and green algal affinities have been proposed for them (Rothpletz 1913:16–17; Wood 1948:18).

Wood (1948:20) regarded *Wetheredella* as a foraminifer, but Loeblich & Tappan (1964:C787) and Copper (1976) suggest that it is an alga. I incline toward Wood's opinion but diagnostic criteria to clarify the nature of *Wetheredella* have still to be obtained. *Rhabdoporella* is regarded as a dasycladacean (Rothpletz 1913:27; Pia 1927:62), a view which is consistent with its porebearing tubiform skeleton.

Stratigraphical remarks

Rothpletzella, Girvanella and *Wetheredella* range throughout the section and *Rothpletzella* and *Wetheredella* commonly show close mutual association. *Solenopora* is markedly more abundant in the upper half of the section above 18 m. *Rhabdoporella* is commonest near the base, below 4 m. *Hedstroemia* and oncolites ("*Spongiostroma*") are virtually restricted to the uppermost part of the section, above 29 m, where they are closely associated.

Rhabdoporella occurs as very small tubular segments or fragments, approximately 0.5 mm long, in fine grained calcilutites. *Rothpletzella, Girvanella* and *Wetheredella* occur as small (up to 3 mm across, but often much less) flat or irregular aggregates in calcarenites. Sometimes they are attached to bioclasts but commonly they are loose and either represent crusts broken from a firm substrate, or original discrete masses. *Solenopora, Hedstroemia* and oncolites occur as nodules up to several centimetres across in coarse grainstones. Those of *Hedstroemia* are the smallest, being round or ovoid masses 1–2 mm across. The oncolites are smooth round, ovoid or bean-shaped bodies 2–10 mm in size.

Solenopora nodules are normally very smooth and round, and range from 0.4–3.3 cm in size mostly being between 1–3 cm. Very occasionally irregularly branched or abraded specimens occur.

Discussion

The two principal modes of occurrence of macroscopic fossils generally regarded as "calcareous algae" on Gotland are both seen in the Vattenfallet section. *Solenopora* nodules are common between 18-30 m and "algal balls" are common above 29 m. However, these balls are "*Spongiostroma*" non-skeletal oncolites, and the "*Sphaerocodium*" skeletal oncolites (for definition of this term see Riding 1977b) constructed by *Rothpletzella* and *Wetheredella* are not seen. The relative environmental significance of skeletal and nonskeletal oncolites and stromatolites has yet to be determined.

The distribution of these macroscopic fossils, together with smaller genera, allows three assemblages to be distinguished within the section:

(1) a lower *Rhabdoporella* assemblage below 4 m,

(2) a middle *Solenopora, Rothpletzella, Girvanella, Wetheredella* assemblage between 4–29 m, and

(3) an upper *Hedstroemia,* non-skeletal oncolite assemblage above 29 m.

Rhabdoporella is a small delicate fossil. It probably lived in relatively quiet-water subtidal environments. Assemblage 2 probably reflects a more agitated shallow subtidal environment with free-living *Solenopora* forming rhodolite-like nodules in a lime sand substrate and with the *Rothpletzella, Girvanella, Wetheredella* crusts perhaps being derived from abrasion of adjacent reef surfaces. Assemblage 3 is a pebbly deposit of rolled calcified and uncalcified algal balls, probably indicative of very shallow subtidal conditions.

Most of these fossils are broken and transported to some degree. *Rhabdoporella* is entirely fragmented and the *Rothpletzella, Girvanella, Wetheredella* crusts are usually detached and broken. The oncolites and *Hedstroemia* bodies do not appear to have been stabilized. The *Solenopora* nodules are possibly closest to their sites of growth and many show asymmetry of their growth layers which suggests stabilization in the substrate.

The uncertain affinities of many of these taxa (see above) make it difficult to use them as specific environmental indicators and prevent any discussion of diversity levels. However, the presence of *Rhabdoporella,* a probable dasycladacean, in what is likely to be the deepest environment in the sequence, can be used to infer a maximum depth for all the environments represented. Calcareous green algae, provided they have not been transported into deeper water after death, are generally restricted to depths above 100 m in the Recent (Riding 1975). Dasycladaceae are usually considered to be commonest in much shallower water still, but it is not possible to confidently state a general maximum depth of less than 100 m at present.

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Sponges

STEFAN BENGTSON

Two kinds of calcitic spicules referrable to sponges have been found at Vattenfallet. They belong to the genera *Astraeospongium* Roemer, 1854, and *Atractosella* Hinde, 1888 (for the range in the section, see Fig. 65).

The *Astraeospongium* spicules are essentially octactines, but the axial rays are usually missing. The observed range of diameter of the spicules is 0.5–2.3 mm, but fragments of larger specimens are present. *Astraeospongium* was previously regarded by most authors as a siliceous sponge; de Laubenfels (1955) referred it to the Order Heteractinida of the Class Hyalospongea (=Hexactinellida). However, Rietschel (1968) argued that *Astraeospongium* was most probably calcareous, and this is supported by its preservation at Vattenfallet: the spicules in the Upper Visby Marl are composed of holocrystalline calcite (thin sections of specimens from a corresponding level at the nearby locality Ygne 3 show that each spicule extinguishes as a unit between crossed nicols), which agrees with the mineralogical structure of modern calcareous sponge spicules (Jones 1970). In the Högklint Beds, the spicules are mostly silicified, and the frequent replacement and overgrowth by quartz crystals indicates that the silicification is secondary; the silicified holothurian(?) sclerites co-occurring with *Astraeospongium* in Högklint *d* also support this interpretation.

The *Atractosella* spicules are strongyles (fusiform monaxons), the rare examples of branching and angularly bent forms being due to fusion between adjoining spicules. The surface is usually granulated, more rarely smooth. They are very common in the Upper Visby Marl, with scattered finds also in Högklint *a* and *b* (Fig. 65). Smooth spicules of this kind from Vattenfallet were described by Regnéll (1955:168, Pls. 3:3, 4:2) as echinoid spines. However, the conchoidal appearance of the fracture surfaces, as well as observations of thin sections under the polarizing microscope, indicate that they are composed of discrete microcrystallites oriented with their *c* axes subparallel to the axis of the spicule, whereas echinoid spines are typically composed of the normal echinoderm stereom, i.e. each spine consists of a continuous calcite lattice with a *c* axis direction parallel to the axis of the spine. The Vattenfallet spicules compare well with the spicules from the British Wenlock described by Hinde (1888) as *Atractosella siluriensis*, although the commonly granulated surface of the Gotland specimens suggests that they probably represent a new species, here referred to as *A.* n. sp. *a*.

Atractosella has not previously been recognized as a calcareous sponge; de Laubenfels (1955) referred it to the Order Epipolasida of the Class Demospongea. The Gotland material shows convincingly that the original composition of the spicules was calcitic. A description of the available material from the Lower and Upper Visby Marls and Högklint Beds, including two natural associations of spicules, is in progress.

Spicules of siliceous sponges have been found only at the level 19.24–19.29 m, from where two hexactine spicules were isolated in an etching residue. They can be referred to as Hexactinellida gen. et sp. indet.

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Stromatoporoids

HELDUR NESTOR

Until recently the stromatoporoid fauna of Gotland was poorly known, but it has now been described monographically by Mori (1969, 1970). The fauna includes numerous species that also occur in the Silurian of Estonia, where they have been monographed by Nestor (1964, 1966).

Material collected from Vattenfallet consists of 83 coenostea or fragments of coenostea (for distribution see Fig. 20).

Annotated faunal list

Clathrodictyidae
Clathrodictyon simplex (Nestor), *C. delicatulum* Nestor, *C.* cf. *gotlandense* Mori.

Actinostromatidae
Densastroma pexisum (Yavorsky), D. aff. *yakovlevi* (Riabinin), *D.* sp. indet. (29.6–30.0 m).

The coenosteum of *Densastroma* aff. *yakovlevi* consists of a very delicate skeletal network, and when the structure is somewhat recrystallized it is difficult to distinguish between this species and *D. pexisum*. Nestor (1966) and Mori (1969) have clearly included such forms in *D. pexisum*.

Pseudolabechiidae
Vikingia tenuis (Nestor), *V.* cf. *nestori* (Mori), "*Pseudolabechia*" *hesslandi* Mori.

Stromatoporidae
Stromatopora impexa Nestor, *S.* sp. indet., *Syringostromella* cf. *yavorskyi* Mori.

Stratigraphical remarks

In the Vattenfallet section stromatoporoids are most common in the upper half of the Upper Visby Marl, where their taxonomic composition agrees with that of other Upper Visby exposures on Gotland. In the section the difference in the stromatoporoid fauna between the Upper Visby Marl and the Högklint Limestone is distinct in that they have only a single species in common.

However, assessment of Mori's (1969) data suggests that elsewhere the difference is not so sharp because *Clathrodictyon simplex* also occurs in places in the Högklint beds, and "*Pseudolabechia*" *hesslandi* together with *Stromatopora impexa* has been recorded from the lowermost Högklint. On Saaremaa (Estonia), typical Upper Visby species characterize the marls of the Jaani Stage, with the particular Upper Visby assemblage of the Vattenfallet section occurring in marls immediately below the base of the Ninase beds.

At Vattenfallet no stromatoporoids have been found in Högklint *a*, and Högklint *b* has yielded relatively few specimens, mostly belonging to species that are difficult to identify and have limited stratigraphical significance. The available material is insufficient to allow any meaningful stratigraphical conclusions to be made.

The lower part of Högklint *c* is relatively rich in stromatoporoids, with *Vikingia tenuis* the dominant species. According to Mori (1969) this species is the most common form in the Upper Högklint reefs and in the Tofta Beds. He also records it from the uppermost part of the Upper Visby Marl and the lower part of the Slite Beds. Most stromatoporoid specimens from Högklint *c* of the section are either rounded pebbles or show signs of wear, and they may belong to debris washed out from contemporaneous Högklint reefs. In his diary Liljevall does not mention any reeflike accumulation of stromatoporoids at these levels in the section (Jaanusson, personal communication). *Vikingia tenuis* is also the principal reef-forming organism in the stratotype exposure of the Jaagarahu Stage on Saaremaa (Nestor 1966).

Most stromatoporoids from Högklint *d* occur as rounded pebbles embedded in the soft "*Pterygotus*" Marl. They are obviously re-deposited. However, some small, unworn coenostea of *Vikingia tenuis* also occur, indicating that this species may have lived there during deposition of the "*Pterygotus*" Marl.

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Foraminifers

SVEN LAUFELD

This account of Foraminiferida is based solely on material from the small rock samples (50 g) used for analysis of the Chitinozoa. When making such analyses I routinely make notes on abundance and sometimes diversity of all other acid-resistant fossils in a sample. Notes on foraminifers are presented here since otherwise an account of these fossils would be lacking in this publication. However, it should be appreciated that 50 g samples are too small for an elaborate study of Silurian foraminifers, and that only tests consisting partly or entirely of organic material are preserved in the sample residues since the samples were processed with hydrochloric, nitric and hydrofluoric acid. This also means that mineral grains originally cemented to and incorporated in the foraminiferal tests were dissolved by the acids. For a summary account such as this, this is no severe objection, but in an elaborate biological and ecological study thin sections should also be scrutinized, together with samples processed specifically for agglutinated material.

Despite the fact that foraminifers are very abundant in the Gotland strata, these fossils have not yet been fully monographed. As far as I am aware, Chapman was the first to report a foraminifer from the Silurian of Gotland (1895:324). The early publications on Gotland material by Chapman (1901) and Smith (1915) are badly in need of revision. Some foraminifers were reported also by Rothpletz (1913). Eisenack (1932, 1954, 1959, 1966a, b, 1967) described several foraminifers from Gotland in a series of useful publications which form the main basis of our knowledge of these fossils on the island.

Only two of the five suborders of Foraminiferida (*sensu* Loeblich and Tappan 1964) are indisputably represented on Gotland, viz. Allogromiina and Textulariina. Specimens of the former suborder have membranous or pseudochitinous tests without or with very little agglutinated material. The Textulariina contain forms with a test of agglutinated foreign matter held by various cements (Loeblich and Tappan 1964: 164, 184). Both suborders are represented at Vattenfallet.

Annotated faunal list

As this is essentially a preliminary study as a by-product of my work on Chitinozoa, the taxonomy used here is chiefly at the generic level. It is beyond the scope of this contribution to discuss the various different species names used by American and European micropalaeontologists, based either on specimens having agglutinated material preserved or on specimens of the same species in which the foreign material has been dissolved by acids. The results of the two schools are incompatible and the large number of species (and genus) names is unwarranted. I have used Loeblich and Tappan's classification (1964) but pending further studies of foraminiferal nomenclature, the genus and species names used are those based only on material described from Gotland. The distribution is shown in Fig. 21.

Textulariina

Blastammina sp.; *Pseudoastrorhiza* sp.; Saccaminidae gen. *a*, sp.; Saccaminidae gen. *b*, sp.

Blastammina and *Pseudoastrorhiza* were described by Eisenack (1932) with *Blastammina polymorpha* and *Pseudoastrorhiza silurica,* respectively, as type species. Most *Blastammina* specimens from Vattenfallet can be referred to *B. polymorpha* but it can not be excluded that other species, e.g. of *B. polyedra* type, are represented in the material. For discussion and illustration of these taxa, see Eisenack (1932:261–265, Pl. 11:11–18; 1954:59–61, 68–69, Pl. 2:1–7, 11–12, 14–15, Pl. 5:11; 1966b:384–389, 392, 395–396, Pl. 29:3, 5–10, Pl. 30:2, 4–6, and Pl. 32:1, 8; 1967:259–261, Fig. 5–6, Pl. 27:5),

Pseudoastrorhiza is represented by scattered specimens probably belonging to only one species.

The Sacamminidae are represented by two other species groups, here referred to as Genus *a* and *b,* respectively. Specimens with a test structure similar to that of *Blastammina striata* (see Eisenack 1966b, Pl. 30:3; 1967, Pl. 27:6–7) are referred to Genus *a*, since the structure of the organic test wall is entirely different from that of the type species of *Blastammina.* Genus *b* embraces specimens with a test structure similar to that of *Blastammina fenestrata* (Eisenack 1954:61, Pl. 2:8–10; 1967:261, Pl. 27:1–3) which differs so much from that of the type species of *Blastammina* and from Genus *a* that a separate generic designation seems warranted.

Allogromiina

Archaeochitinia (Lagynacea, Allogromiidae) is represented by one species only, viz. the type species *A. gotlandica* Eisenack, 1954 (see Eisenack 1954:54–55, 68, 70, Pl. 1:9–10; 1966b:390, Pl. 32:10; 1967:269–270).

Archaeochitosa (Allogromiidae) was described by Eisenack in 1959, the type species being *A. lobosa.* The genus is represented by specimens similar to *A. clausa* Eisenack, 1959 and *A. lobosa* Eisenack, 1959, but a species designation cannot be made until a detailed study of the variation of the vesicle shape in relation to substrate has been made on all Baltic *Archaeochitosa* species and until their nomenclature has been revised. For descriptions and photographs

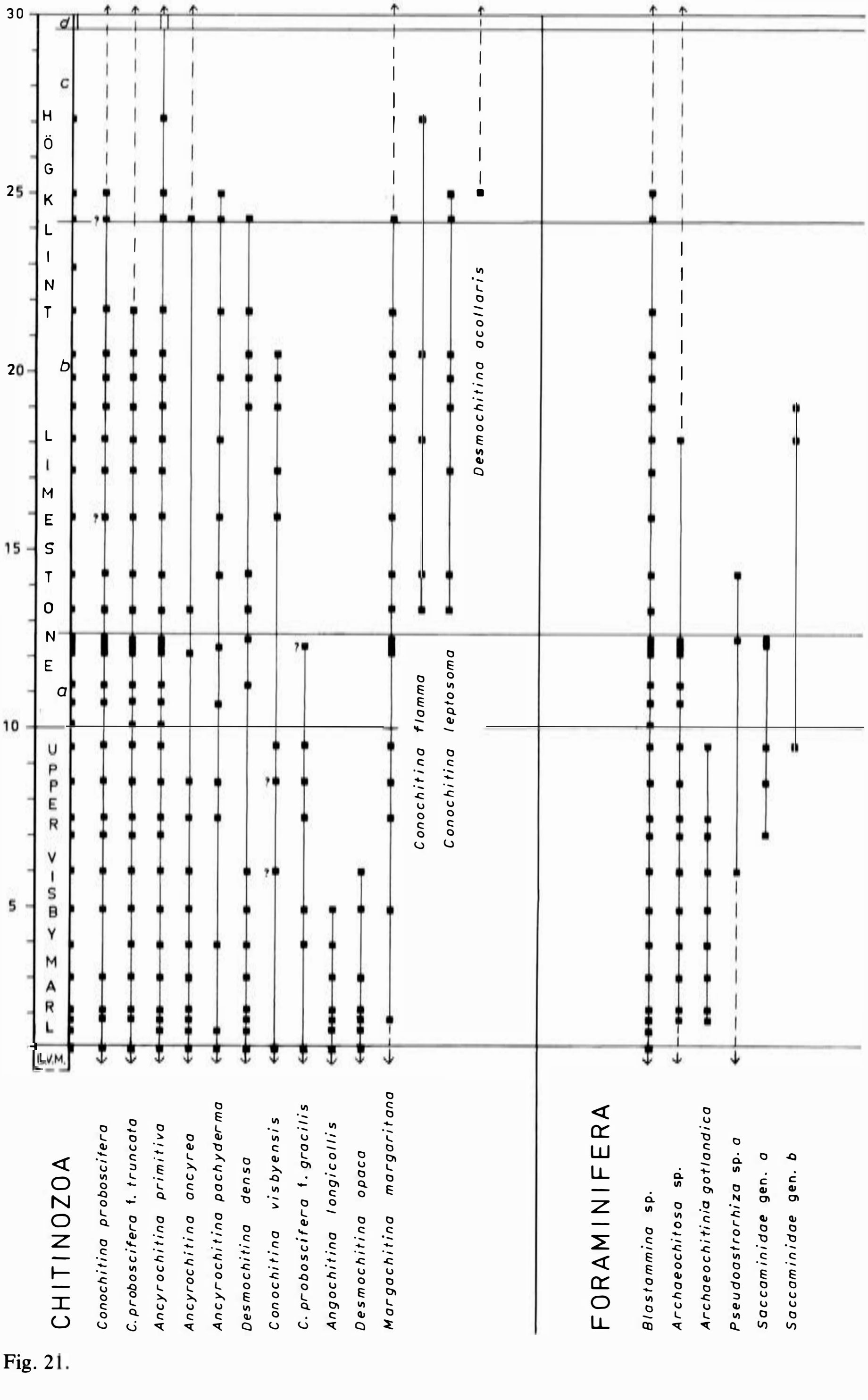
30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
CHITINOZOA
Conochitina proboscifera
C. proboscifera f. truncata
Ancyrochitina primitiva
Ancyrochitina ancyrea
Ancyrochitina pachyderma
Desmochitina densa
Conochitina visbyensis
C. proboscifera f. gracilis
Angochitina longicollis
Desmochitina opaca
Margachitina margaritana
Conochitina flamma
Conochitina leptosoma
Desmochitina acollaris
FORAMINIFERA
Blastammina sp.
Archaeochitosa sp.
Archaeochitinia gotlandica
Pseudoastrorhiza sp. a
Saccaminidae gen. a
Saccaminidae gen. b

Fig. 21.

see Eisenack (1959:90–94, Pl. 9:1–11; 1966:389–391, 395, Pls. 30:8–10, 31:2–5, 32:2–3, 7; 1967:270.

Abundance

Foraminifers occur in all samples studied except for the uppermost four (Fig. 21). The absence of specimens from the middle–upper part of Högklint *c* and from Högklint *d* is possibly the result of the small sample size. It seems probable, however, that local palaeoecological conditions were unfavourable to foraminifers during the time corresponding to this interval, since their frequency appears to decrease upwards through the Högklint Beds. This conclusion is also supported by the fact that *Blastammina* specimens (which occur in all other samples of the section and thus display a fairly strong independence of facies) are the only foraminifers found in the upper part of Högklint *b* and lower part of Högklint *c*.

The most important conclusion to be drawn is that foraminifers played a fairly important role in the Silurian ecosystems of Gotland (the same is true of most Silurian carbonate sequences throughout the world).

Stratigraphical remarks

The stratigraphical range of *Archaeochitosa* is Ordovician–Jurassic and that of *Blastammina* and *Pseudoastrorhiza* late Ordovician–Silurian. (In the "*Treatise*" Loeblich and Tappan give too short ranges for the last two genera.) Thus, as would be expected, taxa at the generic level are of no stratigraphical use in this study.

The type stratum of *Archaeochitinia gotlandica* is within the Upper Visby Marl (Eisenack 1954:54), and according to Eisenack the species has been found definitely only in the Upper Visby Marl (Eisenack 1954:55), with a possible occurrence also in the Lower Visby Marl (Eisenack 1966b:390). *A. gotlandica* disappears close to the uppermost sample of the Upper Visby Marl at Vattenfallet. The absence of the species from the Högklint Limestone in this section corroborates Eisenack's results. It is not improbable that *A. gotlandica* will prove to be a good index fossil for Upper Llandovery, even though its degree of independence of lithofacies remains to be tested.

Other Gotland foraminifers, e.g. *Blastammina* species, seem to have fairly restricted stratigraphical significance. However, they will be of great use in palaeoecological interpretations, since several specimens show impressions of their substrate. Some, for example, lived attached to skeletal fragments of bryozoans, conodont elements and scolecodonts lying on the sea-bed.

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Chitinozoans

SVEN LAUFELD

Chitinozoans are flask-shaped organic-walled microfossils of problematical origin. It seems probable that the first chitinozoan ever figured was a *Conochitina* specimen from the Mulde Beds on Gotland, illustrated and described by Hinde (1882, Pl. 1:5) as a scolecodont of the genus *Eunicites* (see Eisenack 1975:250). It was not until the 1950's that the Chitinozoa of Gotland were reported on, described and illustrated in detail (Eisenack 1955a:178; 1955b:314, 317, Pl. 1:14–15; 1959). Since then, Eisenack has continued his important studies of these fossils in a series of publications entirely or partly dealing with Gotland material (Eisenack 1962a, b, 1964, 1968, 1972). Taugourdeau & De Jekhowsky (1964) and Laufeld (1973, 1974, 1975, 1977, 1979) have also discussed chitinozoans from Gotland. One of my publications (Laufeld 1974) is a monographic study through the complete sequence.

For this account 50 gram samples were processed by my previously described technique (Laufeld 1974:4–6). The chitinozoan taxa were recorded both qualitatively and quantitatively, and with regard to state of preservation. In addition, the following acid-resistant fossils were recorded semiquantitatively: acritarchs with and without spines, foraminifers, "chitinous" hydroids, scolecodonts, eurypterid fragments, graptolite fragments, and melanosclerites. Kerogene was also recorded semiquantitatively.

For distribution of chitinozoans in the Vattenfallet section see Fig. 21.

Faunal list

Ancyrochitina
A. ancyrea (Eisenack, 1931), *A. pachyderma* Laufeld, 1974, *A. primitiva* Eisenack, 1964.

Angochitina
A. longicollis Eisenack, 1959.

Conochitina
C. flamma Laufeld, 1974, *C. leptosoma* Laufeld, 1974, *C. proboscifera* Eisenack, 1937, *C. proboscifera* forma *gracilis* Laufeld, 1974, *C. proboscifera* forma *truncata* Laufeld, 1974, *C. visbyensis* Laufeld, 1974.

Desmochitina
D. acollaris Eisenack, 1959, *D. densa* Eisenack, 1962, *D. opaca* Laufeld, 1974.

Margachitina
M. margaritana (Eisenack, 1937).

Abundance

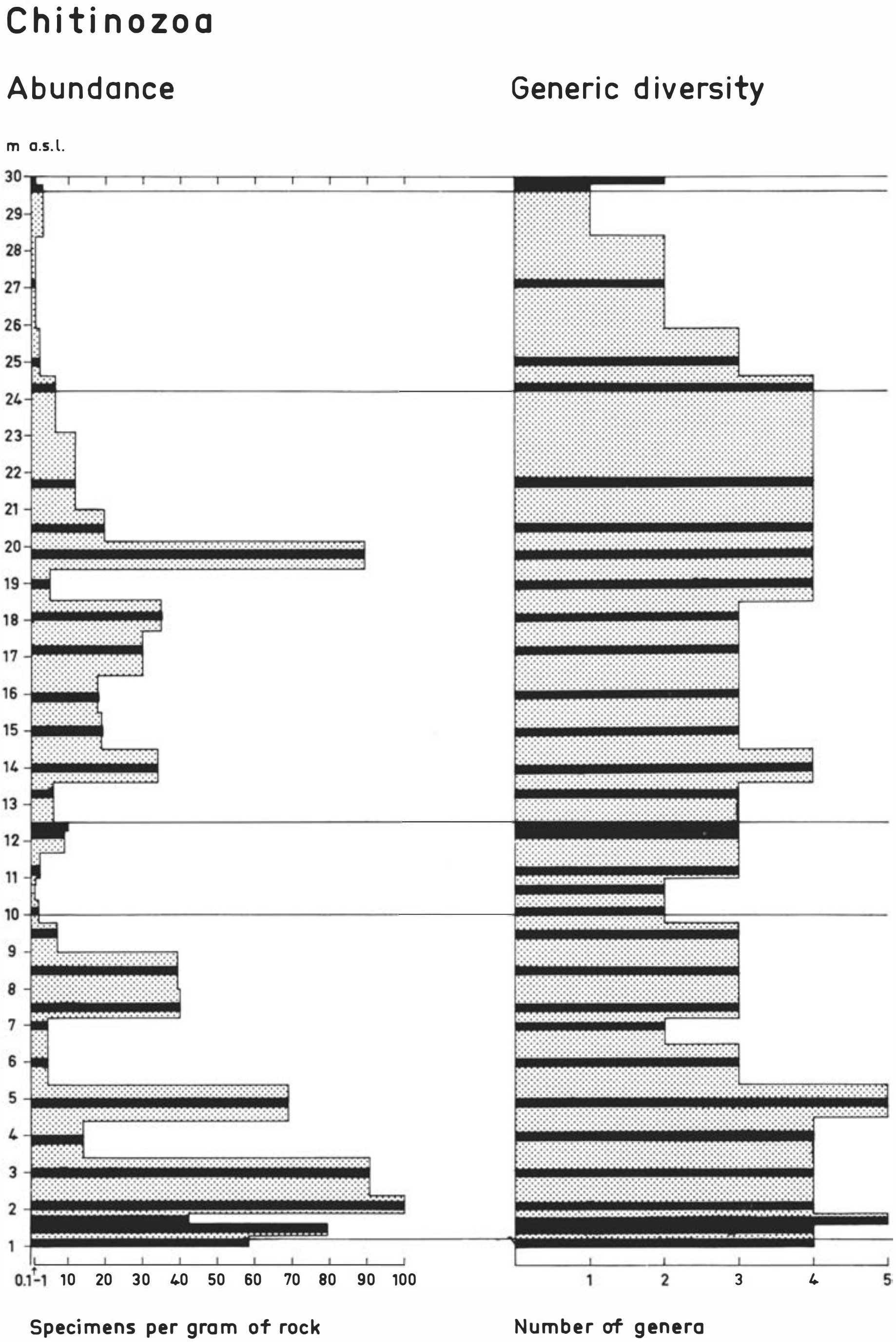
All 33 samples processed yielded chitinozoans. One sample contained more than 5000 specimens (100 per gram), and several others also yielded abundant individuals. Fig. 22 is a graph of abundances through the section. There is a more or less constant decrease of maximum abundance from the lower to the upper part of the Upper Visby Marl. The abundance is low in Högklint *a* and comparatively low to moderate in the lower and middle part of Högklint *b*. In the upper part of Högklint *b* the abundance decreases again and is then low throughout Högklint *c* and *d*. With some deviations, e.g. at 19.8 m, there is thus a general decrease in maximum abundance of chitinozoans from the bottom to the top of the section. This is in good agreement with the pertinent parts of the graph of chitinozoan abundance for all Silurian beds on Gotland (Laufeld 1979, Fig. 1).

Chitinozoans are most abundant in (brachiopod) Benthic Marine Life Zone (BMLZ) 5 on Gotland (Laufeld 1979). They show a high but decreasing abundance through the shallower BMLZ 4 and 3. With few exceptions chitinozoans are rare or absent in the shallowest BMLZ 2 and 1.

Admittedly, several ecological factors, e.g. substrate, food and oxygen supply, currents, temperature, and salinity, play a role in controlling the distribution of brachiopods. It seems evident that factors relating to water depth are very important, at least in low-energy environments such as those of the late Llandoverian to early Wenlockian part of the Gotland sequence. The Lower Visby Marl chiefly represents BMLZ 5, the Upper Visby Marl BMLZ 4, the lower and middle part of the Högklint Beds BMLZ 3, and the upper part of the Högklint Beds BMLZ 2 (Gray et al. 1974:261; Laufeld 1977, 1979; compare with Bassett, this volume).

From an assessment of the general geology, sedimentology and palaeontology of the Lower and Upper Visby and Högklint Beds, it is apparent that there was a general shallowing of the basin during the time of their deposition. Accordingly the graph of abundance of Chitinozoa in the Vattenfallet section reflects bathymetry, as do the brachiopod Benthic Marine Life Zones in late Llandoverian and early Wenlockian time on Gotland. On this assumption, abrupt deviations from the general trend become interesting.

A rapid decrease of abundance might indicate slumping from shallower areas


Chitinozoa
Abundance
Generic diversity
m a.s.l.
30
29
28
27
26
25
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19
18
17
16
15
14
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1
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10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
Specimens per gram of rock
Number of genera

Fig. 22.

or another kind of rapid increase in the rate of sedimentation. On the other hand, a rapid increase of abundance might indicate increasing water depth and/or a decrease of the rate of deposition. It is also possible, though not probable, that the general trend in the graph of chitinozoan abundance reflects a more or less constantly increasing rate of deposition from early Upper Visby through Högklint time at Vattenfallet. A detailed analysis of the total abundance of each species and species diversity through the section will be published elsewhere.

Diversity

The greatest number of chitinozoan species represented in any sample from Vattenfallet is 8. Laufeld (1974:123) pointed out that the main pattern of diversity (expressed as the number of species per sample) on Gotland is similar to that of abundance (expressed as the total number of specimens per gram of rock), i.e. a high species diversity is generally coupled with a high total abundance.

A graph of generic diversity (Fig. 22) reveals general trends in a crude way and is of interest also because the genera represent the five major vesicle types. Furthermore, there can be very little dispute over the generic designations used here, whereas the species taxonomy might be regarded, at least partly, as provincial.

In general the generic diversity is high in the Lower Visby Marl and lower part of the Upper Visby Marl, fairly high in the upper part and in Högklint *a*, fairly high to high in Högklint *b*, and then decreasing through Högklint *c* and *d* from fairly high to moderate or low.

Frequency and palaeoecology

Fig. 23 shows the frequency of specimens referred to genera. *Ancyrochitina* and *Conochitina* predominate, with only two samples dominated numerically by chitinozoans of other genera. The abundance of *Ancyrochitina* specimens fluctuates greatly but the trend increases from the base to the top of the section. The opposite is true of the *Conochitina* specimens. *Angochitina* (represented by *A. longicollis* which is known to have a high abundance in the Lower Visby Marl) is common in the lower part of the Upper Visby Marl but decreases in abundance upwards and disappears in the middle part of this unit. The opposite trend is true of *Margachitina* (represented by *M. margaritana,* a species that seems confined to moderate water depths; it reappears in those parts of the Slite Beds deposited in deeper water than the uppermost part of the Högklint and Tofta Beds).

Chitinozoa

Relative frequencies of specimens within each genus

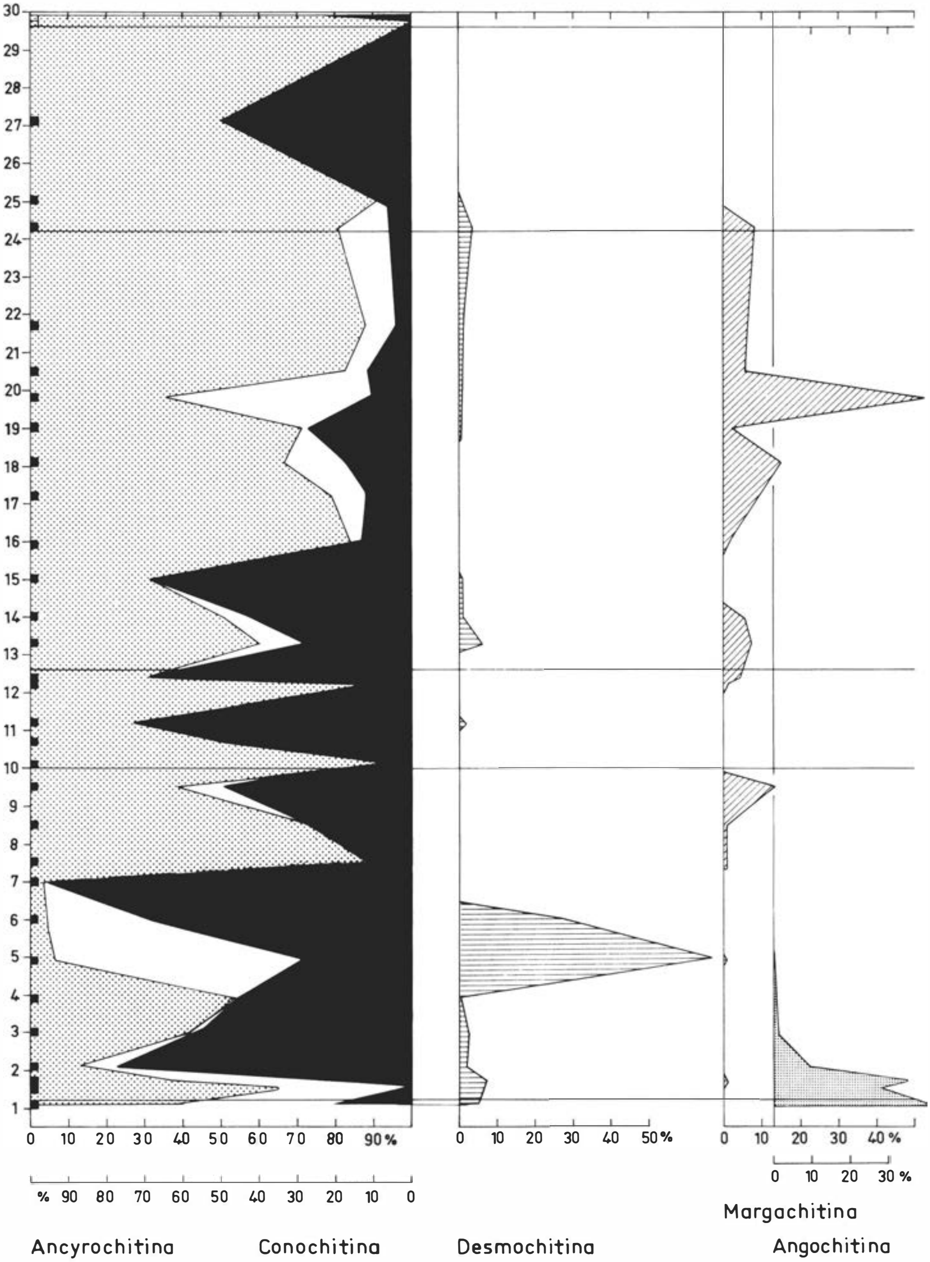

Fig. 23.

Finally, *Desmochitina* specimens also disappear in the uppermost and shallowest part of the Högklint Beds, only to reappear (*D. acollaris*) in the Slite Marl. Of the taxa under discussion only *Ancyrochitina* and *Conochitina* are represented in the uppermost and shallowest part of the Högklint Beds. *Ancyrochitina* specimens almost always dominate where the total abundance of Chitinozoa is low, especially in high-energy environments. This, taken together with the small size and overall morphology of the vesicles of *Ancyrochitina* species, makes it plausible that they were planktic. The large and thick-walled *Conochitina* specimens, however, were probably benthic. This conclusion is supported by the general trend in the frequency graph for *Conochitina*.

Stratigraphical remarks

Thirteen chitinozoan taxa in Fig. 21 occur below the base of the Vattenfallet section. Eight of the taxa in Fig. 21 occur above the Vattenfallet section and the Högklint Beds. The latter chitinozoans reappear in the Slite Beds, since the extremely shallow-water Tofta Beds are barren of these and almost all other acid-resistant fossils. *Ancyrochitina pachyderma, Desmochitina opaca* and *Conochitina leptosoma* were reported to range upwards into the upper, marly southwestern facies of the Högklint Beds (Laufeld 1974, Fig. 77). The facies is possibly correlative with beds somewhere in the lower part of Högklint *c* in the present section, a conclusion that is further supported by the fact that *Desmochitina acollaris* first appears elsewhere on Gotland in the marly SW Högklint facies.

The stratigraphical ranges of the Chitinozoa recorded in the Vattenfallet section agree with those recorded earlier from Gotland by Laufeld (1974, Figs. 77–78) with the important extension of the ranges of *Conochitina proboscifera* forma *truncata, C. visbyensis, C. proboscifera* forma *gracilis,* and *Desmochitina opaca* into at least the topmost bed of the Lower Visby Marl.

The next logical step towards a further refinement of the biostratigraphical use of Chitinozoa on Gotland is to take the graphs of abundance, diversity, frequency, etc., into account. This is the only way to comprehend the influence of various palaeoecological factors and to sort out taxa that are comparatively independent of facies and therefore best suited for the purpose of correlation.

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"Chitinous" hydroids

SVEN LAUFELD

In the hydrozoan order Hydroida, one of the three suborders, Eleutheroblastina,embraces solitary, naked polypoids that are exceedingly rare as fossils (see, however, Schram & Nitecki 1975 and references therein). The second suborder, Gymnoblastina, contains colonial polypoids with naked hydranths and gonophores but with a "chitinous" or (less commonly) calcareous exoskeleton enclosing hydrorhizae and caulomes. In the third suborder, Calyptoblastina, the hydranths and gonophores are enclosed by hydrothecae and gonothecae, forming parts of a "chitinous" periderm that is easily preserved as fossil (Hill & Wells 1956: F83–86).

Despite the fact that "chitinous" hydroids are very common in most Phanerozoic platform mudstones and carbonates, these fossils have attracted remarkably little attention from specialists on coelenterates. This can probably be explained by the difference in techniques needed for the study of "chitinous" hydroids compared with those for coelenterates with a calcareous skeleton. Most publications on fossil "chitinous" hydroids are authored by specialists either on "chitinous" microfossils or graptolites, and are by-products of the digestion of comparatively small rock samples that yield only few and fragmented hydroid periderms. This is true also of this note.

Not only the Vattenfallet section but the entire Silurian of Gotland offers unique possibilities for studies of "chitinous" hydroids preserved in full relief. To my knowledge not one description or illustration of these fossils from the bedrock of the island has yet been published. However, Eisenack described "chitinous" hydroids from Ordovician and Silurian glacial erratics in a series of publications (1932:266–267, Pl. 11:22–23; 1934:54–56, Figs. 1–7, Pl. 4:5–8; 1937:236–238, Figs. 9–20, Pl. 16:6–7; 1971:455–456, Figs. 31–34). Kozłowski's (1959) lucid description and discussion of these fossils from Ordovician erratics of Baltic provenance also deserves mention. As pointed out by Kozłowski (1959:212) it is premature to classify early and middle Palaeozoic "chitinous" hydroids into taxa of suprageneric rank at present. My own records in the Vattenfallet section are based solely on the residues of the 50 gram samples processed for Chitinozoa. Thus I have no basis even for an evaluation of which species and genera are represented in the section. The purpose of this contribution is only to record the occurrence of "chitinous" hydroids at Vattenfallet and to stimulate research on these fossils.

The samples in which "chitinous" hydroids were recorded are shown in Fig. 66. These animals are common in most parts of the Lower and Upper Visby Marl, and Högklint *a* and *b*. They may occur in Högklint *c* and *d*, but if so, they are probably scarce since none of my 50 gram samples from these beds yielded any specimens.

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Melanosclerites

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When studying acid-resistant, "chitinous" microfossils in Ordovician and Silurian erratic limestone boulders from the Baltic area, Eisenack (1932:273–274; Pl. 12:19–23) discovered a kind of problematical microfossils that he described informally as *Schwarze Stäbchen* (=black rodlets), and a few years later he described additional specimens of the same provenance (Eisenack 1934:56–59, Figs. 8–15, Pl. 4:9). In 1942 (pp. 161–174) Eisenack named these problematical fossils "melanoscleritoids" and formalized their taxonomy by applying binominal nomenclature. Sixteen form species were described, and assigned to nine "genera" grouped into two "subfamilies", together forming the "family" Melanoskleritoitidae. Eisenack (1942:158–161) also discussed in detail the chemical composition and systematic affinity of the melanosclerites and added to his earlier (1934:56) interpretation of them as parts of the axial skeleton of Cnidaria (similar to Alcyonacea and Gorgonacea of the subclass Octocorallia, and Antipatharia of the subclass Ceriantipatharia) by suggesting that some of them might represent sclerodermites in octocorals (1942:157, 161, 176). In another paper on fossils from glacial erratics, Eisenack (1950) described macroscopic remains of what he interpreted as more complete "axial skeletons" of "melanosclerite" animals. The largest of the tree-like "axial skeletons" is more than 25 mm long and consists of a 0.8 mm wide "trunk" that is branched "upwards" (Eisenack 1950, Fig. 1).

The first melanosclerites extracted from rocks *in situ* were from the Silurian of Gotland and were described by Eisenack in 1963, who then established a new order – Melanoskleritoitidea – and vernacularized the name to "melanosclerites". Further, he described a number of new "genera" and "species" and discussed the systematics, chemical composition, state of preservation, stratigraphical and geographical occurrence of the melanosclerites. He also described the first complete skeleton of a "melanosclerite" animal (1963:126–127, Pl. 2:5) and characterized melanosclerites as having a fairly small, brown to black, "chitinous", sometimes branched skeleton with axial symmetry and commonly with distal differentiation. The skeleton formed an axial structure of support or sclerite-like elements in benthic animals that probably belong within the Cnidaria. Additional information on melanosclerite morphology was published by Eisenack in 1971 (pp. 349–351). As currently known their stratigraphical range is Middle Ordovician to Middle Devonian (Eisenack 1963:126, 130–132).

According to Eisenack (1963:131), melanosclerites occur more or less abundantly in all the 13 Silurian topostratigraphical units on Gotland, apart from the Tofta Beds.

Melanosclerites are preserved in sample residues prepared for the study of Chitinozoa. However, due to the fact that my technique for processing rock samples is designed primarily for extracting chitinozoans, the melanosclerites are commonly broken and thus unsuitable for systematic work. Nevertheless, this record of melanosclerites in the Vattenfallet section is included here, partly to give complete coverage of the groups of fossils recorded, and partly since this record can be used as a guide for further collecting. The samples in which melanosclerites have been identified are shown in the log, Fig. 66. For a reference to the samples processed, but barren of melanosclerites, see the range chart of chitinozoans (Fig. 21).

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Tabulate and heliolitid corals

EINAR KLAAMANN

The study of Palaeozoic corals can be said to have originated on material from Gotland (Bromell 1728; Linnaeus 1745; Linné 1768), and descriptions of tabulate and heliolitid corals from the island have subsequently been included in, or formed the subject of, many papers (Milne-Edwards & Haime 1851; Lindström 1865, 1873, 1896; Jones 1936; Thomas & Smith 1954; Klaamann 1970; Stasińska 1976, etc.). Lindström's (1899) monograph on the heliolitid corals, with excellent illustrations by G. Liljevall, was based mainly on Gotland material and is still a basic work on the subject. A study of Gotland favositids by Tripp (1933) is difficult to use because of the wide concept of species. An attempt at a monographic study of Gotland tabulates was made by Stasińska (1967) but it comprises only a part of the fauna and much of the material lacked stratigraphical control. Many of the tabulate coral species described from Saaremaa in Estonia (Sokolov 1952; Klaamann 1961, 1966, etc.) have also been identified recently from Gotland.

The material from Vattenfallet comprises 131 tabulate and 56 heliolitid colonies. For distribution see Fig. 24.

Annotated faunal list

Tabulata

Theciidae: *Thecia podolica* Sokolov

Favositidae: *Palaeofavosites forbesiformis porosus* Sokolov, *P. suurikuensis* Klaamann, *P. parilis* Klaamann, *Mesofavosites imbellis* Klaamann, *M.* n.sp. *a*, *Favosites gothlandicus* Lamarck, *F. desolatus* Klaamann, *F. subforbesi* Sokolov, *F. jaaniensis* Sokolov, *F. exilis* Sokolov, *F.* n.sp. *a*, *Barrandeolithus lichenarioides* (Sokolov), *Angopora hisingeri* (Jones), *A. parva* Klaamann.

Syringolitidae: *Syringolites kunthianus* (Lindström).

Pachyporidae: *Pachypora cervicornis* Lindström, *Striatopora calyculata* Lindström, *S. flexuosa* Hall.

Alveolitidae: *Subalveolites panderi* Sokolov, *S. sokolovi* Klaamann, *Planalveolites fougti* (Milne-Edwards and Haime).

Syringoporidae: *Syringopora* sp. indet. The material of *Syringopora* from the section consists only of small fragments of colonies.

Palaeofavosiporidae: *Palaeofavosipora clausa* (Lindström).

Halysitidae: *Halysites senior* Klaamann, *Catenipora quadrata* Fischer-

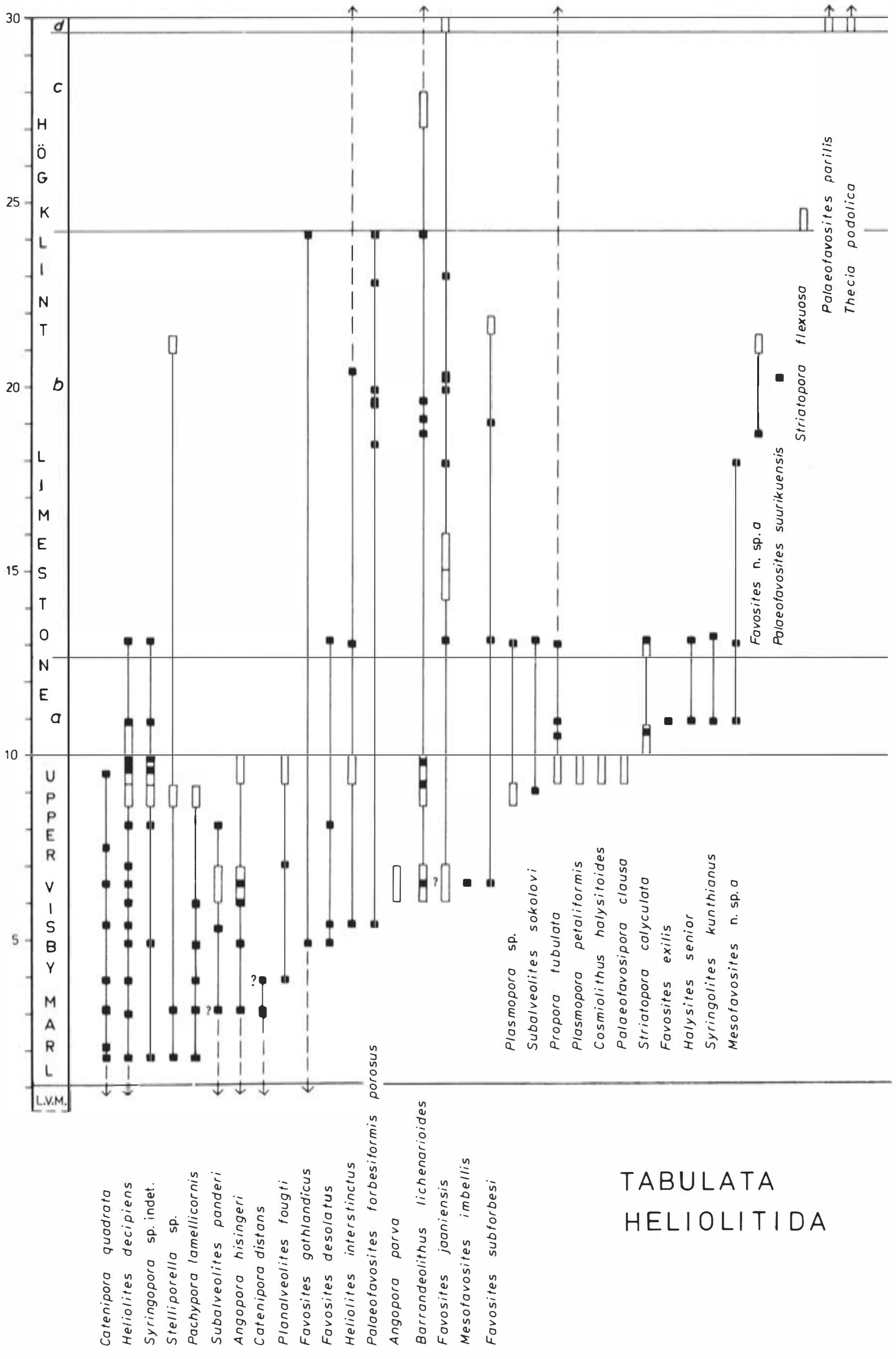
30
25
20
15
10
5
d
c
HÖGKLINT
b
LIMESTONE
a
UPPER VISBY MARL
L.V.M.
Catenipora quadrata
Heliolites decipiens
Syringopora sp. indet.
Stelliporella sp.
Pachypora lamellicornis
Subalveolites panderi
Angopora hisingeri
Catenipora distans
Planalveolites fougti
Favosites gothlandicus
Favosites desolatus
Heliolites interstinctus
Palaeofavosites forbesiformis porosus
Angopora parva
Barrandeolithus lichenarioides
Favosites jaaniensis
Mesofavosites imbellis
Favosites subforbesi
Plasmopora sp.
Subalveolites sokolovi
Propora tubulata
Plasmopora petaliformis
Cosmiolithus halysitoides
Palaeofavosipora clausa
Striatopora calyculata
Favosites exilis
Halysites senior
Syringolites kunthianus
Mesofavosites n. sp. a
Favosites n. sp. a
Palaeofavosites suurikuensis
Striatopora flexuosa
Palaeofavosites parilis
Thecia podolica
?
TABULATA
HELIOLITIDA

Fig. 24.

Benzon, *C. distans* Eichwald. In addition to these species *Catenipora gothlandica* (Yabe) and *C.* n.sp. were found on the top of the Upper Visby reef-like mound.

Heliolitida

Coccoseridida: *Cosmiolithus halysitoides* Lindström.

Heliolitidae: *Heliolites interstinctus* (Linnaeus), *H. decipiens* (McCoy), *Stelliporella* sp.

Plasmoporidae: *Plasmopora petaliformis* (Lonsdale), *P.* sp.

Proporidae: *Propora tubulata* (Lonsdale).

Stratigraphical remarks

A comparison between the Vattenfallet section and the sequence in the northern cliffs of Saaremaa, based on assemblages of tabulate and heliolitid corals, has been discussed by Klaamann (1977). In this contribution therefore only the main points are presented.

Upper Visby Marl

At Vattenfallet this unit has the highest taxonomic diversity of tabulate and heliolitid corals; 24 species are recorded out of a total of 34 species for the whole section. In the uppermost beds of the Upper Visby Marl (8.5 to 10 m), heliolitids abound, particularly *Heliolites decipiens*. A closely comparable heliolitid assemblage occurs on Saaremaa in an interval of about 2 m below the base of the Ninase Beds of the Jaani Stage.

Högklint a

Only eight tabulate and heliolitid species have been found in these beds. *Syringolites kunthianus* has been recorded at other localities in the Upper Visby Marl, whereas *Halysites senior* and *Striatopora calyculata* are restricted to the Högklint Beds on Gotland. The latter species appears on Saaremaa in the Ninase Beds of the Jaani Stage where its appearance coincides with that of *Eocoelia angelini* (Rubel 1976). In the Vattenfallet section *E. angelini* appears at the top of the Upper Visby Marl (Bassett, this volume), only slightly before *Striatopora calyculata*.

Högklint b

The general composition of the tabulate and heliolitid fauna of Högklint *b* is fairly similar to that of the Upper Visby Marl but the taxonomic diversity is lower (19 species). Most of the species that continued from the Upper Llandovery into the Upper Visby Marl do not range into Högklint *b*. The fine-grained limestone in the interval 13.5 to 17 m is very poor in tabulate corals. The commonest species is *Favosites jaaniensis* which is also common in the upper part of Högklint *b.* In the sections on northern Saaremaa this species occurs together with *Palaeofavosites suurikuensis* in the upper part of the Paramaja Beds, that is, in the uppermost beds of the Jaani Stage.

Högklint c

The tabulate fauna here is very poor (2 species) in the section, indicating that environmental conditions were not favourable for colonial corals.

Högklint d

In the *"Pterygotus"* Beds too the rarity of colonial corals indicates unfavourable environmental conditions. Only three species have been found, of which *Favosites jaaniensis* is certainly autochthonous, and probably also *Palaeofavosites parilis,* whereas the recovered colony of *Thecia podolica* probably represents a pebble derived from the older rocks exposed at the same level. *Palaeofavosites parilis* has previously been found in the reefs of the Maasi Beds of the Jaagarahu Stage on Saaremaa, and the Slite beds (Stora Myre 1) of Gotland.

In conclusion, the tabulate and heliolitid assemblages in the Upper Visby Marl, Högklint *a*, and Högklint *b* of the Vattenfallet section closely resemble those from the sequence on northern Saaremaa, with respect to both the composition of the species as well as the succession. In the upper part of the Högklint sequence at Vattenfallet the taxonomic diversity of tabulate corals is low and at present a close comparison is therefore difficult.

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Rugose corals

BJÖRN NEUMAN and NILS-MARTIN HANKEN

Following the pioneer studies of Linnaeus (1745, 1758), rugose corals from Gotland have been described in numerous papers. In early studies species were characterized by external features alone (e.g. Hisinger 1831, 1837; Milne-Edwards & Haime 1851; Lindström 1865) or by external features combined with some internal characters based on one or two thin sections (e.g. Lindström 1870, 1882, 1896; Dybowski 1873; Lang & Smith 1927; Smith & Tremberth 1929). Wedekind (1927) attempted a monographic description of a substantial part of the rugose coral fauna of Gotland but he used an extremely narrow concept of species, in a number of which internal characters were not studied at all. A few recent papers on rugose corals also include material from Gotland (Weyer 1973, 1974; etc.).

Koch (1882) described in some detail the budding of corallites in colonial Rugosa from Gotland. First attempts at ontogenetic studies in solitary forms were published by Ryder (1926) and Vollbrecht (1928). Minato's (1961) very interesting paper on some rugose corals from Gotland unfortunately lacked both locality and stratigraphical data. Neuman (1974) emphasised that during ontogeny, morphological features of solitary forms display a great variation in shape as well as construction. There is also some variation at the same ontogenetic stage between different specimens of a species. For a safe specific identification, study of serial sections, including both adult and pre-adult growth stages, is normally required.

At present the following groups of rugose corals from Gotland are being studied monographically: *Acervularia* by Hanken, and the genera *Phaulactis, Araeopoma, Saucrophyllum,* and *Arachnophyllum* by Neuman.

Because of the lack of modern monographic studies of the Gotland rugose fauna, it is not only difficult to identify, but in many cases also to define a species. Most of the specimens from Vattenfallet were sectioned, and on average two to four dry peels produced from each sectioned corallite (in total approximately 800 peels). In addition, the calices of several specimens were carefully cleaned, with those in colonial forms being prepared by means of a new method elaborated by Hanken (ms. in preparation). The type specimens of species described by Lindström (1865, 1870, 1882, 1896), Ryder (1926), Wedekind (1927), and Vollbrecht (1928) were available for study and comparison. However, despite these factors some of the identifications remain uncertain and may be subject to change when monographic studies are completed.

The total number of specimens of rugose corals in the material from Vattenfallet is 550, distributed among the following families: Streptelasmatidae

(260), Halliidae (99), Arachnophyllidae (37), Acervulariidae (9), Calostylidae (13), Spongophyllidae (5), Ptenophyllidae (8), Trysplasmatidae (57), Cystiphyllidae (34), and Goniophyllidae (4). In addition, there are 20 pre-adult streptelasmatids or halliids and 4 unidentified specimens. In this contribution Hanken is responsible for identification of colonial rugose corals (acervulariids and 5 colonies of *Tryplasma*) and Neuman for solitary corals (all other material).

For distribution in the Vattenfallet section see Fig. 25.

Annotated faunal list

Streptelasmatidae
Dinophyllum involutum Lindström, *Dalmanophyllum dalmani* (Edwards and Haime), *Rhegmaphyllum conulus* (Lindström), *Rhegmaphyllum?* sp. *a*, *Schlotheimophyllum patellatum* (Schlotheim), *Kodonophyllum telescopium* Wedekind, *Crassilasma* sp. *a*.

Halliidae
Holophragma calceoloides Lindström, *Phaulactis cyathophylloides* Ryder, *P.* sp. *a*, *P.* sp. *b*.

Phaulactis cyathophylloides and *P.* sp. *a.* seem to be identical during the early growth stages of the corallite and juvenile specimens can therefore not be identified at species level.

Arachnophyllidae
Entelophyllum visbyense Wedekind, *E.* sp. *a*, *Kyphophyllum lindstroemi* Wedekind.

Acervulariidae
Acervularia breviseptata Weissermel, *A.* sp. *a*, *A.* sp. *b*.

Calostylidae
Calostylis concavotabulata Ma. Weyer (1973, Pls. 1–2) figured the ontogeny of the species based on material from Visby cementfabrik. The material from Vattenfallet seems to be conspecific.

Spongophyllidae
Ketophyllum hoegbomi Wedekind, *K.* sp. *a* (a single specimen).

Ptenophyllidae
Spongophylloides (Actinocystis) sp. *a*.

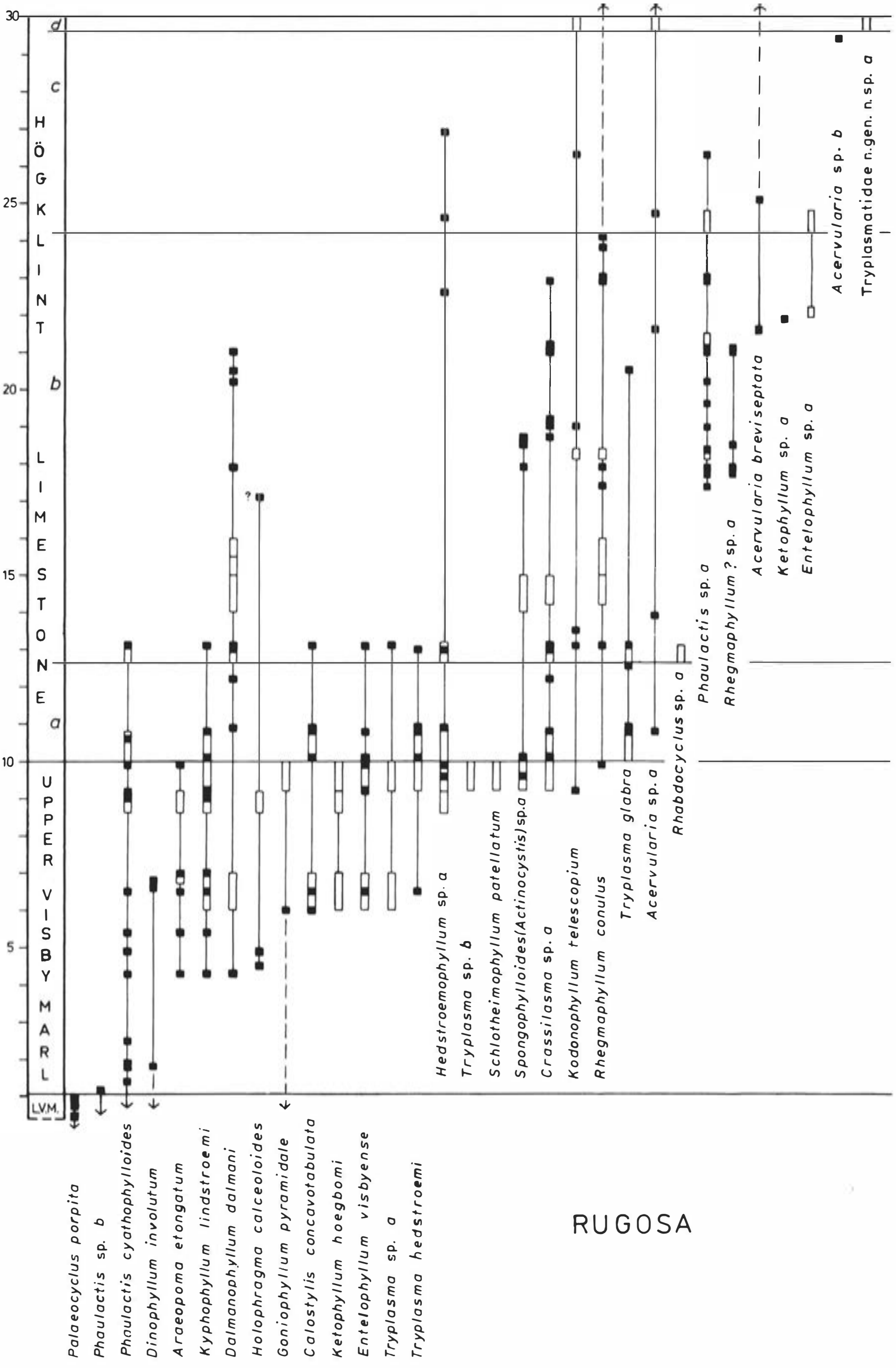
30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
LVM.
?
Palaeocyclus porpita
Phaulactis sp. b
Phaulactis cyathophylloides
Dinophyllum involutum
Araeopoma elongatum
Kyphophyllum lindstroemi
Dalmanophyllum dalmani
Holophragma calceoloides
Goniophyllum pyramidale
Calostylis concavotabulata
Ketophyllum hoegbomi
Entelophyllum visbyense
Tryplasma sp. a
Tryplasma hedstroemi
Hedstroemophyllum sp. a
Tryplasma sp. b
Schlotheimophyllum patellatum
Spongophylloides(Actinocystis)sp.a
Crassilasma sp. a
Kodonophyllum telescopium
Rhegmaphyllum conulus
Tryplasma glabra
Acervularia sp. a
Rhabdocyclus sp. a
Phaulactis sp. a
Rhegmaphyllum ? sp. a
Acervularia breviseptata
Ketophyllum sp. a
Entelophyllum sp. a
Acervularia sp. b
Tryplasmatidae n.gen. n.sp. a
RUGOSA

Fig. 25.

Tryplasmatidae
Tryplasma glabra (Lindström), *T. hedstroemi* Wedekind, *T.* sp. *a*, *T.* sp. *b*, *Palaeocyclus porpita* (Linnaeus), *Rhabdocyclus* sp. *a* (one specimen), Tryplasmatidae n. gen., n. sp. (a single specimen). *Tryplasma hedstroemi* and *T.* sp. *a* are solitary whereas *T.* sp. *b* is colonial.

Cystiphyllidae
Hedstroemophyllum sp. *a, Araeopoma elongatum* (Lindström).

Taxonomic remarks

As noted above, because of the present unsatisfactory knowledge of ontogeny in many species, including type species, a number of specific and generic taxa remain poorly defined. Many subjective synonyms have been established during this study. A preliminary partial synonymy list is included here for some of the Vattenfallet species, based on examination of the type specimens.

Rhegmaphyllum conulus (Lindström, 1868)
Synonym: *Rhegmaphyllum slitense* Wedekind, 1927. For further information, see Weyer (1974:162–163).

Crassilasma Ivanowsky, 1962
The genus (type species: *C. simplex*) was defined by Ivanowsky (1962, 1963, 1965). *Crassilasma* sp. *a* shows the following features characteristic of the genus: Irregularly twisted septa, strongly dilated during early ontogeny; in later stages of ontogeny the dilatations of the major septa become reduced axially; tabulae rare and convex.

Phaulactis cyathophylloides Ryder, 1926
Synonyms: *Lycophyllum tabulatum* Wedekind, 1927, *L. irregulare* Wedekind, 1927, *L. torquatum* Wedekind, 1927, *L.* sp. (Wedekind 1927, Pl. 5:12–13), *Lykocystiphyllum hoegklinti* Wedekind, 1927, *L. oppositum* Wedekind, 1927, *Aulacophyllum* sp. (Wedekind 1927, Pl. 17:11–12), *Phaulactis irregularis* (Wedekind) (in Minato 1961, Pls. 5–7, 17). A more detailed revision may reveal further synonyms. In *Phaulactis* the internal morphology seems to vary widely within a species, probably as a response to various growth conditions. One or two transverse sections of each corallite examined by most previous authors did not reveal the range of intraspecific variation of morphological structures.

Entelophyllum visbyense Wedekind, 1927
Synonym: *E. anschuetzi* Wedekind, 1927.

Kyphophyllum lindstroemi Wedekind, 1927
Synonyms: *Kyphophyllum tenue* Wedekind, 1927, *K. cylindricum* Wedekind, 1927, *K. conicum* Wedekind, 1927, *K. biseriale* Wedekind, 1927 (Pl. 30: 23).

Acervularia sp. *a*
Probable synonym: *Rhabdophyllum conglomeratum* Wedekind, 1927.

Ketophyllum hoegbomi (Wedekind, 1927)
Synonyms: *Dokophyllum annulatum* Wedekind, 1927, *D. lindstroemi* Wedekind, 1927 (Pl. 9:6–12), *D.* sp. (Wedekind 1927, Pl. 9:1–3).

Tryplasma hedstroemi (Wedekind, 1927)
Synonyms: *Pholidophyllum hedstroemi* var. *attenuata* Wedekind, 1927, *P. cylindricum* Wedekind, 1927 (Pl. 3:5), *P. intermedium* Wedekind, 1927, *P. intermedium* var. *articulatum* Wedekind, 1927, *P. tenue* Wedekind, 1927 (Pl. 3:12), *P. coniforme* Wedekind, 1927 (Pl. 3:14), *P. crassum* Wedekind, 1927 (Pl. 3:15), *Zelophyllum hoegklinti* Wedekind, 1927 (Pl. 6:11–13). This species resembles *Tryplasma loveni* (Edwards and Haime) as defined by Hill (1936:206, Pl. 30:46–47) but has a much higher frequency of tabulae.

Hedstroemophyllum sp. *a*
Probable synonyms: *Hedstroemophyllum articulatum* Wedekind, 1927 (Pl. 21:1–2), *H. crassum* Wedekind, 1927, *H. stolleyi* Wedekind, 1927 (Pl. 21:5–9), *H. tenue* Wedekind, 1927 (Pl. 21:10–11), *H. weissermeli* Wedekind, 1927, *H. rugosum* Wedekind, 1927. *Hedstroemophyllum* is very similar to *Holmophyllum* Wedekind, 1927. A thorough study of type material is required in order to understand the relationships between these genera.

Remarks

In terms of numerical abundance of rugose corals, *Crassilasma* sp. *a* (186 specimens), *Dalmanophyllum dalmani* (37) and *Phaulactis cyathophylloides* (28) comprise the main elements of the fauna. The greatest taxonomic diversity at Vattenfallet is in the upper part of the Upper Visby Marl, Högklint *a*, and the base of Högklint *b*. Hanken observed that five of the six colonies of *Acervularia* were worn prior to final deposition.

Details of the vertical range of various rugose coral species in the stratigraphical interval under consideration are poorly known. *Phaulactis cyathophylloides, Dinophyllum involutum* and *Goniophyllum pyramidale* also occur in the Lower Visby Marl, and the two latter species range farther into the underlying *Arachnophyllum* Beds. *Rhegmaphyllum conulus* and *Acervularia* *breviseptata* are common in the Slite Beds. The former species is here recorded for the first time from the Högklint Limestone.

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Polychaete jaws

CLAES BERGMAN

There are very few previous reports of polychaete jaws (scolecodonts) from the Silurian of Gotland. Although, according to Hinde (1882:4) and Thorell & Lindström (1885:4), Angelin had identified specimens from Gotland as jaw elements of annelids as early as 1864, the paper by Hinde (1882) is the first published account of these fossils from the island. Hinde's report is a well illustrated account of scolecodonts from two localities, one of which was in "decomposed shale from the neighbourhood of Wisby", later stated by Thorell & Lindström (1885:4) to be from the "*Pterygotus*" Beds of Vattenfallet.

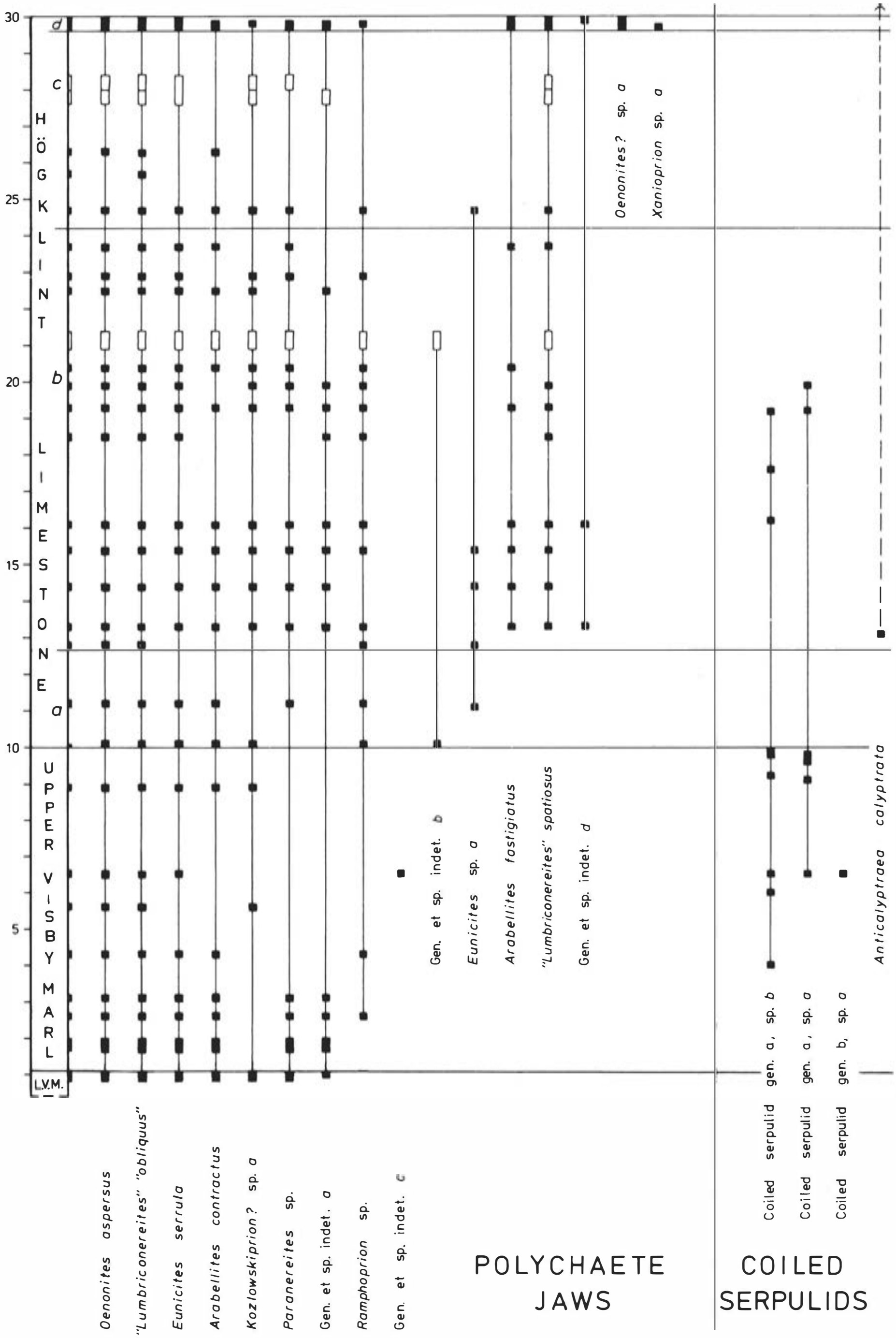
Hede recorded the occurrence of annelid jaws from a large number of localities on Gotland in the descriptions of the geological map sheets. More recently Martinsson (1960) described two clusters of jaws from the Mulde Marl, and Eisenack (1975) discussed some scolecodont material from the island within a more general study of the group.

I am currently studying both fused and dispersed polychaete jaws from the Silurian of Sweden, mainly from Gotland. A full discussion of the taxa tentatively identified here is in preparation. Specimens have been picked from the same residues as those prepared for conodont extraction. For further information on the samples and their treatment, see Jeppsson (this volume). 13,581 jaw elements from Vattenfallet have been examined, but only a few of these were fused. 16 separate species are distinguished (Fig. 26), 10 of which were not described by Hinde (1882). He named 26 different species from about 1 kg of soft "*Pterygotus*" marl, but in my opinion about 20 of these are synonyms.

Taxonomy, nomenclature and terminology

Various authors have proposed that a parataxonomic system should be used for disaggregated jaw elements and that clusters should be named separately. A proposal of this kind by Moore & Sylvester-Bradley (1957) was rejected by the 15th International Congress of Zoology in 1958 (Kielan-Jaworowska 1968), and thus the only valid nomenclatorial basis is that which follows current I.C.Z.N. rules (e.g. article 23). Similar problems have been widely discussed with regard to conodonts, and the success in attempting to apply strictly biological criteria for taxonomy suggests that the same success can be achieved for polychaetes.

In this study I have mainly used the morphology of the first maxillae (MI) to distinguish different species, although some of the other jaw elements of each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15
10
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d
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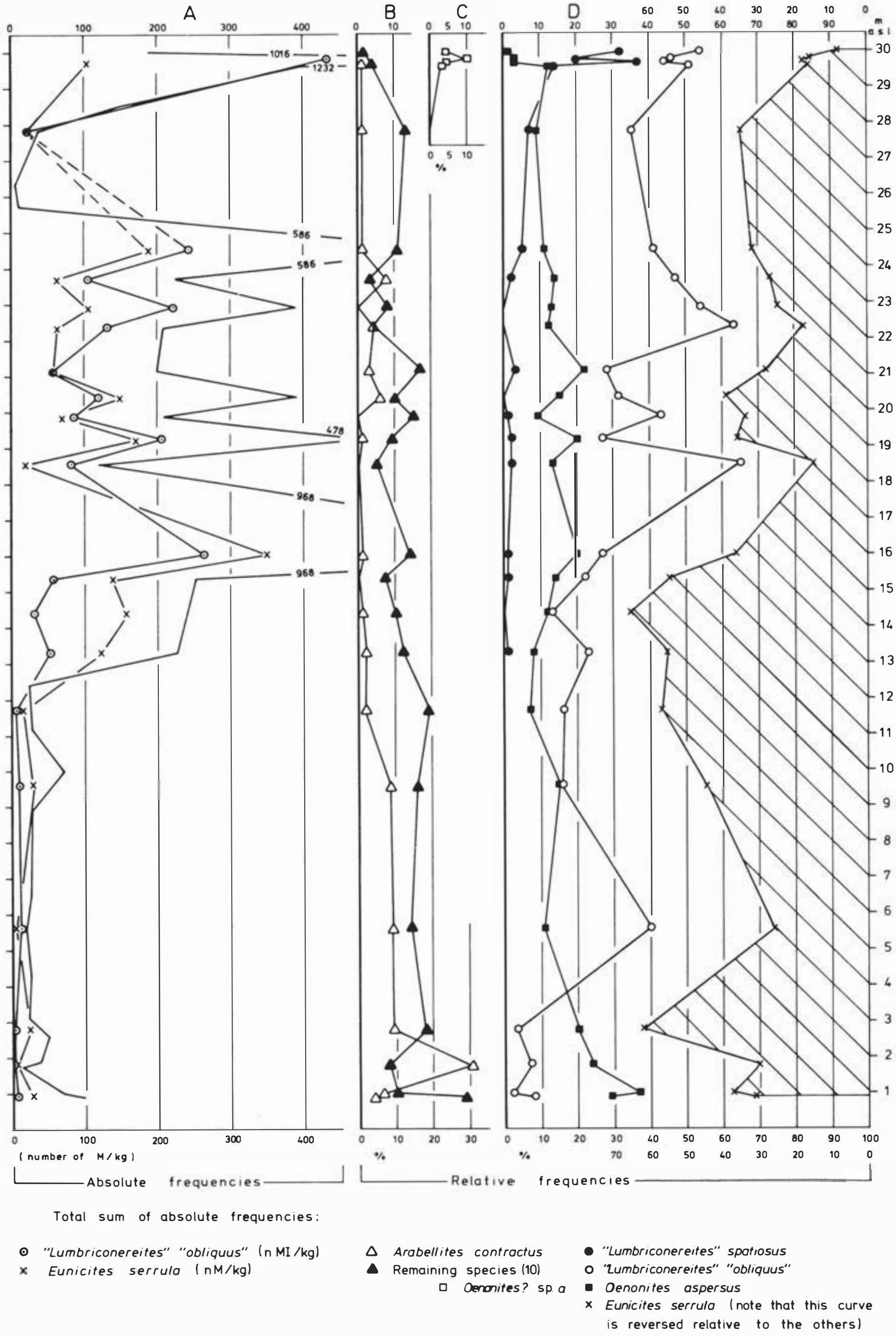
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
Oenonites? sp. a
Xanioprion sp. a
Gen. et sp. indet. b
Eunicites sp. a
Arabellites fastigiatus
"Lumbriconereites" spatiosus
Gen. et sp. indet. d
Coiled serpulid gen. a, sp. b
Coiled serpulid gen. a, sp. a
Coiled serpulid gen. b, sp. a
Anticalyptraea calyptrata
Oenonites aspersus
"Lumbriconereites" "obliquus"
Eunicites serrula
Arabellites contractus
Kozlowskiprion? sp. a
Paranereites sp.
Gen. et sp. indet. a
Ramphoprion sp.
Gen. et sp. indet. c
POLYCHAETE JAWS
COILED SERPULIDS

Fig. 26.


A
B
C
D
0 100 200 300 400
0 10
0 5 10
0 10 20 30 40 50 60 70 80 90 100
60 50 40 30 20 10 0
m a.s.l.
1016
1232
586
586
478
968
968
30 29 28 27 26 25 24 23 22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
0 5 10
%
0 100 200 300 400
(number of M/kg)
0 10 20 30
%
0 10 20 30 40 50 60 70 80 90 100
%
70 60 50 40 30 20 10 0
Absolute frequencies
Relative frequencies
Total sum of absolute frequencies:
⊙ "Lumbriconereites" "obliquus" (n MI/kg)
× Eunicites serrula (nM/kg)
△ Arabellites contractus
▲ Remaining species (10)
□ Oenonites? sp. a
● "Lumbriconereites" spatiosus
○ "Lumbriconereites" "obliquus"
■ Oenonites aspersus
× Eunicites serrula (note that this curve is reversed relative to the others)

species have also been identified using the same methods as those employed in reconstructing conodont apparatuses. Further work is required to identify the remaining jaw elements of these species.

I have not yet studied the type specimens of the species involved, and thus it is impossible at this stage to determine which of the many names used for single jaw elements has priority. Since the elements in my samples from the *"Pterygotus"* Beds can be compared easily with those figured in Hinde's (1882) paper, I have tentatively used his names where possible. As this is one of the oldest papers on scolecodonts it is reasonable to assume that most of Hinde's species names have priority, although some of the generic names that he used (Hinde 1879, 1880, 1882) will probably be replaced by others when full taxonomic revisions are made.

Descriptive terms used here are those in the "glossary of descriptive terms" of Jansonius & Craig (1971:257). I use 'cluster' in the sense of Pollock (1969:929) rather than 'assemblage' since the latter has been used with different meanings by different authors.

Annotated faunal list

Arabellites contractus Hinde, 1880 (Fig. 28:2A–B); *A. fastigiatus* Hinde, 1882 (Fig. 28:1A–B). The type species of *Arabellites* Hinde, 1879, is *A. hamatus* Hinde, 1879, and according to Hinde (1880, 1882) the two species here identified from Vattenfallet are congeneric. However, there may be some doubt as to whether both *contractus* and *fastigiatus* should be included in this genus. At present MII and MIV of *Arabellites* can not be identified at the species level and they are here referred to as *A.* sp. indet.

Kozlowskiprion? sp. *a* (Fig. 28:9). The MI of this species are similar to those of *K. longicavernosus* described by Kielan-Jaworowska (1966:98).

"Lumbriconereites" "obliquus" (Eichwald, 1854) (Fig. 28:7A–C). It is doubtful whether Hinde was correct in placing this species in the genus *Lumbriconereites,* and whether he correctly identified specimens with those of Eichwald's species. The jaws of the type specimen of the type species of *Lumbriconereites* Ehlers, 1868 are poorly preserved (Jansonius & Craig 1971:273), making a comparison between them and the specimens described by Hinde very difficult. The specific name *obliquus* Pander, 1856 was used by

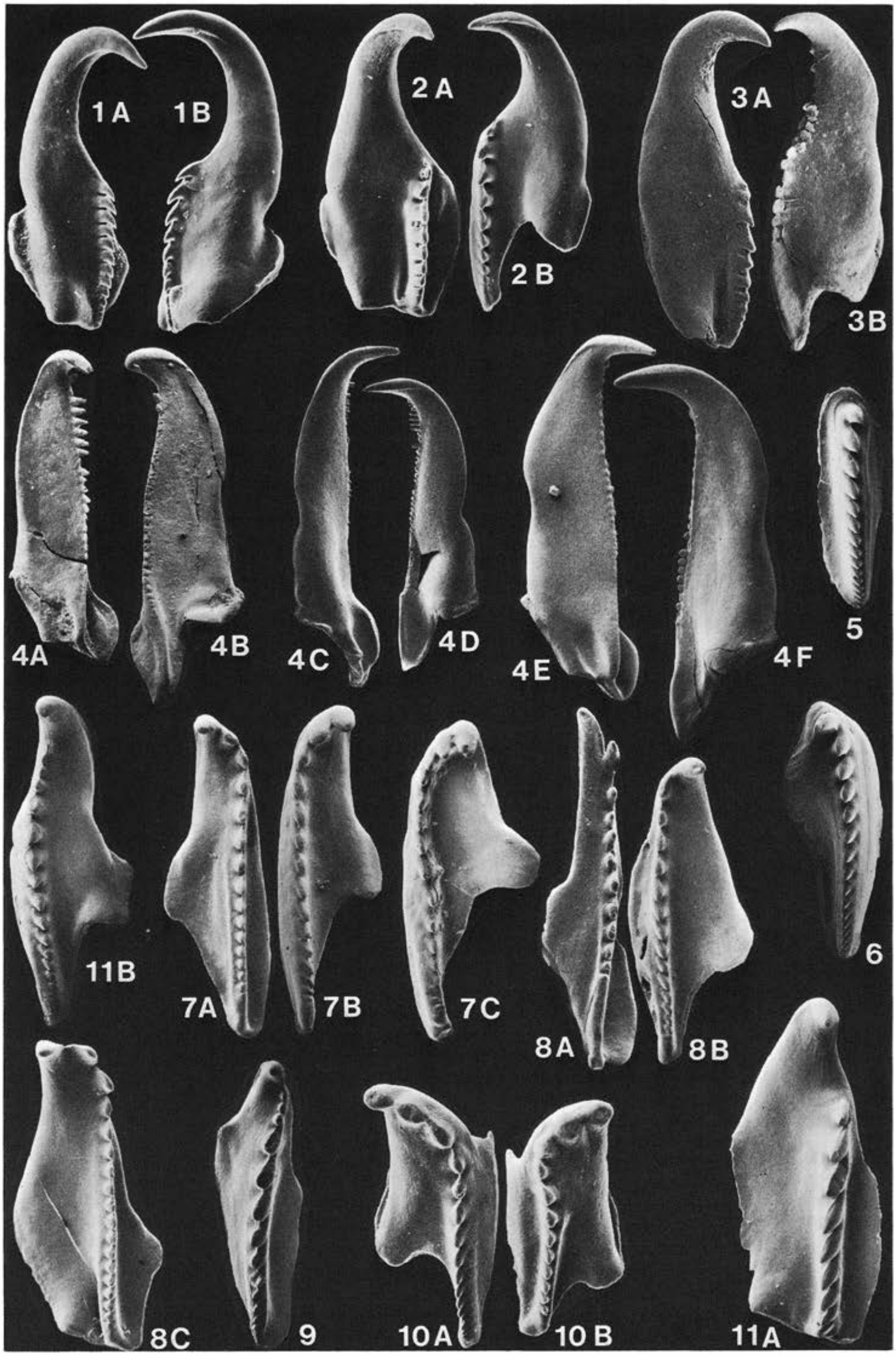
Fig. 27. Absolute and relative frequencies of jawed polychaete species at Vattenfallet. Adjacent samples having a low absolute frequency have been grouped together. The data are based on counts of MI except for *Eunicites* and Gen. et sp. indet. *b* and *c,* for which all maxillae have been counted. In B, C and D, samples containing less than 35 specimens have been grouped with the nearest sample below or above.

POLYCHAETE JAWS FROM VATTENFALLS-PROFILEN 1

SAMPLE NUMBER	LEVELS IN M A.S.L.	AMOUNT DISSOLVED MTRL (GRAM)	NUMBER OF ELEMENTS PER KILOGRAM	TOTAL NUMBER OF ELEMENTS	*Oenonites aspersus*		*"Lumbriconereites" "obliquus"*								*Eunicites serrula*	*Arabellites contractus*		*Kozlowskiprion? sp. a*		*Paranereites sp.*	*Gen. et sp. indet. a*		*Ramphoprion sp.*	
					l.MI	r.MI	l.MI	r.MI	l.MII	r.MII	l.MIV	r.MIV	bp	cr	M	l.MI	r.MI	l.MI	r.MI	MI	l.MI	r.MI	l.MI	r.MI
G. HOLM Pteryg. RM	29.6-30.0	?	?	784	5	8	220	263	4	10	4	5	57	–	28	2	5	–	3	–	–	1	–	–
LJUS KST RM	29.6-30.0	500	306	152	1	–	26	25	–	4	1	1	9	–	8	–	–	–	–	–	–	–	–	–
HERRMAN. RM	29.6-30.0	930	1688	1570	10	14	229	204	28	49	16	14	56	4	154	5	6	1	3	29	2	–	–	2
VALDARIA. RM	29.6-30.0	? 2000	1696	3392	34	48	582	502	58	94	26	40	240	–	207	18	32	5	5	6	–	6	–	–
LJUS SK RM	29.6-30.0	385	875	337	9	9	40	37	2	2	6	5	9	2	24	1	–	–	–	3	2	–	–	–
SGU	28.0-28.4	475	240	114	4	2	9	17	1	1	–	1	4	–	25	–	–	3	2	4	–	–	–	–
SGU	27.65-28.00	400	60	24	1	1	2	4	–	–	–	–	–	–	3	–	–	1	1	–	–	1	–	–
SGU	26.28-26.37	500	6	3	1	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
SGU	25.6-25.8	270	26	7	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SGU	24.6-24.7	145	979	142	7	2	15	20	1	4	4	3	1	1	27	–	1	–	2	3	–	–	–	3
SGU	23.70	285	393	112	7	2	13	17	3	2	2	–	3	2	17	–	5	–	–	1	–	–	–	–
SGU	22.90	195	677	132	2	8	18	25	4	2	1	1	3	–	20	–	–	1	–	3	–	–	2	–
SGU	22.40-22.50	245	384	94	4	2	13	19	3	2	1	–	4	–	9	2	–	1	–	–	–	1	–	–
SGU	20.9-21.4	180	339	61	5	3	3	7	2	1	–	1	–	–	10	–	1	–	1	3	–	–	1	–
SGU	20.40	185	849	157	5	6	9	13	5	7	1	5	3?	–	28	1	3	1	–	3	–	–	2	–
G70-1 LJ	19.87	500	312	156	6	4	15	27	1	13	–	–	5	–	35	–	–	1	1	4	–	2	4	4
G70-2 LJ	19.24-19.29	2500	785	1962	57	51	264	246	52	73	16	14	58	12	428	3	10	3	1	25	–	2	34	31
G70-3 LJ	18.52-18.57	500	198	99	6	2	20	19	–	9	1	–	–	–	9	–	–	–	–	–	–	1	2	–
G70-5 LJ	16.0-16.10	500	1518	759	51	46	57	76	18	22	3	5	12	13	175	2	2	4	3	22	2	1	2	12
G70-6 LJ	15.33-15.41	2500	393	982	51	39	49	90	19	30	6	1	13	6	342	1	1	4	8	25	–	1	5	2
G70-7 LJ	14.38-14.48	500	366	183	4	10	5	10	6	8	–	1	2	–	78	1	–	–	5	3	1	–	–	–
G70-8 LJ	13.33	2500	352	879	23	22	63	65	15	25	9	10	9	1	309	6	5	5	5	23	3	–	9	13
G70-9 LJ	12.38-12.43	500	50	25	1	–	–	2	2	1	–	–	1	–	–	–	–	–	–	–	–	–	1	–
G70-21 LJ	11.20-11.23	2500	44	110	1	4	4	7	1	1	2	–	1	–	46	–	1	–	–	2	–	–	2	1
G70-20 LJ	10.02-10.04	3670	112	412	17	21	19	24	6	9	6	6	8	–	121	12	8	8	19	–	–	–	5	7
G70-22 LJ	8.94	500	40	20	1	1	1	1	–	4	–	–	–	–	5	–	1	1	2	–	–	–	–	–
G70-19 LJ	6.49-6.54	500	40	20	1	–	1	4	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–
G70-18 LJ	5.59	500	48	24	1	–	3	3	–	1	–	–	1	–	–	–	–	1	–	–	–	–	–	–
G70-17 LJ	4.26-4.33	500	46	23	2	–	2	1	–	1	–	–	1	–	3	2	1	–	–	–	–	–	1	1
G70-16 LJ	3.06-3.16	500	48	24	3	1	–	–	1	1	–	1	1	–	5	1	–	–	–	4	1	–	–	–
G76-8 LJ	2.58-2.62	2000	100	199	10	6	1	2	6	8	2	2	2	–	57	2	7	–	–	8	1	–	6	6
G70-15 LJ	1.86-1.96	1300	75	98	9	3	2	2	–	2	2	–	–	–	10	11	10	–	–	1	1	–	–	–
G76-7 LJ	1.73-1.78	2000	19	37	2	4	–	1	–	–	–	–	–	–	12	1	1	–	–	3	–	1	–	–
G70-14 LJ	0.99-1.06	840	142	119	10	13	1	–	1	1	3	2	–	–	23	3	7	–	1	4	–	1	–	–
G76-6 LJ	0.94-0.99	2000	184	368	31	24	4	12	1	5	1	2	1	2	60	4	3	21	25	9	–	–	–	–
				13580	382	356	1694	1745	240	392	113	120	504	43	2284	79	110	61	87	187	13	18	76	82

TABLE 2. Frequencies of various polychaete jaw elements in the samples from Vattenfallet. The sample "Valdaria RM" was processed at the Riksmuseum and the other samples by L. Jeppsson. Abbreviations in sample numbers: RM=Riksmuseum; SGU=Geological Survey of Sweden (Liljevall's samples); LJ=L. Jeppsson, Lund. Note the small sample weight in some samples from Högklint *b* and *c*.

Gen. et sp. indet. c	Gen. et sp. indet. b	*Eunicites* sp. a	*Arabellites fastigiatus*		"*Lumbriconereites*" *spatiosus*					Gen. et sp. indet. d	*Oenonites*? sp. a		*Xanioprion* sp. a	*Oenonites* sp. indet.			*Arabellites* sp. indet.				Sp. a	Gen. et sp. indet.	Mandibel sp. indet.					Anterior and lateral teeth
M	M	M	l.MI	r.MI	l.MI	r.MI	lbp	bp	cr	MI?	l.MI	r.MI	bp	l.MII	r.MII	cr	l.MII	r.MII	l.MIV	r.MIV	bp?	M?	MIII?	MIV	A	B	C	
–	–	–	1	3	60	59	1	–	–	1	–	2	–	11	13	–	–	–	–	–	–	–	5	–	1	–	–	12
–	–	–	1	–	12	18	2	1	–	–	1	3	–	1	–	–	–	–	–	–	–	3	9	–	2	–	–	25
–	–	–	2	2	93	94	11	6	–	–	51	44	–	66	51	–	1	–	–	–	–	54	59	53	17	2	–	138
–	–	–	9	6	442	469	8	–	–	–	36	56	–	50	74	–	2	8	1	3	1	25	96	40	18	–	–	145
–	–	–	1	–	7	15	8	2	–	–	2	3	1	14	5	–	–	–	–	–	–	7	39	72	–	1	–	9
–	–	–	–	–	3	2	–	–	–	–	–	–	–	2	3	–	–	–	–	–	–	–	2	10	2	1	–	16
–	–	–	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	–	2	–	–	4
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1	1	–	–	–	–	–
–	–	1	–	–	2	2	–	–	–	–	–	–	–	1	4	–	–	–	1	–	–	–	18	4	2	–	–	13
–	–	–	1	–	–	1	–	–	–	–	–	–	–	3	3	1	–	1	–	–	–	–	5	3	3	–	–	17
–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	–	1	–	–	1	–	1	6	5	4	1	–	17
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	7	11	3	–	–	10
–	1	–	–	–	–	1	–	–	–	–	–	–	–	1	2	–	1	1	–	–	–	–	3	2	1	–	–	10
–	–	–	1	–	–	–	–	–	–	–	–	–	–	6	3	–	1	2	1	1	3	–	9	3	4	1	1	29
–	–	–	–	–	–	1	–	–	–	–	–	–	–	2	1	–	1	–	–	–	–	2	7	4	7	1	–	8
–	–	–	8	4	6	21	3	3	2	–	–	–	–	25	48	1	5	4	1	1	1	23	115	77	63	13	6	152
–	–	–	–	–	1	–	–	–	–	–	–	–	–	3	2	1	1	–	–	–	–	–	5	4	6	–	–	7
–	–	–	12	11	3	2	1	–	–	1	–	–	–	32	28	5	3	1	–	–	–	1	28	27	28	4	–	44
–	–	1	1	–	4	4	–	2	–	–	–	–	–	23	38	1	–	–	–	–	1	–	52	48	29	–	6	79
–	–	1	–	1	–	–	–	1	–	–	–	–	–	7	4	–	–	1	1	1	–	–	7	12	6	–	–	7
–	–	–	8	13	1	4	–	5	–	1	–	–	–	16	19	2	2	1	1	–	–	–	44	22	41	4	3	72
–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	7
–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	6	–	1	–	–	–	–	1	2	8	6	–	–	11
–	1	–	–	–	–	–	–	–	–	–	–	–	–	5	11	2	2	2	3	2	1	–	27	14	19	–	3	24
–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	1	–	–	–	–
1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	3	3	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	2	–	8	–	1	–	–	2
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	2	–	–	–	–	1	–	1	–	–	2
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	2
–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	15	–	1	2	1	2	–	–	17	9	12	1	1	6
–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	6	–	4	4	1	2	2	–	7	6	–	–	–	7
–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	1	–	1	–	1	–	–	–	1	–	–	–	–	3
–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	6	–	4	2	2	2	2	–	8	8	5	–	–	2
–	–	–	–	–	–	–	–	–	–	–	–	–		27	24	3	–	6	3	1	2	–	49	15	7	6	–	20
1	2	12	45	40	634	694	34	20	2	3	90	108	1	329	375	16	31	38	17	16	15	118	645	463	290	35	20	900


1A
1B
2A
2B
3A
3B
4A
4B
4C
4D
4E
4F
5
11B
7A
7B
7C
8A
8B
6
8C
9
10A
10B
11A

Hinde without having studied the type material. Therefore I use *"L."* *"obliquus"* only as a tentative name. The possibility that some of the MII, MIV, basal plates, and carriers which I include here might belong to other species cannot be excluded.

"Lumbriconereites" spatiosus Hinde, 1882 (Fig. 28:10A–B).

Oenonites aspersus Hinde, 1879 (Fig. 28:4A–F). Hinde referred the MI of this species to *O. aspersus* and the MII to *Arabellites anglicus*. As both species names were published in the same paper either may be used and I provisionally use the name that was based on the MI. Lange (1947) noted that the MI of *O. aspersus* were similar to those of the specimens he named *Paulinites paranaensis*. Two clusters from Gotland were described by Martinsson (1960) as strikingly similar to the MI and MII of *P. paranaensis*. In my opinion the clusters described by Martinsson as *P. burgensis* are even more closely related to *O. aspersus* than to *P. paranaensis*. In fact, *P. burgensis* and *O. aspersus* may well be conspecific. So far I have not been able to distinguish the MII and carriers of *O. aspersus* from those belonging to *Oenonites?* sp. *a*, so I have therefore referred all these elements of *Oenonites* to *O.* sp. indet.

Oenonites? sp. *a* (Fig. 28:3A–B). The MI show a slight similarity to the illustrations of the MI of *Arabellites hamatus* Hinde (1879, Pl. 18:12; 1882, Pl. 2:42–44).

Paranereites sp. The MI of this species are somewhat similar to those figured by Eisenack (1939:168, Fig. 13) as *Paranereites*.

Ramphoprion sp. (Fig. 28:8A–C). The left MI (Fig. 28:8C) is similar to that of *Ramphoprion* sp. *b* of Kielan-Jaworowska (1966:11).

Eunicites serrula (Hinde, 1880) (Figs. 28:5–6). This name is used here for a group of jaws of which some are similar to those figured by Hinde (1880, Pl.

Fig. 28. All figures are SEM photographs of specimens from Vattenfallet. Specimen numbers preceded by LO refer to the collections of the Department of Historical Geology and Palaontology, University of Lund, and those by An to collections of the Section of Palaeozoology, Swedish Museum of Natural History, Stockholm. All specimens from the *"Pterygotus"* Beds (29.0–30.0 m) are from a Riksmuseum sample crowded with *Valdaria testudo*. 1. *Arabellites fastigiatus:* A, left MI, ×60, 29.6–30.0 m, An 2644; B, right MI, ×60, 29.6–30.0 m, An 2645. 2. *Arabellites contractus:* A, left MI, ×60, 29.6–30.0 m, An 2646; B, right MI, ×60, 29.6–30.0 m, An 2647. 3. *Oenonites?* sp. *a*: A, left MI, ×37, 29.6–30.0 m, An 2648; B, right MI, ×45, 29.6–30.0 m, An 2649. 4. *Oenonites aspersus:* A, left MI, ×45, Sample G70–10 L.J. (13.33 m), LO 5082; B, right MI, X30, 29.6–30.0 m, An 2650; C, left MI, ×45, 29.6–30.0 m, An 2651; D, right MI, ×45, 29.6–30.0 m, An 2652; E, left MI, ×45, 29.6–30.0 m, An 2653; F, right MI, ×45, 29.6–30.0 m, An 2654. 5. *Eunicites serrula,* M?, ×30, Sample G70–20 L.J. (10.02–10.04) m, LO 5083. 6. *Eunicites serrula:* M?, ×30. Sample G70–20 L.J. (10.02–10.04 m), LO 5084. 7. *"Lumbriconereites" "obliquus":* A, left MI, ×40, 29.6–30.0 m, An 2655; B, right MI, ×50, 29.6–30.0 m, An 2656; C, left MI, ×150, Sample G70–20 L.J. (10.02–10.04 m), LO 5085. 8. *Ramphoprion* sp.: A, left MI, ×55, Sample G70–20 L.J. (10.02–10.04 m). LO 5086; B, right MI, ×75, Sample G70–20 L.J. (10.02–10.04 m), LO 5087; C, left MI, ×90, Sample G70–20 L.J. (10.02–10.04 m) LO5088. 9. *Kozlowskiprion?* sp., left MI, ×60, Sample G70–20 L.J. (10.02–10.04 m), LO 5089. 10. *"Lumbriconereites" spatiosus:* A, left MI, ×45, 29.6–30.0 m, An 2657; B, right MI, ×45, 29.6–30.0 m, An 2658. 11. Gen. et sp. indet. *a:* A, left MI, ×60, Sample G70–8 L.J. (13.33 m), LO 5090; B, right MI, ×15, 29.6–30.0 m, An 2659.

14:18–20; 1882, Pl. 1:11,12). Some of the jaws designated as MIV without any generic and specific name might also belong to *E. serrula*.

Eunicites sp. *a*. The jaws resemble those figured by Kielan-Jaworowska (1966:62) as *Pristioprion* sp. *b*.

Xanioprion sp. One basal plate is similar to the specimen figured by Szaniawski (1970, Pl. 4:2) as *X. borealis* Kielan-Jaworowska, 1962.

Gen. et sp. indet. *a* (Fig. 28:11A–B). Only the MI are as yet identified. They are somewhat similar to "*L.*" "*obliquus*" but differ in having a more prominent fang which forms a hook.

Gen. et sp. indet. *b*. Only two MI were found.

Gen. et sp. indet. *c*. The one jaw element found is somewhat comparable with that discussed and figured by Kielan-Jaworowska (1966:117, Pl. 15:1c–d) as *Kalloprion* sp. *a*.

Gen. et sp. indet. *d*. Three jaw elements (MI?) resemble the one figured by Stauffer (1933:1200) as *Paleonereites*.

Basal plates? sp. *a*. Under this designation I include elements that are presumably basal plates of one species, probably one of those listed above.

MIII?. Jaw elements that might be MIII from several species.

MIV. Most of these jaw elements probably belong to *Eunicites serrula*.

M?, Gen. et sp. indet. Specimens that have neither been identified taxonomically nor assigned to a type of element. The elements are of the same type and they all belong to the same species.

Mandibles. Three different types have been found. *A*, similar to those figured by Eisenack (1939:169) as *Palaeosigma*. *B*, similar to those figured by Stauffer (1933:1205) as *Northrites*. *C*, resembling *Northrites* but more slender.

Anterior and lateral teeth. A general "wastebasket" group in which different indeterminate anterior and lateral elements have been placed.

Eight clusters were found in the material from the section, of which seven, with two or four elements fused, are from Högklint *b*. Five of the clusters are identified as *O. aspersus* and the others as *A. fastigiatus* and "*L. obliquus*", respectively. A single cluster found on a bedding plane in the "*Pterygotus*" Beds by Lindström is referred to "*L.*" "*obliquus*". The nine elements in this cluster are not fused.

Discussion

The abundance of polychaete jaws in the Upper Visby Marl and Högklint *a* is relatively low, between 10 to 100 MI/kg (Fig. 27:A), and this low abundance is coupled with a fairly low taxonomic diversity (Fig. 26). There is a pronounced increase in abundance in Högklint *b*, where it varies from 125 to 968 MI/kg (Fig. 27:A). This high figure might not be a reflection only of the shallower water depths, since variation in abundance can also depend on differences in the rate of sedimentation. Högklint *c* shows a high variation in abundance, from 6 to 540 MI/kg. The taxonomic diversity is somewhat lower than in Högklint *b*. Högklint *d* (*"Pterygotus"* Beds) shows a variation in abundance from 140 to 1200 MI/kg.

The relative frequencies of various species is shown in Fig. 27D. Data on *Eunicites serrula* may be incomplete because its jaw apparatus may include elements additional to MI, making a comparison between this and the other species somewhat tenuous. In order to distinguish the *E. serrula* curve easily from those of the other species, it has been drawn reversed. *"Lumbriconereites" "obliquus"* and *Eunicites serrula* are the most abundant taxa in the section (Fig. 27A), forming together 40 to 80 per cent of the total counts. It is interesting to note that the curves of these two species show a conspicuous correlation in that they change almost simultaneously and with about the same magnitude. This might indicate that the variation in absolute frequency reflects variations in the rate of deposition. The relative frequency curve of *"L." "obliquus"* is roughly reversed in comparison with that of *Oenonites aspersus* (Fig. 27D). The relative frequency of *Arabellites contractus* (Fig. 27B) is lower in the Högklint Beds than in the Upper Visby Marl and it thus appears that this species is relatively more common in deep water deposits than those of shallower water environments.

It is not always appreciated that the polychaetes represented by the jaw elements were large animals. In some modern nereid species the body of a complete individual is 20 to 50 times longer than its MI (Forney 1974). At Vattenfallet the largest MI element found belongs to *"Lumbriconereites" "obliquus"* and is about 9 mm long. The complete animal may have had a body length of up to half a metre.

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Coiled serpulid polychaetes

KENT LARSSON

Silurian coiled serpulids are largely undescribed. Lindström (1884) described a form from Gotland as *Autodeteus* (=*Anticalyptraea*) *calyptrata* Schrenk and referred it to phorid gastropods, but more likely it represents a serpulid. The rest of the Gotland serpulids have never been described, and the species and genus concept applied herein to the Vattenfallet material must be regarded as highly tentative.

Coiled serpulids occur encrusting various skeletal remains, but are particularly abundant on the lower side of tabulate and stromatoporoid colonies. The material from Vattenfallet comprises about 40 specimens (for the range see Fig. 29).

Faunal list

Anticalyptraea calyptrata (Schrenk), coiled serpulid gen. *a*, sp. *a*, coiled serpulid gen. *a,* sp. *b,* coiled serpulid gen. *b*, sp. *a.* In addition, indeterminate specimens have been recorded at 1.1–1.3 and 7.0 m, and a specimen of coiled serpulid n. gen. *a,* sp. indet. in Högklint *d*.

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Monoplacophorans

JOHN S. PEEL and KRISTINA WÄNGBERG-ERIKSSON

Monoplacophorans from Gotland were described in Lindström's monographic study mentioned in the chapter on gastropods. In the Vattenfallet material the group is represented by 4 specimens of the large species *Pilina unguis* (Lindström) (for distribution see Fig. 29). *Pilina* appears to have been a relatively mobile, deposit feeding or browsing member of the epifauna (Peel 1977).

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Polyplacophorans

KRISTINA WÄNGBERG-ERIKSSON

Representatives of polyplacophorans are rarely found in the Silurian of Gotland. The existing museum material has been described by Bergenhayn (1943, 1955). At Vattenfallet only one unidentifiable fragmentary valve has been found at the 28.60–28.80 m level (Högklint *c*).

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Gastropods

JOHN S. PEEL and KRISTINA WÄNGBERG-ERIKSSON

The Silurian gastropods and monoplacophorans of Gotland are principally known through the monographic study of Lindström (1884) – a classic work summarising in detail earlier studies and describing 174 species with superb illustrations made by G. Liljevall. Lindström's monograph has remained essentially unrevised. Several of his described species have subsequently been renamed or designated type species of new genera, although often only on the basis of the original descriptions and illustrations. Lindström's unusual conception of Gotland stratigraphy and the passage of time have left their mark, but the work remains a scholarly and uniform treatment of the entire fauna as then known. As such, it inevitably forms the basis for the identification of the material from Vattenfallet.

The total number of gastropod specimens from the section is 235. A large proportion of species entered in the log (Fig. 29) is only identified at an ill-defined systematic level, e.g. Platyceratacea sp. indet. *a*. To some extent this open nomenclature reflects material which needs to be revised monographically before a meaningful identification can be presented. The principal reason, however, is poor preservation. Many specimens are represented by internal moulds without any remaining trace of the shell. This is in itself a common feature of gastropod faunas from many areas and is due to the preferential solubility of aragonite. Other forms, such as *Euomphalopterus*, *Oriostoma* and *Platyceras*, frequently have an excellently preserved shell surface, owing to a thin outer calcitic layer in the shell that is apparently missing in many of the other taxa.

Annotated faunal list

Bellerophontacea

Prosoptychus sphaera (Lindström), *Boiotremus* n.sp. *a*, *Liljevallospira tubulosa* (Lindström), Bellerophontacea sp. indet. *a*, *b* and *c*.

Boiotremus n.sp. *a* (Peel, in ms.) differs from the characteristic *B. longitudinalis* (Lindström) from the Upper Visby Marl in being smaller, having a less expanding aperture, and in frequently developing coarser ornamentation.

Euomphalacea

Poleumita discors (Sowerby), *P. rugosa* (Sowerby), Euomphalidae sp. indet. *a* (15–16 m).

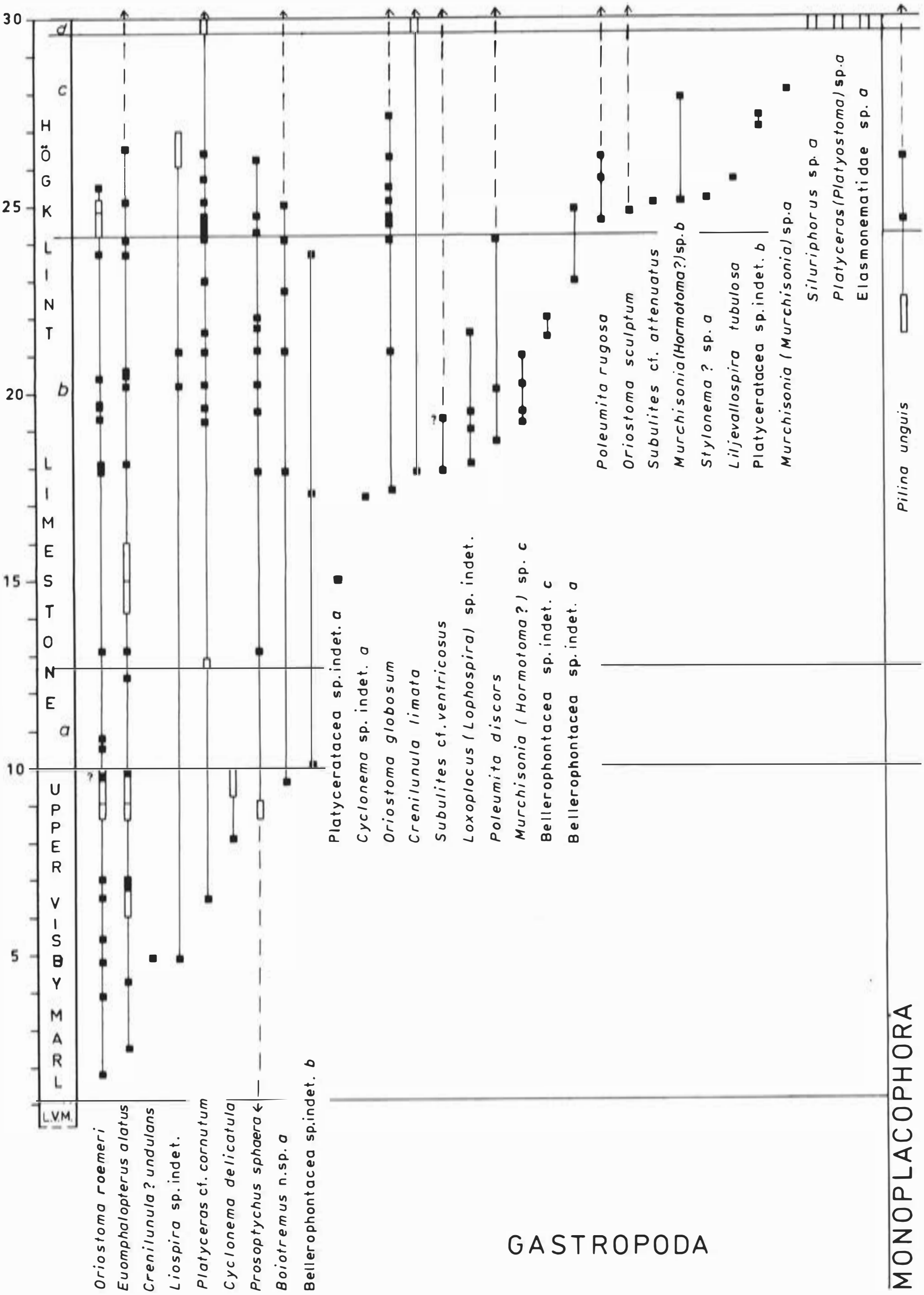
30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
Oriostoma roemeri
Euomphalopterus alatus
Crenilunula ? undulans
Liospira sp. indet.
Platyceras cf. cornutum
Cyclonema delicatula
Prosoptychus sphaera
Boiotremus n.sp. a
Bellerophontacea sp.indet. b
Platyceratacea sp.indet. a
Cyclonema sp. indet. a
Oriostoma globosum
Crenilunula limata
Subulites cf. ventricosus
Loxoplocus (Lophospira) sp. indet.
Poleumita discors
Murchisonia (Hormotoma ?) sp. c
Bellerophontacea sp.indet. c
Bellerophontacea sp.indet. a
Poleumita rugosa
Oriostoma sculptum
Subulites cf. attenuatus
Murchisonia (Hormotoma?) sp. b
Stylonema ? sp. a
Liljevallospira tubulosa
Platyceratacea sp.indet. b
Murchisonia (Murchisonia) sp. a
Siluriphorus sp. a
Platyceras (Platyostoma) sp. a
Elasmonematidae sp. a
Pilina unguis
GASTROPODA
MONOPLACOPHORA

Fig. 29.

Pleurotomariacea

Crenilunula limata (Lindström), *C.? undulans* (Lindström), *Euomphalopterus alatus* (Wahlenberg), *Liospira* sp. indet., *Loxoplocus (Lophospira)* sp. indet.

Knight (1945) in designating *Pleurotomaria limata* Lindström, 1884 as type species of *Crenilunula* equated the Gotland species with *Euomphalus carinatus* Sowerby in Murchison, 1839. Unfortunately, most of Sowerby's Silurian gastropods are poorly known and inadequately illustrated and there is little to be gained from enforcing the synonymies without a thorough revision.

Platyceratacea

Platyceras (Platyostoma?) cf. *cornutum* (Hisinger), *P. (Platyostoma)* sp. *a*, *Cyclonema (Cyclonema) delicatulum* (Lindström), *C. (C.)*. sp. indet. *a*, Elasmonematidae sp. *a*, Platyceratacea sp. indet. *a* and *b*.

A variety of platyceratids, compared to *P. cornutum* (Hisinger), occurs throughout the Vattenfallet section. The coprophagous mode of life of these gastropods produces tremendous variation in shell morphology. In the absence of monographic revision it is not considered meaningful to attempt to recognize distinct species within this complex.

Oriostomatacea

Oriostoma globosum (Schlotheim), *O. sculptum* (Sowerby), *O. roemeri* Lindström.

Murchisoniacea

Murchisonia (Murchisonia) sp. *a*, *M. (Hormotoma?)* sp. *b*, *M.* (*H.*?) sp. *c*, Murchisoniidae sp. indet. *a* (1.7–1.9 m) and *b* (22.80 m).

Pseudophoracea

Siluriphorus sp. *a*.

Loxonematacea

Stylonema? sp. *a*.

Subulitacea

Subulites cf. *attenuatus* Lindström, *S.* cf. *ventricosus* Hall, *S.* sp. indet. (2.5 m).

Ecological comments

The great majority of Lower Palaeozoic gastropods were referred to the Archaeogastropoda by Knight et al. (1960). In contrast, two thirds of present day prosobranchs are referred to the Caenogastropoda (= Mesogastropoda + Neogastropoda) and have relatively advanced ctenidia capable of coping with fine suspended sediment in soft substratum environments. Lower Palaeozoic archaeogastropods are generally considered to be herbivores living on relatively firm substrata in conditions of clear water, by analogy with most extant members of the order. However, many Lower Palaeozoic archaeogastropods display morphological characters which are readily interpreted as adaptation to life on relatively soft substrata. Others are associated with fine-grained sediments possibly indicative of similar bottom conditions. Their presence in such environments can partly be explained in terms of various types of foliage support but the frequent large size and heavy calcification of shells of many species provides difficulties in this respect. It is becoming increasingly evident that close ecological comparison between extant archaeogastropods and Lower Palaeozoic supposed archaeogastropods provides a seriously limited picture of the range in modes of life followed by gastropods in the Lower Palaeozoic.

Most of the Vattenfallet gastropods were probably epifaunal deposit feeding microherbivores, although some may have browsed on algal foliage. It is difficult to find evidence of carnivorism but the rare caenogastropod *Subulites* possibly lived in this way. Platyceratids are frequently coprophagous, living on the calices of echinoderms and ingesting their expelled faeces. Other, more regularly coiled platyceratids, e.g. *Cyclonema,* were probably sluggish carnivores or scavengers.

Several species of *Oriostoma* are of common occurrence at Vattenfallet. Their abundance, large size and thick, heavily ornamented shells suggest a deposit feeding existence. The common pleurotomariacean *Euomphalopterus alatus,* also probably a deposit feeder, is characterized by a wide flange at the whorl periphery which may be an adaptation to prevent sinking into a soft substratum by increase in surface area.

The development of an explanate aperture in bellerophontaceans has been interpreted as an adaptation to life on a soft substratum (Peel 1974). *Boiotremus* n.sp. *a*, and to a lesser extent *Prosoptychus sphaera,* develop such expanded apertures during the later growth stages.

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Pelecypods

JOHN POJETA, Jr

Present knowledge of the Silurian pelecypods of Gotland is meager. Many of the reported taxa are known only from faunal lists, various taxa were described in more general faunal studies (Hisinger, 1837, 1840; Lindström 1880), and to my knowledge only two studies have been devoted entirely to pelecypods (Walmsley 1962; Soot-Ryen 1964). Although pelecypods are reasonably abundant at Vattenfallet (89 specimens), they are not well preserved, and most of the forms mentioned herein are treated within open nomenclature.

For distribution in the section see Fig. 30.

Faunal list

Ambonychiacea: *Mytilacra* sp. *a*.

Pteriacea: *Actinopteria* sp. *a*, *A*. sp. *b*, *A*. spp. indet., *Pteronitella?* sp. *a*, Pteriacea gen. et sp. indet.

Mytilacea: Modiomorphidae? sp. indet., *Goniophora* sp. *a*.

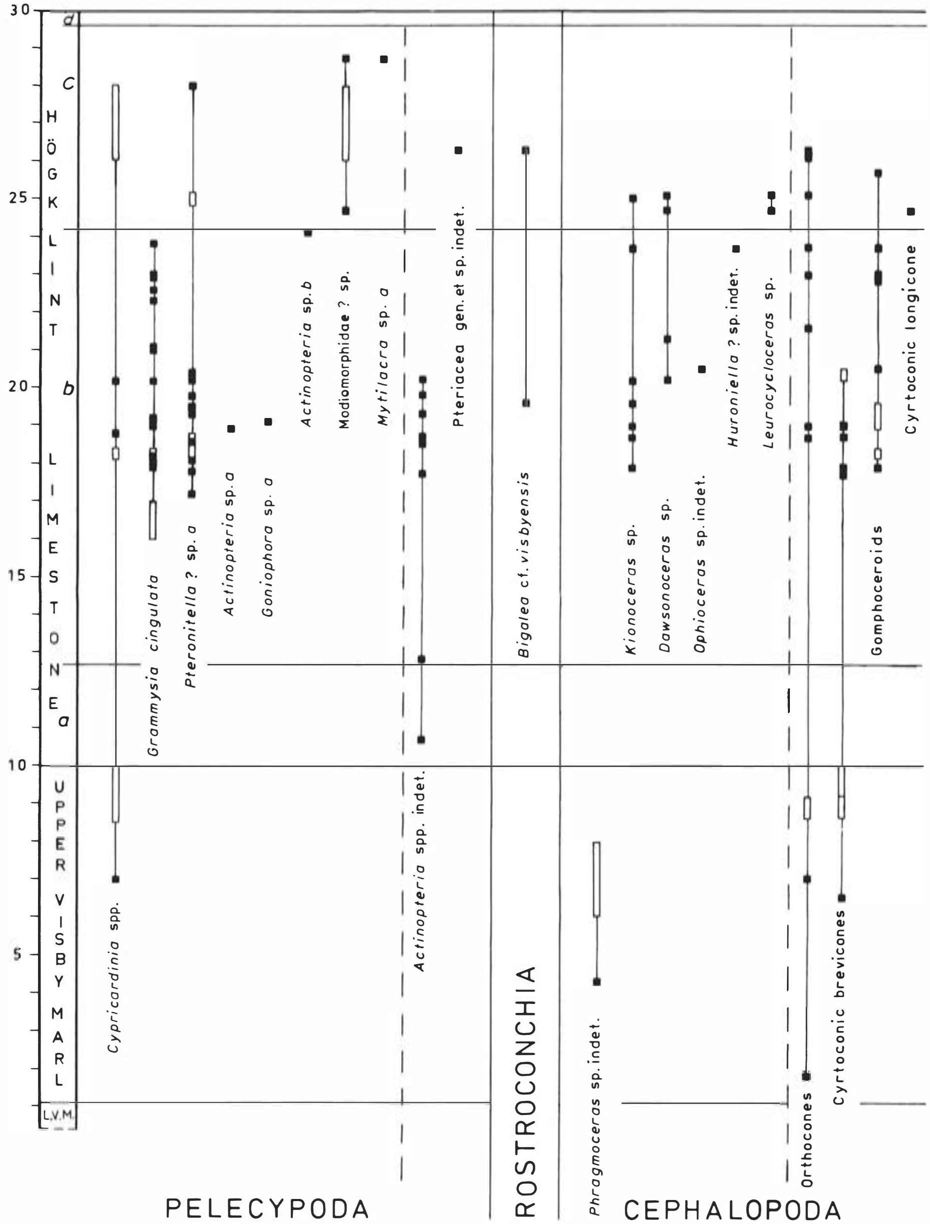
Crassatellaceas: *Cypricardinia* spp.

Pholadomyacea: *Grammysia cingulata* (Hisinger).

Discussion

The most common pelecypods in the material from the section are *Grammysia cingulata* (28 specimens), *Pteronitella*? sp.*a* (18) and *Actinopteria* spp. (13).

Pteronitella is a reasonably common genus in the Ludlovian rocks of Gotland (Walmsley 1962, 1964). The Lower Wenlockian species herein assigned to that genus has the general form of *Pteronitella* in that it lacks a prominent posterior wing, has prominent comarginal ornament, and the anterior auricle is not strongly delimited from the rest of the shell. However, the dentition of the Vattenfallet specimens is not known, furthermore they are biconvex and possibly equivalved. Thus, the Vattenfallet specimens are identified as *Pteronitella*? sp. *a*. *Pteronitella retroflexa* (Wahlenberg), the type species of


30
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5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
Cypricardinia spp.
Grammysia cingulata
Pteronitella ? sp. a
Actinopteria sp. a
Goniophora sp. a
Actinopteria sp. b
Modiomorphidae ? sp.
Mytilacra sp. a
Actinopteria spp. indet.
Pteriacea gen. et sp. indet.
Bigalea cf. visbyensis
Phragmoceras sp. indet.
Kionoceras sp.
Dawsonoceras sp.
Ophioceras sp. indet.
Huroniella ? sp. indet.
Leurocycloceras sp.
Orthocones
Cyrtoconic brevicones
Gomphoceroids
Cyrtoconic longicone
PELECYPODA
ROSTROCONCHIA
CEPHALOPODA

Fig. 30.

Pteronitella, has very prominent dentition and is markedly inequivalved (Walmsley 1962, 1964).

With the possible exception of *Grammysia cingulata*, all the pelecypods known from Vattenfallet were byssally attached to the substrate (for discussions of various bysally attached Paleozoic pelecypods see Pojeta 1962, 1966; Bambach 1971; Stanley 1972; Runnegar 1974), and all known forms were suspension feeders. There are two modes of life among byssate pelecypods, partial burial in the substrate (endobyssate or semi-infaunal) and attachment to the surface of the substrate (epibyssate or epifaunal).

Bambach (1971) has presented evidence that *Grammysia obliqua* (McCoy) from the Upper Silurian rocks of Nova Scotia, was an endobyssate filter feeder. His documentation for this mode of life for that species includes the presence of a byssal gape and the finding of specimens of *G. obliqua* in life position. Runnegar (1974:914) has suggested the same mode of life for Devonian species of *Grammysia;* he noted that in Devonian forms, the anterior adductor muscle scar is very small, which is a common feature in byssally attached pelecypods.

None of the known specimens of *G. cingulata* from Vattenfallet preserve the muscle scars or show evidence of a byssal gape, although some of them suggest the presence of a posterodorsal gape in the species. Various pelecypods that have a prominent byssus do not have an obvious byssal gape (Pojeta 1962, 1966); however, such forms usually show a byssal sinus in lateral view. Neither *G. cingulata* nor *G. obliqua* show a byssal sinus. *Grammysia cingulata* may have been endobyssate like younger species of *Grammysia,* or it may have been a sluggish shallow burrower. The latter mode of life was suggested as possible for the genus *Cuneamya* (Runnegar 1974:914), the likely ancestor of *Grammysia*.

Mytilarca has a highly reduced anterior end and lacks an anterior lobe (Pojeta 1966); it was probably epibyssate (Stanley 1972). All other pelecypods from Vattenfallet are in Stanley's (1972) endobyssate category, although their inclusion there needs to be documented by the finding of specimens in life position.

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Rostroconchs

JOHN POJETA, Jr

The rostroconchs from Gotland were included in a general revision of rostroconch molluscs by Pojeta & Runnegar (1976). In the material from Vattenfallet rostroconchs are represented only by six specimens of which three (26.28–26.37 m and from the *"Pterygotus"* Beds) are unidentifiable and one (*Hippocardia* sp.) lacks any information about the level. Two specimens have been identified as *Bigalea* cf. *visbyensis* Pojeta and Runnegar and entered into the log (Fig. 30). The rostroconchs from the section were probably infaunal deposit feeders (Pojeta & Runnegar 1976).

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Cephalopods

HARRY MUTVEI

In *Fragmenta Silurica* nine species of cephalopods were described from Gotland (Angelin *in* Angelin & Lindström 1880), but by 1885 Lindström estimated the total number of Gotland species to be at least 100. However, it is more likely that the actual number exceeds 200. To date, the only major groups which have been described monographically are ascoceratids (17 species) and ophidioceratids (2 species; both by Lindström 1890), and phragmoceratids (32 species; Hedström 1917). Occasional species of actinoceratids and orthoceratids have been described or revised by Teichert (1934) and Mutvei (1957, 1964a). Thus, only a small fraction of the Gotland material has been adequately described, forming a serious obstacle to the identification of specimens from Vattenfallet.

The total number of cephalopod specimens in the Vattenfallet material is 64, comprising at least 16 genera. Of these, six taxa have been identified at the generic level. The remainder were grouped according to the shape of their shells: gomphoceroids, cyrtoconic brevicones, cyrtoconic longicones and orthocones. The preservation is variable with the shell wall partially or wholly dissolved in several specimens. Many shells have been crushed during the compaction of the sediment. The shell chambers are frequently filled by a coarse calcitic spar, and the structure of the wall of the siphonal tube is poorly preserved. Under these circumstances, identification of the majority of the cephalopods has not been possible.

For distribution see Fig. 30.

Faunal list

Orthoceratidae: *Leurocycloceras* sp., *Kionoceras* sp.

Dawsonoceratidae: *Dawsonoceras* sp.

Phragmoceratidae: *Phragmoceras* sp. indet.

Ophidioceratidae: *Ophioceras* sp. indet.

Huroniidae: *Huroniella*? sp. indet.

A very rough estimate of the possible number of different cephalopod species in the material from each lithostratigraphical unit of the section gives the following data: Upper Visby Marl 4 species, Högklint *b* 11 species, and Högklint *c* 7 species. No cephalopod has been found in Högklint *a* and Högklint *d*.

Ecological remarks

The only survivor of the ectocochleate cephalopods, *Nautilus*, has a specialized mode of life, in being a mobile benthic scavenger. It lives in deep waters (300–500 m), but migrates seasonally to the shore, probably when spawning (Hamada & Mikami 1977). The recent coleoids are active carnivores, having a vagile benthic, or nektic to pseudoplanktic mode of life. The oceanic squids belonging to the last category are particularly numerous. Many of them float with the aid of ammonium chloride in their tissues, thus maintaining buoyancy without possessing chambered shells (Denton 1974). The mantle musculature and swimming ability are often more or less reduced. The majority of living coleoids catch live prey with their long tentacles.

The orthocones, cyrtoconic brevicones and cyrtoconic longicones from Vattenfallet certainly had poor swimming ability. This conclusion is supported by the fact that, to judge from their attachment to the shell, the retractor muscles were small and their relationship to the main mantle cavity was different from that in *Nautilus* (Mutvei 1964b). The structure of the siphonal tube clearly indicates that it was used in regulation of the volume of cameral liquid and thus these nautiloids were not benthic but pseudoplanktic, and undertook vertical migration.

The gomphoceroid nautiloids, together with *Phragmoceras*, were not efficient swimmers, as indicated by their poorly streamlined shells. Adult gomphoceroids are especially common in reef mounds and their mode of life may have been adapted to that general environment. Only mature specimens with constricted apertures have been found. The young animals probably lived in a different biotope. The constricted apertures allowed only microphagous feeding. It is interesting to note that the retractor muscles were numerous and arranged uniformly around the body (Mutvei 1964b). Their unique arrangement may have been somehow connected to a microphagous feeding habit. It is not possible to determine whether the gomphoceroids were benthic or pseudoplanktic.

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Trilobites

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DEREK J. SIVETER, and RONALD TRIPP

The last comprehensive review of the trilobites from Gotland was that by Lindström (1885). Since then a few additional species have been described but only some small groups have been thoroughly revised (Odontopleuridae, Bruton 1967; *Encrinurus punctatus* group, Tripp 1962). Proetids and calymenids are currently being described monographically by R.M. Owens and D.J. Siveter, respectively, but most of the remainder of the fauna is badly in need of revision.

The total number of specimens of trilobites in the material from Vattenfallet is 846, distributed among the following families: Odontopleuridae (14 specimens), Illaenidae (39), Cheiruridae (8), Proetidae (265), Aulacopleuridae (1), Phacopidae (225), Dalmanitidae (1), Calymenidae (120), Encrinuridae (150), and Lichidae (23). The total number of individuals may have been somewhat smaller than the number of specimens recorded, since in any one bed several specimens might have belonged to a single disarticulated specimen, but it is impossible to determine this. Moreover, occasionally, small specimens may have been moult stages of individuals represented in the same bed by large specimens.

In this paper Bruton is responsible for odontopleurids, Jaanusson for illaenids and cheirurids, Owens for proetids, aulacopleurids, phacopids, and dalmanitids, Siveter for calymenids, and Tripp for encrinurids and lichids.

For ranges in the section see Fig. 31.

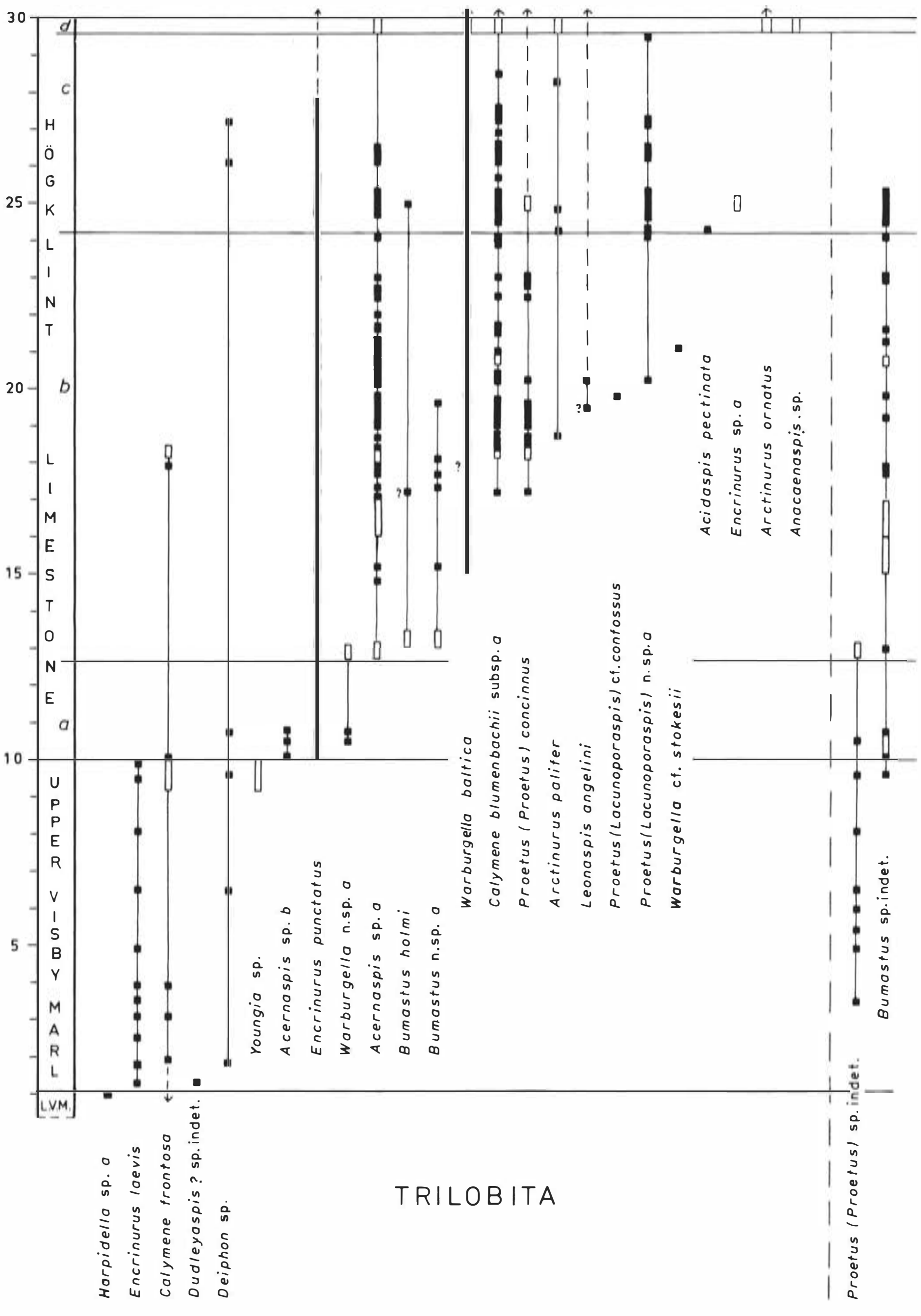
Annotated faunal list

Odontopleuridae

Dudleyaspis? sp. indet., *Leonaspis* sp. indet. (13.1 m), *Leonaspis angelini* (Prantl and Přibyl), *Acidaspis pectinata* Angelin, *Anacaenaspis* sp. (cf. *A*. aff. *gotlandensis,* Bruton 1967, Pl. 35:9 only).

Illaenidae

Bumastus holmi Lindström, *Bumastus* n. sp. *a, Bumastus* sp. *b* (8–10 m). *Bumastus* is not uncommon in the Högklint beds but most specimens are either fragments, internal moulds, or juvenile pygidia (see *Bumastus* sp. indet. in the log, Fig. 31).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c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
LVM.
?
TRILOBITA
Harpidella sp. a
Encrinurus laevis
Calymene frontosa
Dudleyaspis ? sp. indet.
Deiphon sp.
Youngia sp.
Acernaspis sp. b
Encrinurus punctatus
Warburgella n.sp. a
Acernaspis sp. a
Bumastus holmi
Bumastus n.sp. a
Warburgella baltica
Calymene blumenbachii subsp. a
Proetus (Proetus) concinnus
Arctinurus palifer
Leonaspis angelini
Proetus (Lacunoporaspis) cf. contossus
Proetus (Lacunoporaspis) n. sp. a
Warburgella cf. stokesii
Acidaspis pectinata
Encrinurus sp. a
Arctinurus ornatus
Anacaenaspis sp.
Proetus (Proetus) sp. indet.
Bumastus sp. indet.

Fig. 31.

Cheiruridae

Deiphon sp. (only very small cranidia), *Youngia* sp.

Proetidae

Proetus (Proetus) concinnus Dalman, *P. (Lacunoporaspis)* cf. *confossus* Owens, *P. (L.)* n.sp. (aff. *signatus* Lindström), *Warburgella (Warburgella)* n.sp. *a, W. (W.) baltica* Alberti, *W. (W.)* cf. *stokesii* (Murchison), *Warburgella* sp. indet. (9.20–10.0 m, 13.55 m, 13.85 m). The specimens of *Proetus (Proetus)* from the Upper Visby Marl (given in the log, Fig. 31, as *P. (P.)* sp. indet.) may include *P. (P.) concinnus* but the material is too fragmentary to resolve the problem.

Aulacopleuridae

Harpidella sp. *a*. This species, represented by a single cranidium, appears to be specifically distinct from the common Mulde Marl species *H. elegantula* (Lovén).

Phacopidae

Acernaspis sp. *a, A.* sp. *b*.

There are two closely related, and apparently new phacopid species represented, both referable to *Acernaspis*. Detailed comparison with other species is not possible here, since with a few exceptions, most are badly in need of redescription.

Dalmanitidae

Acastocephala cf. *macrops* (Salter) (Högklint *c,* exact level unknown).

Calymenidae

Calymene frontosa Lindström, *C. blumenbachii* Brongniart n. subsp. *a*.

Encrinuridae

Encrinurus laevis (Angelin), *E. punctatus* (Wahlenberg), *E.* sp. *a*.

In *E. punctatus,* variation in the arrangement of tubercles on the glabella and anterior border of the cranidium have been recorded on specimens from the Högklint Limestone, Slite Marl and Jaani Marl (Tripp 1962: 467, Table 1). Comparable statistics for lithostratigraphical subdivisions *a, b,* and *c* of the Högklint Beds, Vattenfallet, are as shown on Table 3. A rare variant is a cranidium from 18.45 m, in which there is a pair of small 1 – 1 tubercles in place of 1 – 0. Hypostomes are similar to the specimen from the Slite Beds figured by Tripp (1962, Pl. 67, figs. 8a, b). In most pygidia the mucro appears to have been large, but is broken off. There is one non-mucronate pygidium, from

19.45–19.50 m, comparable in most respects with the lectotype (Tripp & Whittard 1956, Pl. 3).

One free cheek, from 24.80–25.20 m., here referred to *E.* sp. *a*, is distinguished from species of the *E. punctatus* species group in the coarse pitting of the field of the cheek.

Lichidae
Arctinurus ornatus (Angelin), *A. palifer* (Lindström), an euarginid hypostome (10.0–10.8 m; not likely to belong to *Trochurus* as listed by Hedström 1910).

Stratigraphical remarks

Details of the vertical range of various trilobite species in the stratigraphical interval under consideration are still poorly known on Gotland, in part because the precision of stratigraphical and geographical data on labels accompanying extensive old collections is insufficient for modern needs. In the Vattenfallet material the replacement of *Encrinurus laevis* by *E. punctatus* at the base of Högklint *a* is particularly noteworthy (Fig. 31). The latter species has repeatedly been recorded also from the Upper Visby Marl but its occurrence there requires confirmation.

It is interesting to note that the taxonomic diversity of trilobite species (see also Fig. 76) is much higher in Högklint *b* (estimated number of species in the material 14) and Högklint *c* (13) than in the Upper Visby Marl (9). Högklint *a* has yielded about as many trilobite species (7) as the Upper Visby Marl.

TABLE 3. Comparison of specimens of *Encrinurus punctatus* from the lithostratigraphical subdivisions *a*, *b*, and *c* of the Högklint Limestone, Vattenfallet.

	Metres above sea-level		
	10.0– 13.0	13.0– 24.0	24.0 29.6
Number of specimens:			
Cranidium			
Cranidia studied	1	12	5
With tubercle iii-0	1	12	4
With any of the 4 iii-2 ${}^{*}_{*}$	1	9	4
With 8 tubercles on anterior border	—	7	1
With 9 tubercles on anterior border	—	—	—
With 10 tubercles on anterior border	—	1	—
Uncertain	1	4	4
Pygidium			
Pygidia studied	2	15	14
With first tubercle on first ring	—	3	1
With first tubercle on second ring	2	11	12
With first tubercle on third ring	—	1	1
Specimens showing correlation of position of axial and pleural tubercles	—	6	4

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Eurypterids

ERIK N. KJELLESVIG-WAERING

At Vattenfallet Eurypterida are restricted almost entirely to Högklint *d*. Two other horizons (18.9–19.1 and 20.20–20.25 m) contain rare eurypterids, represented respectively by a single leg spine of *Holmipterus* and by small patches of skin also referable to that genus. For the distribution of eurypterid skin fragments in the insoluble residue of Laufeld's samples (not examined by me) see Fig. 66. In the past Högklint *d* has commonly been referred to as *Pterygotus* Marl, with reference to the abundant pterygotids in its well-preserved eurypterid assemblage; this assemblage was previously considered to be equivalent to the famous assemblage from the Lower Ludlovian Rootsiküla Stage (K_1) of Saaremaa, but the Vattenfallet eurypterids are now known to be of early Wenlock age and are thus much older. They comprise five genera, one of which is described here as new, and five species, four of which are new, as follows:

Holmipterus suecicus n.gen., n.sp. (common)
Baltoeurypterus serratus (Jones and Woodward) (rare)
Dolichopterus gotlandicus n.sp. (rare)
Truncatiramus serricaudatus n.sp. (common)
Erettopterus carinatus n. sp. (rare)

It seems probable that all these species were known to Gerhard Holm, as in his posthumous plates (Wills 1963) he figured nearly all specimens reported here. The famous scorpion *Palaeophonus nuncius* Thorell and Lindström also occurs in this bed and various fragments have been noted in addition to the original specimen. Clearly, this assemblage, consisting mainly of *Holmipterus* and Pterygotidae, belongs in the eurypterid assemblage No. 1 (Kjellesvig-Waering 1961:794), which comprises mainly pterygotids and carcinosomatids (or Mixopteridae and Megalograptidae) associated with a rich marine fauna.

The Vattenfallet eurypterids are all fragmentary. Nevertheless, the preservation is remarkable, much like that in the Rootsiküla eurypterid beds of Saaremaa, where the chitin is preserved without change and retains original colors. Many Vattenfallet specimens had been dissolved out of the limestone by Holm and mounted in Canada Balsam. This type of preservation necessitates that all specimens be covered with a thin coating of lacquer or some suitable fixing compound, otherwise flaking of the fragile skins will occur until practically nothing is left but the external imprint of the skin. The flaking begins immediately upon exposure at the collecting site. It is therefore highly important that the lacquer is administered as soon as exposure occurs.

The fragmentary state of the eurypterids indicates that currents or other agencies have disarticulated the various components of the exuviae. In this connection, Brower & Reyment (in Andrews et al. 1974:89) ascribed a catastrophic termination as the cause of the accumulation of nearly entire eurypterids, as in the Silurian Fiddlers Green eurypterid assemblage of Passage Gulf, New York. This was in contradiction to the general view that the great majority of all eurypterids, whole or fragmentary, represented moulted instars (Clarke & Ruedemann 1912:25; Størmer 1934:57). Although the purpose of this paper is not to refute Brower's & Reyment's supposition, it must be acknowledged that, of nearly all exoskeletons preserved in which the venter of the carapace is exposed to reveal whether or not the eurypterid had moulted, there is no doubt that the specimens are cast-off exuvia and in no way indicate either a catastrophic termination or accumulation. Indeed, in the few instances known where thanatosis is involved (as attested by preservation of the alimentary canal) each event has been so unusual as to merit a separate notice in the literature. The eurypterid exoskeletons in areas such as Saaremaa and Passage Gulf could only have accumulated by either being transported by currents – and the evidence is to the contrary – or by the animals themselves seeking a quiet, current-free area in which to moult. The process of moulting in arthropods involves a highly hazardous period, one requiring a quiet area free from disturbing influences, both mechanical and biological. Apparently, Passage Gulf, Saaremaa and the other areas where eurypterids occur concentrated, represented such areas.

The lack of scavenging activity is also cited by Brower & Reyment (1974:89) as one of the reasons for a catastrophic burial. I would suspect that the lack of scavenging activity is more properly due to the important fact that the exuviae did not contain any organic matter that could be scavenged such as would occur had catastrophic death been involved.

Suborder Eurypterina Burmeister, 1843

Superfamily Mixopteroidea Caster and Kjellesvig-Waering, 1955; Family Megalograptidae Caster and Kjellesvig-Waering, 1955.

Holmipterus n. gen.

Megalograptidae of large size, male mesial organ consisting of three parts, a long tubular basal with an expanded, rounded end consisting of the terminal joints; walking legs carcinosomatoid; telson spike-like with expanded anterior and serrated dorsal platform, with articulating cercal blades on each side of the platform.

Derivation of name. – In honour of the great Swedish paleontologist Gerhard Holm, Head of the Department of Paleozoology at Riksmuseum 1901–1922, whose work remains as a model for all who study arthropods.

Remarks. – There is little doubt in my mind that *Holmipterus* is so different from *Megalograptus* that when more specimens of the former are known, it will be best to separate them into different families. The legs of *Megalograptus* are differentiated and not of the carcinosomatoid type as in *Holmipterus.* The serrated telsonic platform is a unique morphological feature of the latter, and certainly is sufficient to separate this genus from all other eurypterids. Again this surprising telson merely emphasizes the great diversity of the Eurypterida, and also how little we really know of this Order.

Holmipterus suecicus n. sp.

Figs. 32–33

All specimens reported here were known to Holm, who figured them in plates that were printed but never released for publication, nor was a description ever made. The important cercal blades were not identified, nor figured by Holm, but this is not surprising as these structures were unknown in Eurypterida until much later (Caster & Kjellesvig-Waering 1964). The chelicera is known from a paratype (Ar. 31832) of which only the 3rd joint is preserved (assuming that Megalograptidae have four joints as in the Eurypteridae and Pterygotidae). Most of the hand is present showing that it is about as broad as long, with a socket for the articulation of the condyle of the 4th joint. The pincer is long, very narrow, falcate and colored very dark brown to black on the extremities. The hand is light brown on the outer parts, grading towards black on the inner edges. The hand is 11.5 mm long, 11.9 mm wide, and the falcate pincer is 12.4 mm long (see Fig. 32F).

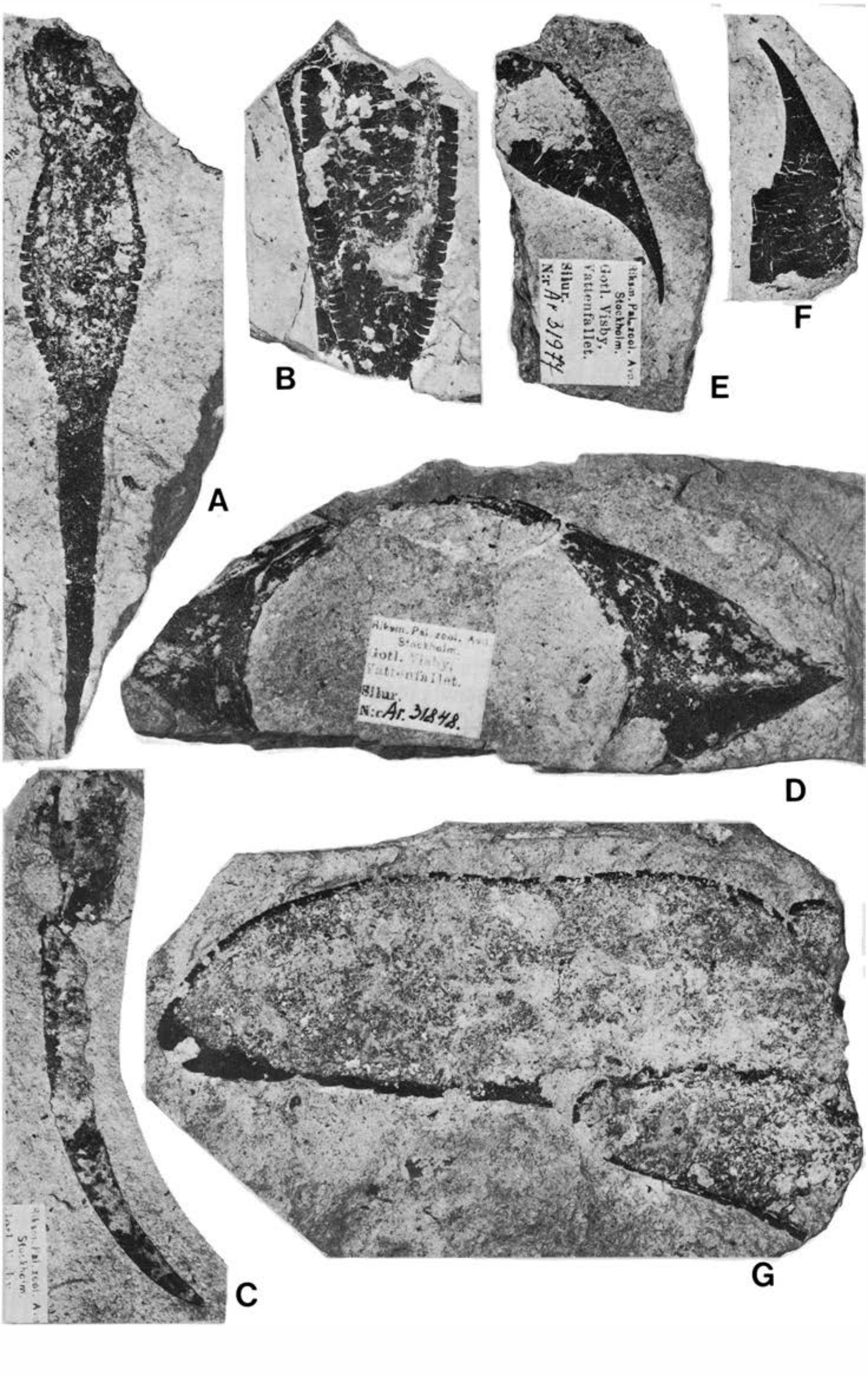
The walking legs are practically unknown except for two joints (Ar.31833 and Ar.32002). Both have large, curved spines, one on each side and characteristic of most of the Carcinosomatidae wherein the legs are flattened and with the venters turned anteriorly. These carcinosomatoid legs are very different from the highly differentiated legs of *Megalograptus.* The spines of the legs are striated with narrow, longitudinal ridges along the posterior of the curved part (Fig. 33F).

The swimming leg or sixth appendage is known from a nearly complete paddle retaining part of the sixth and all of the seventh segment which constitutes most of the paddle, and several pieces containing the distal end of the paddle which is important in identification of these mixopteroid eurypterids (Ar. 31828, Ar. 31836, Ar. 31857, Ar. 31859).

The triangular lobe of the sixth joint is very long and has linear scales along most of the posterior or outer edge which grade into serrated scales at the distal end. The seventh joint is also very long, finely serrated along the anterior edge and increasingly coarser along the distal end. The posterior edge is coarsely serrated (Fig. 33G). The eighth joint is a small triangular spine (Fig. 33G). The seventh joint (Ar. 31828) measures 78.8 mm in length and 25.8 mm in width at midsection. The other paratypes indicate individuals of considerably greater size, possibly reaching 1.5 m in total length.

The operculum and median organ is known only from two well preserved specimens, both of Type A, considered by Størmer & Kjellesvig-Waering (1969) to be male, but by Wills (1965) to be female. The male operculum is deeply cleft at the anterior median edge, separating the opercular lobes; thus there is no development of the usual anterior median suture. Deltoidal plates are well developed, triangular in shape and covered with small semilunar scales, black in color and contrasting with the light brown background.

Two distinct, curved slits occur on each side of the hastate section of the mesial appendage. These slits separate a lighter colored brown area which also has much finer semilunar scales than the adjacent part of the lobe, indicating that these areas, on each


A
B
Riksm. Paleozool. Avd.
Stockholm.
Gotl. Visby,
Vattenfallet.
Silur.
N:r Ar 31977
E
F
Riksm. Pal. zool. Avd.
Stockholm.
Gotl. Visby,
Vattenfallet.
Silur.
N:r Ar. 31848.
D
C
G

side of the mesial appendage, are the anchylosed lateral lobes. The entire opercular lobes are covered by even sized, small semilunar scales, black in color and evenly distributed on light brown integument.

The mesial appendage is composed of three distinct parts, a long, slightly tapering basal joint which comprises almost the entire organ, and which probably extended to the succeeding two abdominal plates. The haft part is, as in many eurypterids, triangular. The base is an inverted triangular area with a small, median, triangular protrusion. Attached to this area is a bulbous part which seems to have been rather inflated, because in the holotype the left side was noted to be larger, suggesting that in compaction this part was laterally dislocated. The terminal joints are unique, consisting of two nearly elliptical plates.

The mesial appendage is devoid of any ornamentation except at the hastate part and also on the anterior, median part of the shaft where small black semilunar scales are present.

The holotype (Ar.31827) is 102.5 mm wide across the middle of the opercular lobes. The mesial appendage is 57.4 mm long. A paratype (Ar.31845) measures 105 mm in reconstructed length indicating that *H. suecicus* reached an overall length of about one metre from the anterior of the carapace to the distal end of the telson.

Specimen Ar.31901 possibly represents the distal end of the Type B, or female, mesial appendage. It is round, apparently club shaped and is ornamented at the edge by a row of scales which appear to represent the distal part of radiating striations. The outside (ventral) part of this organ is black but the inside (covered dorsal in life) is light brown. I cannot at present conceive of this fragment belonging to anything but the female appendage of this eurypterid (see Fig. 33E). The colors indicate this interpretation, as well as the improbability, if not impossibility, of it belonging to the other known associated eurypterids. The distal end is 9 mm wide, indicating a specimen comparable in size with other adult *H. suecicus* found in this horizon.

The preabdomen is known from three large fragments.

An irregular piece (Ar.31850) 50 mm by 33 mm, reveals that the ornamentation consisted of black, rather small, semilunar to mucronate scales on a background of very dark brown. The underside is known by a large incomplete abdominal plate (Ar. 31879) which is possibly the first plate succeeding the operculum. The plate is bilobate, dark brown, lighter anteriorly than posteriorly, and rounded at the outer posterior angles. The central part is covered with very small semilunar scales, much smaller than those occurring on the dorsal plates. The semilunar scales decrease in size anteriorly and posteriorly; the entire posterior part of the abdominal plate is smooth. The plate is estimated at 150 mm in width of which 130 mm are preserved, and is 40 mm long. Another fragment (Ar. 31578 and counterpart Ar. 31579) is apparently part of the epimera of the first tergite. The edge slopes posteriorly, thus positive proof that the entire mesosoma was highly tumid, much as in the Carcinosomatidae.

Fig. 32. *Holmipterus suecicus* n.sp. Magnification ×1.2. A. Telson from the dorsal side showing the enlarged, serrated, flattened platform against which the cercal blades operate as double forceps (for cercal blade see Fig. 32E). Ar. 31696. B. Anterior platform of telson revealing the serrated, but truncated, teeth. Ar. 31691. C. Telson from the side; the horizontal serrated platform is seen on the left side of the photograph which represents the dorsal side. Ar. 31804. D. Pretelson preserved from the anterior (vertical on the bedding plane) end, thus revealing the round cauda and the flaring epimera. Ar. 31848. E. A cercal blade. Ar. 31977. F. The hand and fixed ramus of the chelicera, showing the condyle for the articulation of the free ramus. Ar. 31832. G. The distal part of the sixth, and all of the seventh joints of the paddle; the notch at the end of the seventh joint represents the site of the small terminal or eighth joint. Ar. 31828. All specimens from Högklint *d* at Vattenfallet. Photograph U. Samuelson.

An abdominal plate of a young individual (about 36 mm wide) also verifies that these plates were bilobed and joined in the center line by a suture. Only half of the plate is preserved (Ar. 31679).

Small pieces of integument, possibly tergites of the dorsal side of the mesosoma (Ar. 31695 and Ar. 31834) were dissolved out of the rock by Holm and reveal that the ornamentation probably covering the main part of the eurypterid consisted of scales,

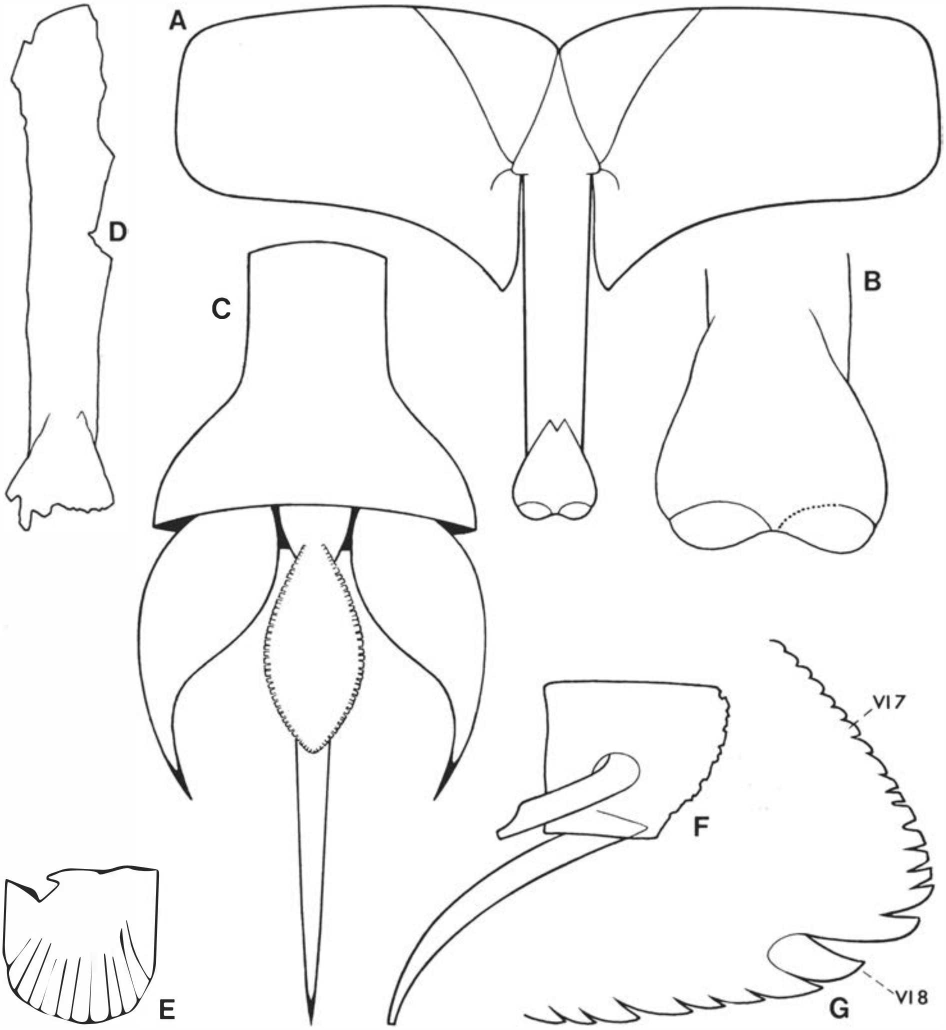


Fig. 33. *Holmipterus suecicus* n.sp. A. Restoration of operculum and Type A mesial appendage, based mainly on the holotype. Approxim. ×1. B. Distal end of the mesial appendage of the holotype. Ar. 31827, ×3. C. Restoration of pretelson, cercal blades and telson. D. Unattached male mesial appendage of considerably greater size than the holotype. Ar. 31845, ×0.8. E. Possible Type B median appendage. Ar. 31901, ×2. F. Joint and attached spines of a walking leg. Ar. 31833, ×1.5. G. Distal part of swimming leg. Ar. 31859, × 1. All specimens from Högklint *d* at Vattenfallet.

hemi-elliptical in shape, about as long as wide and all of a distinct, regular size interspersed by very small, semilunar scales. In areas such as edges the scales become mucronate. All these scales are very dark brown to black and contrast against the light brown of the rest of the integument.

The metasoma is known from three large fragments (Ar. 31849) which would include the last tergite (7th) of the preabdomen, and the first two tergites (8th and 9th) of the postabdomen or cauda. Although width measurements cannot be made as parts are missing, it is possible to measure the lengths, which are as follows: tergite 7–31.0 mm, tergite 8–41.3 mm, tergite 9–60.4 mm. The tergites are covered with small mucronated scales. The cauda seems to be black, at least dorsally, as the doublures are dark brown in color and therefore the black coloring is primary and has not been altered. There is an indication that strong constriction occurs between the seventh and eighth tergites as in other eurypterids, but preservation does not permit determination of the amount of constriction.

The most surprising morphological feature of this eurypterid, as in other megalograptids, is the pretelson-telson assemblage which includes the cercal blades. The pretelson is preserved in a flattened condition, but flattened from the anterior end; thus in burial it was covered upright and perpendicular to the bedding plane. Although only one specimen is preserved (Ar. 31847–Ar. 31848), it can be stated that the anterior, and therefore probably the entire cauda, was nearly round in cross-section. This would be in keeping with many genera of Carcinosomatidae, Mixopteridae and Megalograptidae which had rounded, or tubular cauda capable of being thrust "overhead" as in the scorpions. The basal part is widely flaring, very probably to accomodate the wide cercal blades (see Fig. 32D). The pretelson measures 45 mm "in the round" and each flaring end is 28.3 mm long; therefore, the basal end of the flaring pretelson measures 91.6 mm in width.

The cercal blades are known from two specimens (Ar. 31977, Ar. 32003) both of which are nearly complete except for the bases. The part preserved shows the specimen to be bulbous/flattened and produced into a long, falcate termination (Fig. 32E).

The remarkable telson is unique among eurypterids. Fortunately it is represented by four specimens (Ar. 31691, Ar. 31696, Ar. 31804, and Ar. 32083). The telson is robust in lateral view, curved downward in life (Fig. 32A), and has a flat, serrated platform on the anterior part near the bulbous articulation of the telson. The serrated edge of the telsonic platform is laterally rounded and overlaps the underlying shaft of the telson. The teeth along the serrated edge are truncated at the apical ends, so that each tooth appears to be squarish. These serrations are clearly visible in both Ar.31691 and Ar.31696 from the dorsal side, and laterally in Ar. 31804 and Ar. 32083 (see Fig. 32A–C).

By comparison with numerous specimens of the American Upper Ordovician *Megalograptus ohioensis* (Caster & Kjellesvig-Waering 1964) it is possible to assemble the various parts which compose the terminal part of the cauda with considerable confidence. The cercal blades fit on each side of the flaring pretelson and articulate against the raised, serrated, telsonic platform (see restoration Fig. 33A). The entire downwardly-bent telson acted as a third or middle pincer between the two falcate, forceps-like cercal blades, and because the cauda could be thrust over the carapace, as in scorpions, this combination formed a particularly formidable grasping weapon. The complete telson (Ar. 31696) is 86.5 mm long, 14.5 mm estimated at the base, 8 mm at the anterior of the platform, 14.6 mm in greatest width of the platform, and 10.8 mm at the posterior of the platform or anterior of the spike. The telsonic platform of Ar.31691 is much larger, measuring 18.2 mm in greatest width.

Remarks. – The scorpion-like cauda and telson was a formidable weapon although there is no evidence that a pair of poison glands occurred as in the scorpions. In fact, although it has been suggested in the past that some of the Mixopteridae and Carcinosomatidae may have possessed poison glands in the curved telson, this does not seem possible. The eurypterid telson is far too thick or blunt, and the double poison glands, if present at the base of the telson, would be located too far away from the terminal end to be effective. In contrast, the scorpion has a very sharp point, with openings on each side, and the paired poison glands are close to the openings for instantaneous injection of the poison.

The upward thrust-action of the downwardly-curved telson, and the rounded tubular cauda are features that are common in scorpions and some eurypterids such as *Holmipterus, Mixopterus* and *Paracarcinosoma*. This was apparently a development in the eurypterids for the use of the forcep-like cercal blades and not for a supposed poison-injecting telson. In genera such as *Mixopterus* and *Paracarcinosoma,* the cercal blades disappeared, and evidence for this conclusion will probably be forthcoming in older eurypterids such as those from the Lower Silurian and Ordovician. This also implies that early scorpions, older than Middle Silurian, might have developed the up-thrusting tail primarily for the accomodation of cercal blades and later developed the vesicle and aculeus with the paired poison glands.

Superfamily Stylonuracea Diener, 1924; Family Dolichopteridae Kjellesvig-Waering and Størmer, 1952

Dolichopterus gotlandicus n. sp.

Fig. 34

This large *Dolichopterus* is represented by a metastoma (Ar.31697) designated as the holotype and by three coxae of the swimming leg.

The metastoma, although not complete, is sufficiently preserved so that most of the important characters of the plate can be described and compared with other species. Anteriorly it is cordate, with an inverted, obtuse angular notch in the middle. Each side of the notch is superimposed with a single row of seven, evenly shaped, squarish, even-sized denticles. The lateral margins of the metastoma are nearly parallel, with a

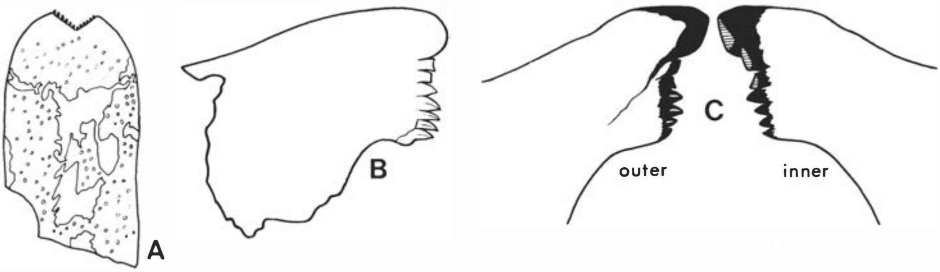


Fig. 34. *Dolichopterus gotlandicus* n.sp. A. Metastoma. Holotype, Ar. 31697, ×2. B. Part of coxae of swimming leg. Ar. 31840, ×2. C. Gnathobase of swimming leg; the principle or anterior tooth is on a lower level than the rest of the teeth. Ar. 37698, ×2 (see also Fig. 36F). All specimens from Högklint *d* at Vattenfallet.

slight constriction posteriorly; therefore, the sides are slightly convergent posteriorly. The ornamentation comprises evenly spaced and even sized, pilious pustules. Each pustule is surmounted with a round opening or setal site, and each is black in color and contrasts with the rich, shiny brown color of the integument (see Fig. 34A).

The three paratypes reveal the typical *Dolichopterus* type of coxae, being very wide with a long neck and the gnathobase at the inner end. The gnathobase of *Dolichopterus* is very similar to that of *Baltoeurypterus,* having a ventral anterior, or principle tooth, which is truncated and striated on the inside. On a higher plane is a row of smaller teeth. This row contains two much smaller truncated teeth, followed on the same row by four triangular teeth which decrease in size posteriorly. Specimen Ar. 37698 has been freed from the matrix by Holm, and all details are available (Fig. 34C). Another, about 50 per cent larger specimen reveals the same arrangement. The coxae are covered with hughmilleriid type of linear scales or ridges, and are dark brown in color, contrasting against the rich shiny dark brown color of the integument.

Remarks. – By comparison with other Dolichopteridae, the two species from Saaremaa, *Dolichopterus stoermeri* Caster and Kjellesvig-Waering and *Dolichopterus* sp. show considerable differences. The peculiar ornamentation of the metastoma in *D. stoermeri* is sufficient for differentiation. In *D. stoermeri,* the much deeper anterior notch and the smaller and lesser number of teeth also represent differences from the Vattenfallet species. From *Dolichopterus* sp. (Holm 1898, pl. 10:11) the differences are immediately apparent in the highly constricted metastoma in comparison with the nearly parallel sides of the Gotland form. It is very likely that *Dolichopterus* sp., although belonging within the Dolichopteridae, will not be retained within the limits of the genus *Dolichopterus* when more parts are known.

Superfamily Eurypteracea Burmeister, 1845; Family Eurypteridae Burmeister, 1845.

Baltoeurypterus serratus (Jones and Woodward)

Fig. 35B–C

1888 *Phasganocaris pugio* (Barrande) var. *serrata* Jones and Woodward, p. 149, pl. VI, figs. 3–6.

The various fragments of *Baltoeurypterus* reported below had been described and figured in manuscript form when Dr. W. D. Ian Rolfe forwarded to the writer the syntypes and other specimens of the supposed phyllocarid *Phasganocaris pugio* (Barrande) var. *serrata* Jones and Woodward, as he had properly recognized that all represent eurypterids rather than phyllocarids. Nearly all the specimens were determined as belonging to *Baltoeurypterus* including at least one syntype of the Jones & Woodward species (1888, Pl. VI:4, refigured here as Fig. 35D). This specimen (Ar.31589) is here designated as the lectotype. It is a Type A telson which is considered to represent the male. It is not as well preserved nor as complete as some of the telsons described below.

Besides the lectotype and three other syntypes the material comprises six male (Type A) telsons (Ar.31803, 31808, 31811, 31812, 31819, and 31845, the last being associated on the same bedding plane with a large paratype of *Holmipterus suecicus*), a large female metastoma (Ar.31716), a 10th tergite (Ar.31715), an 11th tergite (Ar.31716), and two basitarsal (6th) joints (Ar.31718 and 31717 which are on the same bedding plane as the metastoma).

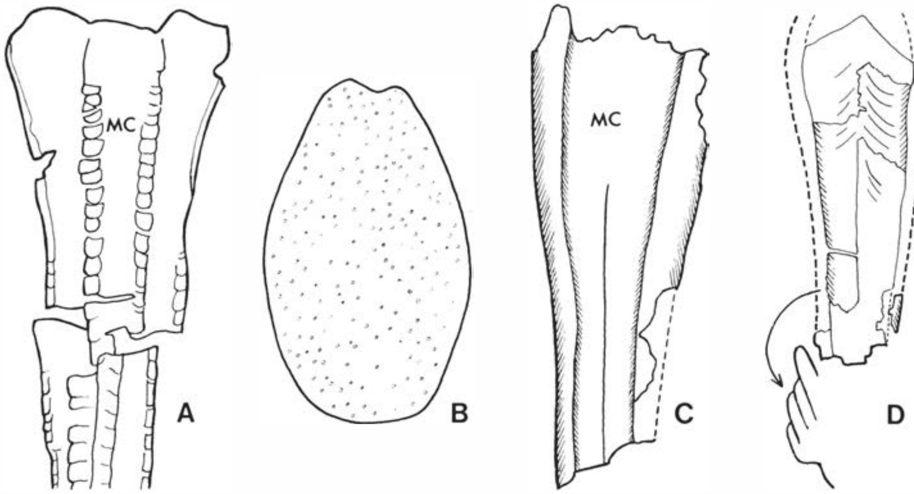


Fig. 35. *Baltoeurypterus tetragonophthalmus* (Fischer): A. Details of the anterior, ventral part of the male (Type A) telson. Ar. 48931, ×3. Saaremaa, Viita quarry; Rootsiküla (K_1) Stage.
Baltoeurypterus serratus (Jones and Woodward): B. The Type A metastoma. Ar 31717, ×3. C. Details of the anterior, ventral part of the male (Type A) telson. Ar. 31811, ×3. D. Telson, lectotype. Ar. 31589, ×3 (enlargement of "serrations" ×12). Högklint *d*, Vattenfallet.

The telson is of prime importance in the differentiation of eurypterids. In the Eurypteridae it is one of the most consistently preserved parts, and fortunately of more diagnostic importance for the separation of minor taxa than even the carapace. *Eurypterus remipes* DeKay and *Eurypterus lacustris* Harlan, can easily be distinguished by the ornamentation on the telson. The same is true of species of *Baltoeurypterus*. I have material of several further species of *Baltoeurypterus* from Gotland and Saaremaa which also reveal the importance of the telson for the separation of species. Comparison has been made directly with specimens from Holm's collection of preparations so that comparisons are possible with as much accuracy as if one were using tissues from living specimens. The great number of specimens studied show that the characteristics of the telson are constant.

Specimen Ar.31803, consisting of a nearly complete male telson, is bulbous anteriorly and tapers to a spike. The anterior bulbous area is 7.7 mm wide, and its overall length is estimated at 36.5 mm. The ventral side is bounded by a flat, wide carina which is bounded on the edges by an ornamentation of fine diagonal, plumose striations in single narrow rows (see Fig. 35C). The central part of the flat carina is smooth. A median groove separates the median carina. The lateral margins of the telson are also bounded by a margin of fine, diagonal, plumose striations, but these are slanting in the opposite direction to those on the median carina. No scales are present on the lateral margins which appear to be entirely smooth. In contrast, male telsons of the same size in *B. tetragonophthalmus* (Fischer) (Fig. 35A) have a much narrower, inferior carina which is bounded on each side by a row of large semilunar scales on the anterior, and which grade into a narrow ridge on each side of the carina and converge posteriorly. The lateral margins are bounded by a serrated edge of long, flat scales.

Incredible as it may seem in dealing with middle Silurian fossils, the coloration can be compared. In *B. serratus*, the rows of striations on the lateral margins of the carina and telson are black; the lateral margins of the carina in *B. tetragonophthalmus* are black, but the scales on the lateral margins of the telson are dark brown. The central part of the carina in *B. serratus* is dark brown to black; the same area in *B. tetragonophthalmus* is light brown. The rest of the venter of the telson, that is the area between the carina and the margins of the telson in both species, is light brown. The dorsal part of the telson of *B. tetragonophthalmus* is flat and is bounded on each side of the telson by a single row of dark brown, elongated scales (about 2–3 times as long as wide). The rest of the telson is light brown and smooth. In *B. tetragonophthalmus* the median groove on the dorsal carina is not as prominent except distally.

The distal end of the telson is known from specimen Ar. 31845 which has the telson lying on its side. This reveals that the striated spines, particularly on the lateral margins of the telson, grade distally into coarse mucronated scales.

The female (Type B) telson is considerably narrower, and although the piece known (Ar. 31819) is only from the central dorsal part, it is probably safe to assume that it is long, and downwardly bent as in other species of *Baltoeurypterus*. The central carina and the edges of the telson are ornamented as in the male.

The two joints of the paddle (Ar. 31717 and Ar. 31718) comprise the basitarsus or 6th joint and are typical of the genus in being very short and wide. Ar. 31717 is 10.0 mm in greatest width and 5.2 mm long, measured through midsection to the suture of the triangular lobe, whereas Ar. 31718 is 10.2 mm wide and 7.2 mm long.

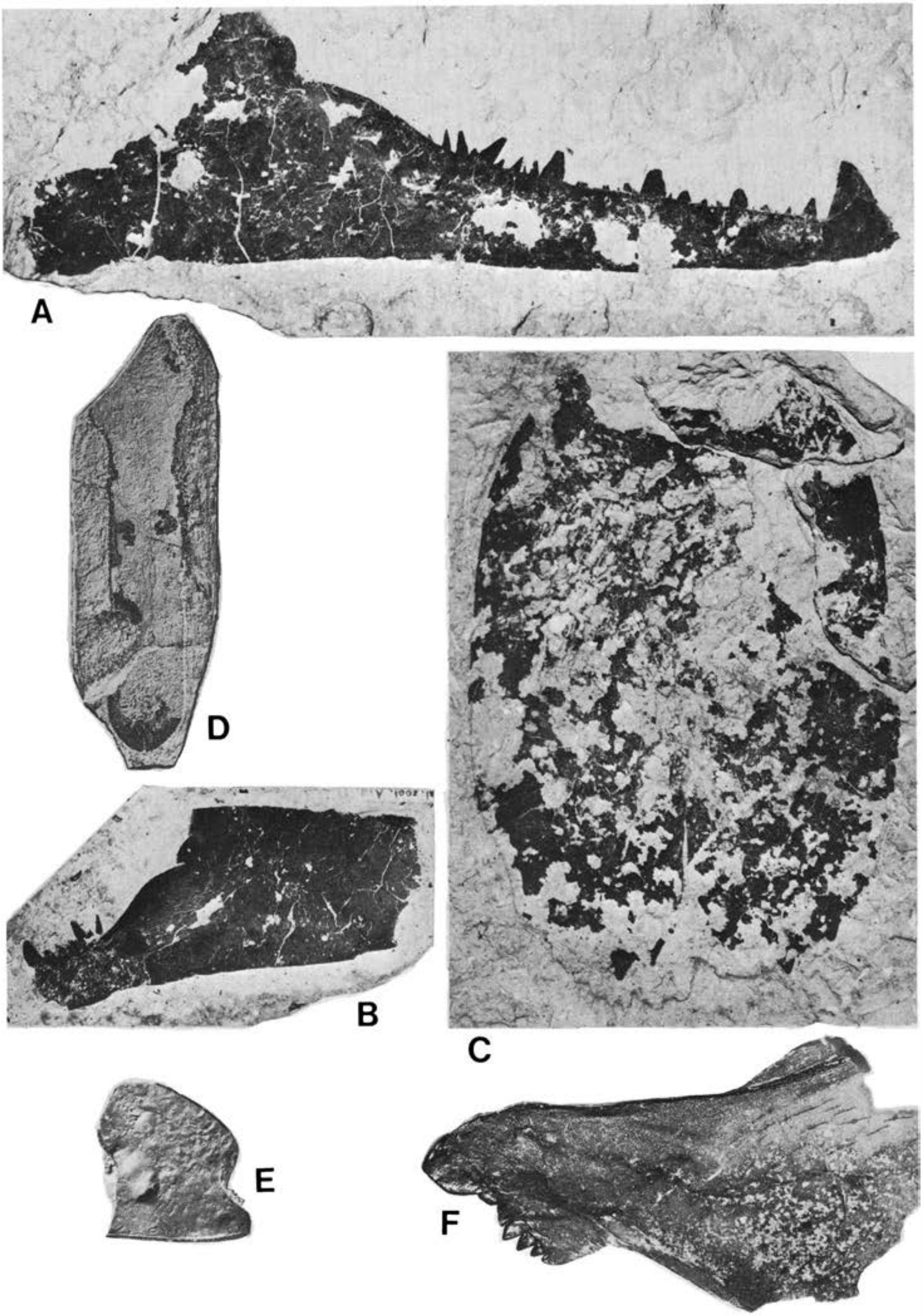
The metastoma (Ar. 31717) is ovoid as in *B. tetragonophthalmus* except that it is narrower at the anterior end, and the development of denticles on the indented anterior end is not as great. If this metastoma is typical of the species, it differs from *B. tetragonophthalmus* in being more pyriform. The surface of the metastoma is covered with small pustules, all of which are pileous as each has an opening at their apices. This type of ornamentation on the metastoma (see Remarks), as well as being the broad type, denotes a female (Type B). The metastoma has a maximum length of 13.7 mm and is 8.7 mm wide.

The tenth tergite of the metastoma is rather piceous at the centre, thus denoting a female. The basal border is bounded by a single row of evenly spaced scales, giving the tergite a serrated edge. The genal angles are produced into short horns, and the ventral side, which is the only side exposed, reveals that the lateral pleural areas are covered with mucronated scales, whereas the central part is thickened with imbricating scales, all of which are piceous. The pleural areas are light brown. A well developed anterior marginal rim is defined by a row of small scales, which continue anteriorly. The tergite is 22.5 mm wide and 10 mm long, both measurements through the center.

In the eleventh tergite the ventral side is not complete, but enough is preserved for a fair description and comparison with *B. tetragonophthalmus*. The central part is piceous, plumose and thickened. The pleural areas are devoid of scales. This contrasts with the imbricating, semilunar, large irregular scales of the central part of the corresponding segment in *B. tetragonophthalmus*. The 11th tergite is obviously from a female specimen.

Suborder Pterygotina Caster and Kjellesvig-Waering, 1964

Superfamily Pterygotoidea Clarke and Ruedemann, 1912; Family Pterygotidae Clarke and Ruedemann, 1912


A
D
B
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E
F

Truncatiramus serricaudatus n. sp.

Figs. 36, 37A–D

1964 *Erettopterus osiliensis* (Schmidt): Waterston, p. 18, Pl. 2, figs. 1–3.

By far the most common eurypterid at Vattenfallet is a large pterygotid represented by many disjointed pieces, of which the diagnostic telsons and cheliceras can be correlated as belonging to the same species. This is important as there is definitely another pterygotid present (*Erettopterus carinatus* n. sp.). A metastoma, also of diagnostic value, is referred to *T. serricaudatus*. Many other pieces, very likely belonging to *T. serricaudatus*, cannot safely be referred to either pterygotid as the parts represented – coxae, tergites – are not sufficiently diagnostic.

The holotype (Ar. 31886) is the fixed ramus with part of the hand of a large chelicera. Other specimens are Ar. 31888, 31890, 31891, 32013, 32026, 32071, 32073, and 32075; telsons Ar. 31894, 32084 and metastoma Ar. 31893. The holotype reveals a fixed ramus with acute termination and considerably smaller teeth of uneven size, placed at right angles to the ramus. There are two large central teeth and in the rear of the ramus is a cluster of diagonally opposed teeth which are characteristic. The condyle for the articulation of the free ramus is located within one third of the width of the hand. Paratype Ar. 31888, also a fixed ramus and an entire hand, reveals that the hand is long and without ornamentation, as are both of the rami. The color of the chelicera is dark reddish-brown, with the teeth and condyle, as well as the terminal tooth, being black. The holotype measures 56 mm from the terminal tooth along the ramus to a line drawn from the condyle to the base of the ramus. The width of the hand in the area of the condyle (greatest width) is 23.3 mm. The hand of paratype Ar. 31888 has a maximum width of 18.5 mm and is 25.7 mm long from the condyle to the base of the cheliceral hand.

The free ramus has a double acute termination that straddles the main tooth of the fixed ramus. This is notably present in all pterygotids but in preservation is nearly always covered. This double termination is well shown on the paratypes of this species. The ramus is also very straight on the outer edge and is surmounted by small teeth, all of which, except at the base, are bent evenly backward. Two central teeth are more prominent than others but details of the teeth are best revealed by comparison of the photographs.

The metastoma is represented by only one specimen (Ar. 31893) which reveals a form typical of the genus. It is highly cordated anteriorly, the major width of the structure lies in the anterior half and is tapering posteriorly into a rounded termination. It is covered with small, semilunar to mucronated scales, all of even size and densely distributed.

Fig. 36. *Truncatiramus serricaudatus* n.sp.: A. Fixed ramus and part of the hand of the chelicera. Holotype, Ar. 31886, ×1.5. B. Hand and part of the fixed ramus of the chelicera. Ar. 31888, ×1.2. C. Telson. Ar. 32084, ×1.2. D. Type A mesial appendage. This photograph is from Holm's posthumous plate; the specimen has not been located and is assumed here that the original came from Vattenfallet. ×1.

Baltoeurypterus serratus (Jones and Woodward): E. The sixth joint of the paddle which has been freed from the matrix. Ar. 31718, ×1.6.

Dolichopterus gotlandicus n.sp.: F. Gnathobase and neck of the coxa which has been freed from the matrix. Ar. 37698, ×3 (see also Fig. 34C). All specimens from Högklint *d* at Vattenfallet. Photograph (except for Fig. D) U. Samuelson. Fig. D was photographed by G. Holm and retouched by G. Liljevall.

The telson is represented by four specimens (Ar. 31894, 31898, 32084, and 32085), all well preserved and retaining the original color which is dark reddish-brown, darkening to black at the edges, particularly on the coarse serration of triangular bordering spines. More important, two specimens are preserved so that it is possible to determine dorsal from ventral sides. In specimen Ar. 31894 the dorsal side is preserved, showing that it is devoid of any median or slight flat ridge as in *T. osiliensis* (Schmidt). The ventral side is indented in the central part, with both lobes gently sloping from the centre line. Both sides are covered with semilunar to sub-mucronated scales on the anterior, and bordered by a row of about two or more flat and rhombic scales, which increase in length to become large, triangular scales on the rounded cordated end of the telson. These large scales are separated by much smaller triangular scales, which together with the coarse scales account for the serrated termination. Ar. 31894 has an estimated length of 95 mm and is 57 mm wide; Ar. 32084 is 65.3 mm long and 44.3 mm wide; and Ar. 32085 is 43 mm in estimated length and 30.5 mm in width.

Many other specimens in the Riksmuseum collections could very likely be referred, with only slight doubt, to this species, but these parts are gnathobases and coxae which, with our present knowledge, are not diagnostic. Some of these could represent *Erettopterus carinatus.*

A Type A median appendage requires description as this organ is of considerable diagnostic value. Unfortunately, the specimen has been misplaced and my description is based only on the excellent photograph in Holm's posthumous plate (Fig. 11 of an unlabelled plate; Fig. 36D herein). Inasmuch as the specimen is surrounded by figures of Vattenfallet specimens, it is quite safe to assume it is from Vattenfallet. The mesial appendage (estimated length 60 mm) consists of an unjointed organ, triangular anteriorly, with parallel sides and rounded posteriorly where it appears to be divided by a narrow notch. It is unusual in not retaining an enlarged bulbous terminalia of the mesial appendage as in most pterygotids. It is rather safe to assume that the specimen is referable to *Truncatiramus serricaudatus* or *Erettopterus carinatus,* as these are the only pterygotids at Vattenfallet, and because nearly all of the recognizable specimens belong to the most common pterygotid, it seems reasonable to assign this specimen to *T. serricaudatus.*

Remarks. – In comparison with the outwardly bowed rami of the type species *T. osiliensis* (Schmidt) from the Rootsiküla Stage (K_1) of Saaremaa differs from the straight rami of *T. serricaudatus.* The details of the form and grouping of the teeth are also completely different in both. Apart from the chelicerae, the telson of both are easily separated on the basis of the serrations as well as the low median ridge on the anterior of the telson of *T. osiliensis* which is totally lacking in *T. serricaudatus.*

A specimen (Ar. 32089) of unusual interest is referred with hesitation to *T. serricaudatus.* This comprises parts of the first and second joints of the chelicerae in articulation. The joints in articulation between the two joints are rarely found, as they are nearly always broken and this has led to the erroneous assumption that the pterygotid chelicerae consisted of three, rather than four joints (see Kjellesvig-Waering 1964:334–339). At that time, I thought that the pterygotid chelicerae articulated with the base of the epistoma, but although it was very close to the epistoma in position it did not in fact articulate with it, but occupied a position as in *Eurypterus, Baltoeurypterus* and *Limulus,* adjacent to the doublure, and articulating against each side of the labrum. This condition has not been found in the pterygotids but is highly likely as it is present in *Eurypterus* and *Baltoeurypterus.* The chelicerae consist of part of the first joint, which is considerably narrower than the second, articulating inside the second joint, and

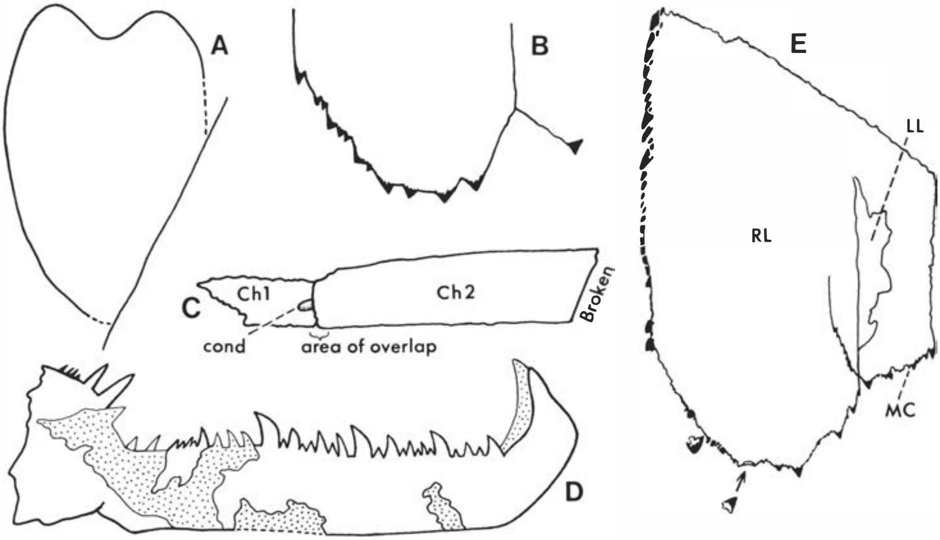

Fig. 37. *Truncatiramus serricaudatus* n.sp.: A. Metastoma. Ar. 31893, ×1. B. Details of well preserved, posterior part of the telson. Ar. 31898, ×2. C. First and second joints of the chelicera. Ar. 32089, ×0.6. D. Free ramus of chelicera; the stippled areas represent parts where the skin has been flaked off; however, the impression of the structures, such as the teeth, is present – the double termination of the terminal teeth is particularly well preserved. Ar. 31891, ×2.7.

Erettopterus carinatus n.sp.: E. Details of telson seen from the ventral side. RL, right lobe; LL, left lobe; MC, median carina. Holotype, Ar. 31896, ×3. All specimens from Högklint *d* at Vattenfallet.

attached by a condyle and socket of the second joint. The second joint is slightly bent against the first and is straight on the outer edge and bowed outward on the inner. This results in the second joint being thicker proximally. The color of the entire chelicerae is bright brown.

The Type B median appendage has been fully described by Waterston (1964:18, Pl. 2:1–3).

Erettopterus carinatus n. sp.

Fig. 37E

This species is based on a fragment of the base of the telson (Ar.31896) which has been freed from the matrix by Holm. It is mounted in Canada Balsam and reveals that a true *Erettopterus* is present at Vattenfallet. The fragment measures 20.5 mm by 13 mm, and indicates a telson of 40 mm estimated length, 20 mm in maximum width (each horizontal lobe is 10 mm wide) with a carina or vertical lobe of at least 5 mm in height (3 mm preserved).

The right lobe is represented by a large fragment showing a highly serrated terminal part which is acutely cordated and is bordered by at least three large triangular spines. The border of spines continues on the lateral edges where they become more linear and with the points close to the edges of the telson but pointed posteriorly. The middle carina extends to the centre of the cordated notch, has considerably thinner or narrower spines, and more mucronated, smaller spines than the lateral or horizontal lobes (see Fig. 37E).

Remarks. – The differences between *T. serricaudatus* and *E. carinatus* are apparent in the presence of the carinated telson of the latter. From the Scottish Upper Llandovery *Erettopterus bilobus* Salter, it differs in having each lateral lobe much narrower and in having coarse serrations on the cordated area.

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Phyllocarids

W.D. IAN ROLFE

In the Vattenfallet collections phyllocarids are represented by *Ceratiocaris* sp. indet. from the *"Pterygotus"* Beds (Högklint *d*). The material comprises a distal part of a large telson and many cutting edges of mandibles. The telson shows characteristic microstructure in a calcified cuticle, 0.2 mm thick. The gnathal lobes of mandibles, found in acid resistant residues, correspond in general form with those described by Rolfe (1962:923–925).

The material submitted for identification also included five specimens identified as phyllocarids by Holm. These specimens include also the syntypes of *Phasganocaris pugio serrata* Jones and Woodward, 1888. Gürich (1929:58) has already pointed out that this material is better not classified as a phyllocarid crustacean. Presuming these specimens might be non-phyllocarid, they were sent to Kjellesvig-Waering who identified them as telsons of *Baltoerypterus*. This material is thus confirmed as non-phyllocarid and may henceforth be known as *Baltoeurypterus serratus* (Jones and Woodward). The Lower Devonian *Phasganocaris* (Novák 1886) bears ornament resembling the present material, but *Phasganocaris* may well be the telson of *Aristozoe memoranda* Barrande in Bigsby, 1868. *Phasganocaris* thus becomes a junior synonym of *Aristozoe* (Rolfe 1969). Similar ornament is found on the telson of *Ceratiocaris*? *coherbaria* Chlupáč, 1963. The further question of the identity of *Phasganocaris* s.s. with eurypterids has been much discussed, but restudy of the type Bohemian material is required to solve this problem.

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Leperditiid ostracodes

ANDERS ANDERSSON

Leperditiacean ostracodes are fairly common in the Silurian sequence of Gotland. Hisinger (1831) described two species and Kolmodin (1869, 1880) added some, but since then no descriptive work on this group from the island has been attempted.

Annotated faunal list

Leperditiacea: *Eoleperditia*? *baltica* (Hisinger) (6 specimens from Högklint *c*), *Herrmannina phaseolus catarractensis* n. subsp. (25 specimens from Högklint *c* and innumerable specimens in a limestone bed from Högklint *d*, where in places the rock is crowded with valves). For ranges see Fig. 43.

Eoleperditia? *baltica* has a simple, non-denticulate hinge and lacks a chevron scar. These characters, as well as the general shape of the valves, agree with those of *Eoleperditia*, but further studies are required for a definite generic assignment. *Herrmannina phaseolus catarractensis* is described below.

Herrmannina phaseolus catarractensis n. subsp.

Figs. 38–40

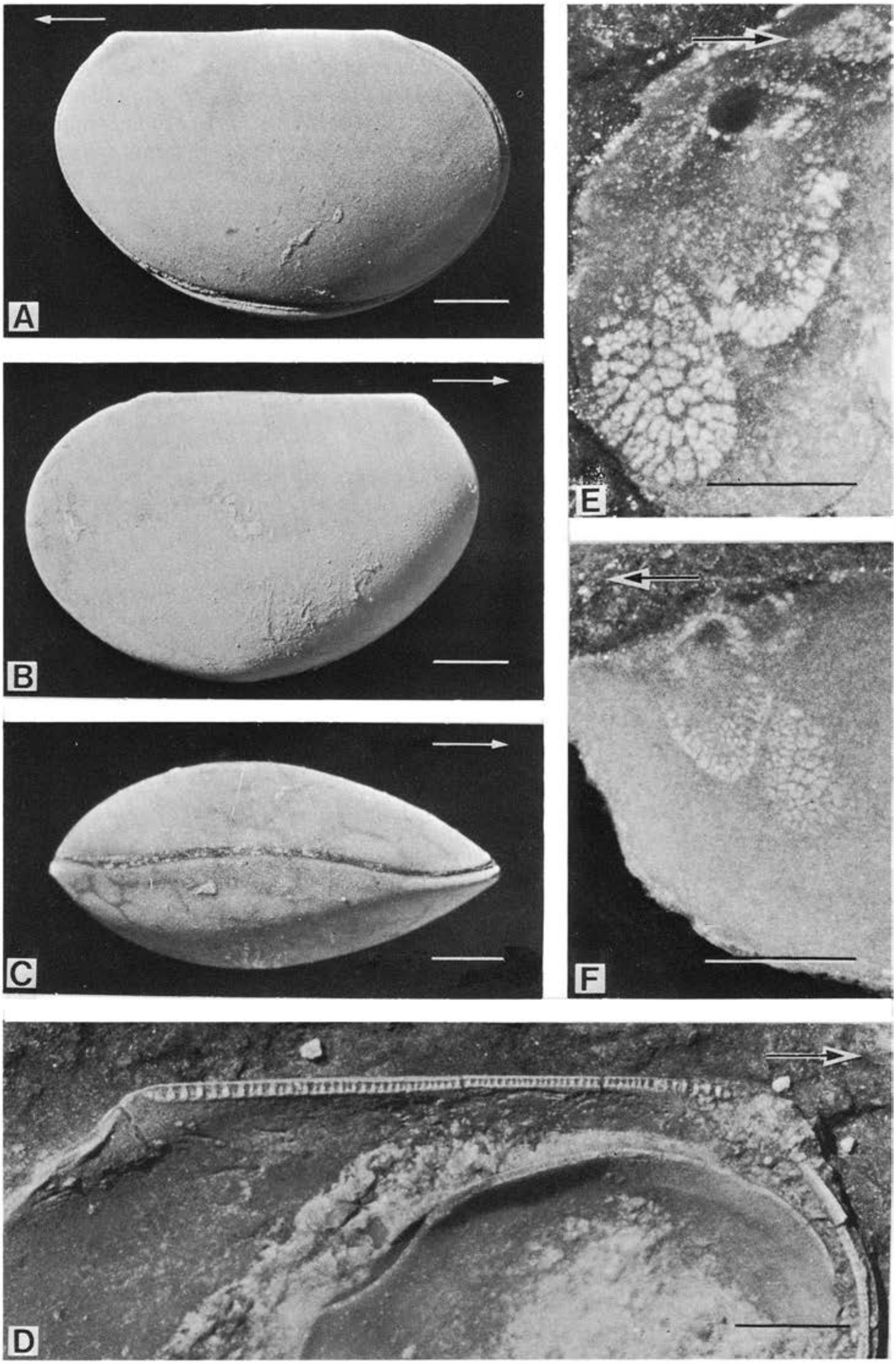
1923 *Leperditia phaseolus* (His.) – Hedström, p. 336, Figs. 1–2.

Holotype. – Carapace RM Ar.49767, Fig. 38A–C; Vattenfallet, *"Pterygotus"* Beds (29.60–30.00 m).

Diagnosis. – Valves almost completely smooth, relatively convex; anterior cardinal corner somewhat swollen; ventral surface of left valve smooth; venose markings absent.

Description. – Valves smooth, with occasional very faint traces of puncta. The holotype is 6.3 mm long and 4.2 mm high (hinge-line 3.8 mm). The largest specimen in the collection is 9.0 mm long and 5.8 mm high (hinge-line 5.6 mm). For further variation in length and height, see Fig. 40. Maximum height at a position two thirds of the way

Fig. 38. *Herrmannina phaseolus catarractensis* n. subsp. A–C. Carapace in lateral and ventral view; holotype, Ar. 49767. D. Hinge of left valve; Ar. 49733. E. Anterior part of interior surface, left valve, showing chevron and adductor muscle scars; Ar. 49735. F. Anterior part of interior surface, right valve; Ar. 49734. All specimens from Högklint *d* at Vattenfallet; photograph U. Samuelson. Arrows point anteriorly, bars represent 1 mm.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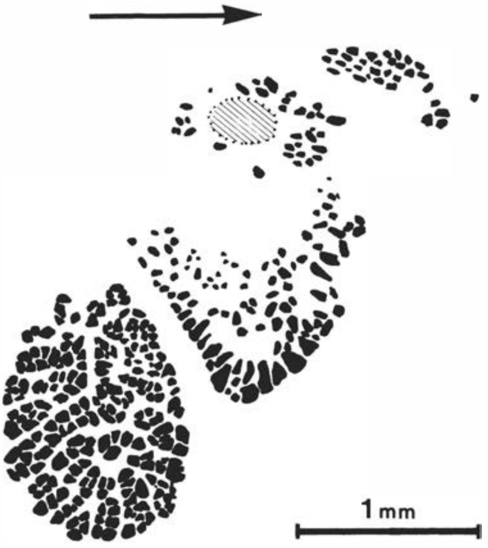

Fig. 39. *Herrmannina phaseolus catarractensis* n. subsp. Camera lucida drawing of adductor, chevron and dorsal muscle scars based on specimen Ar. 49735 (see Fig. 38E). The arrow points anteriorly.

along the hinge-line from the anterior cardinal corner. Maximum convexity of the valves close to the adductor muscle scar. The overlapped area of the left valve is smooth. Anterior cardinal corner somewhat accentuated with a faint subjacent depression. Eye tubercle weak, but represented by a deep pit on interior of valve, surrounded with about 200 muscle spots (Fig. 39). Marked chevron scar situated subjacent to eye tubercle, on interior surface of the valve limited by a distinct ridge ventrally. Limbs of chevron scar form an angle of about 70°. Venose markings absent. Hinge finely denticulate (Fig. 38 D).

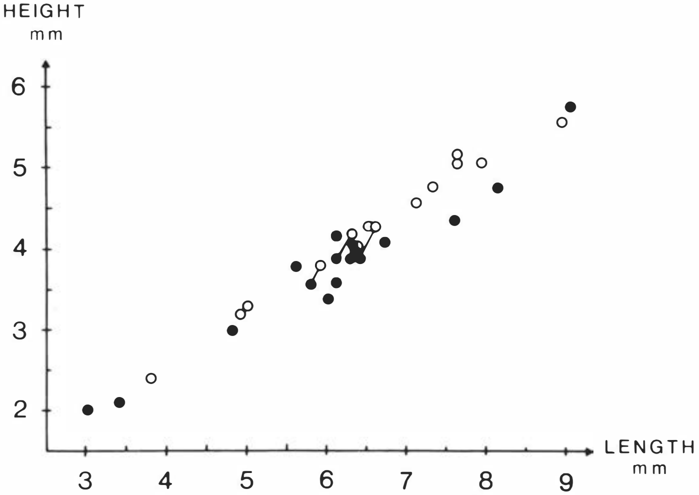

Fig. 40. *Herrmannnina phaseolus catarractensis* n. subsp. Diagram showing relationship between length and height of valves based on measured specimens from Högklint *d* at Vattenfallet. Dots and circles denote left and right valves, respectively; symbols connected by a line refer to the same carapace.

Remarks. – *Herrmannina phaseolus phaseolus* and *H. phaseolus catarractensis* are similar in shape. However, the former has a larger average size and is also finely punctose all over the whole exterior surface, whereas specimens from the *"Pterygotus"* Beds do not possess distinct puncta, although most are well preserved. The overlapped flat ventral area of the left valve in *H. phaseolus phaseolus* shows a faint, elongate depression, which is not present in *H. phaseolus catarractensis*. Moreover, the anterior cardinal corner is less pronounced in *H. p. phaseolus*. On well preserved valves of this subspecies, the venose markings are easily distinguished; such markings have not been observed on any valves from the *"Pterygotus"* Beds.

Occurrence. – The exact vertical range of *H. p. catarractensis* cannot be determined without further studies. It is common to abundant in the uppermost Högklint Limestone and seems to occur also in the Tofta Limestone.

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Palaeocope and eridostracan ostracodes

DALIP K. SETHI

Our current knowledge of palaeocope ostracodes from Gotland is very uneven. Beyrichiaceans have been described in an exellent monograph by Martinsson (1962). Silurian primitiopsaceans have been studied in some detail in Estonia (Sarv 1968) and Latvia (Gailite 1967), but only a few species have recently been described from Gotland (Martinsson 1955, 1956). The remainder of the palaeocopes are poorly known, not only on Gotland but also in the Silurian of the Balto-Scandian region in general. Although a number of species have been described their firm identification is frequently difficult if type or topotype material is not available for comparison. For a few species relevant to the present study such material could be examined but for the remainder open nomenclature has had to be used. This extensive use of open nomenclature also reflects the presence in the Vattenfallet material of numerous new taxa, some of them of uncertain affinity.

Eridostracans are here regarded tentatively as a separate order-group category. To my knowledge this group has not been reported previously from Gotland, and without a special study of comprehensive material, definition of eridostracan genera and species from Vattenfallet is difficult.

The bulk of palaeocopes and eridostracans from Vattenfallet have been obtained from limestone samples which were broken down into small chips that were scanned under a binocular microscope at ×20 magnification. The rock samples were collected by Liljevall, apart from a few obtained by me in 1975. Prior to identification many specimens had to be prepared with a fine needle, and the total time spent on preparation over five years was considerable. A minor fraction of the palaeocopes was obtained from marl samples many of which had previously been picked for ostracodes by Liljevall. The total material of palaeocope ostracodes examined comprises more than 15,000 specimens from some eighty different levels in the section. About 60 eridostracan valves were found.

Annotated faunal list

Palaeocopa

Leperditellacea

Neoprimitiella versipella (Neckaja), *N.* cf. *litvaensis* (Neckaja), *Pseudoaparchites decoratus* (Jones), *Bollia amabilis* Neckaja, *B.* sp. *a, Parahippa vis-*

byensis n. gen., n. sp., *Ulrichia* sp. *a, U.? palisadica* n. sp., *Monoceratella* n. sp. *a* (a single carapace), *Vattenfallia spinosa* n. gen., n. sp., *Opistoplax* sp. *a, O.* sp. *b* (a single valve), *Mirochilina* sp. *a, Aechmina* sp. *a, A.* sp. *b, Aechminaria* sp. *a, A.* sp. *b, A.* sp. *c, A.* sp. *d* (2.3 m, a single valve), Leperditellacea? gen. *a,* sp. *a*, Lepertitellacea gen. *b,* sp. *a,* Leperditellacea? gen. *c,* sp. *a* (12.35 m), Leperditellacea gen. *d,* sp. *a.*

The genus *Brevidorsa* Neckaja, 1973 (type species *Brevidorsa brevidorsa* Neckaja, 1973) is here regarded as a junior subjective synonym of *Pseudoaparchites* Krandijevsky, 1963 (type species *P. latus* Krandijevsky, 1963; junior subjective synonym of *Leperditella gregaria* Sarv, 1962, according to Abushik 1971). *Pseudoaparchites gregaria* Sarv is probably a junior subjective synonym of *Aparchites decoratus* Jones, 1889. Associated with specimens exhibiting the shape and ornamentation of *P. decoratus* are specimens with a smooth surface but otherwise similar to *P. decoratus*. In our present state of knowledge it is not clear whether these specimens fall within the range of variation of *P. decoratus* or belong to a separate species. In the log (Fig. 41) the smooth specimens are recorded as *P.* cf. *decoratus.*

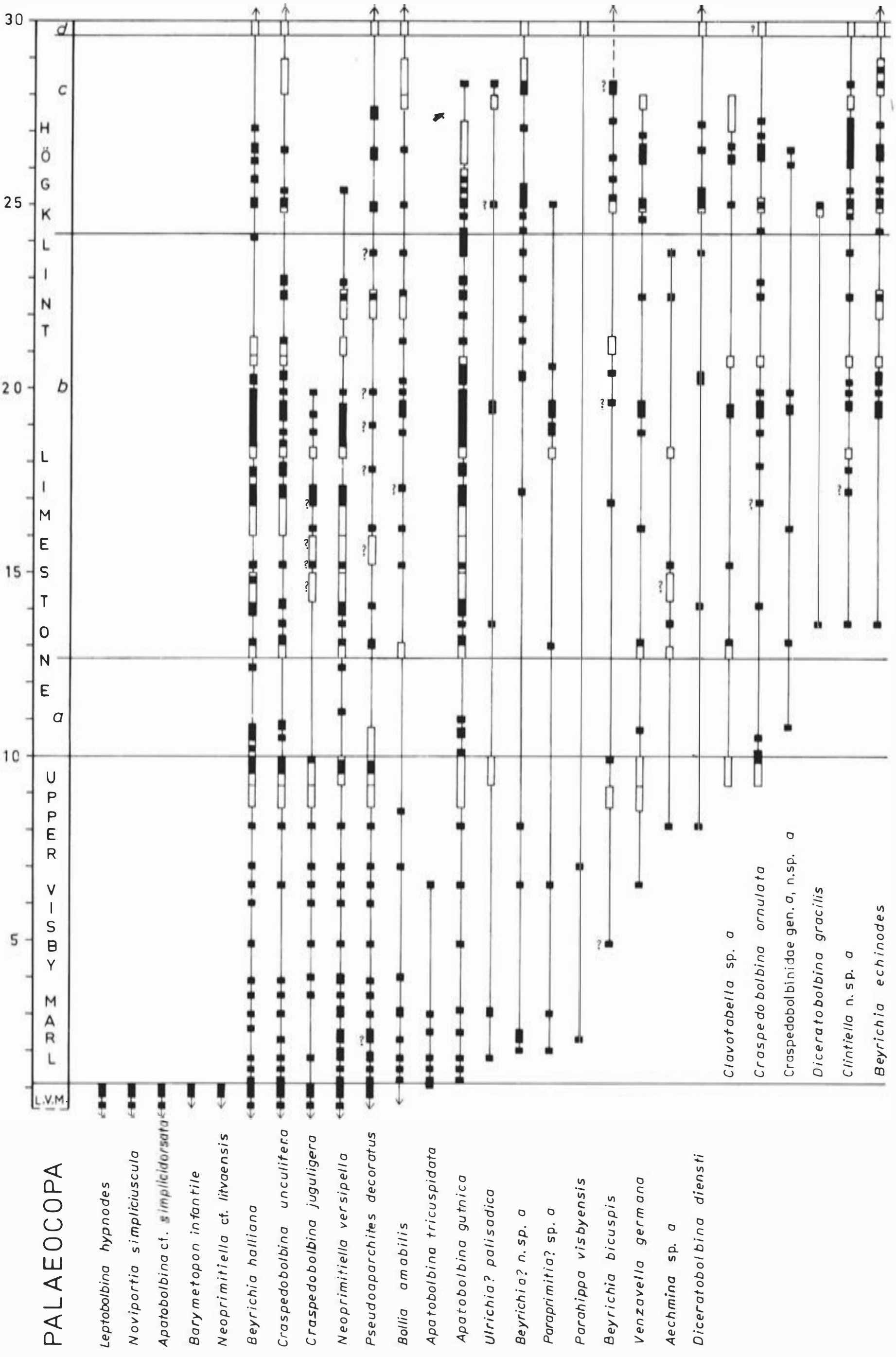
Eurychilinacea
Platybolbina (incertia subgeneris) *lunulifera* Henningsmoen, Eurychilinacea? gen. *a,* sp. *a.*

Primitiopsacea
Clavofabella sp. *a, Venzavella germana* Sarv, *V.* sp. *a, Signetopsis* sp. *a,* Primitiopsidae gen. *a,* sp. *a,* Primitiopsidae gen. *b,* sp. *a* (one tecnomorphic valve).

Primitiopsidae gen. *a,* sp. *a* has a *Clavofabella*-like shape to both valves and the dolon, but it lacks an adductorial pit and has a smooth surface. Primitiopsidae gen. *b,* sp. *a* has a coarsely reticulated surface and tecnomorphic velar ridge, but lacks an adductorial pit. The specimens of *Venzavella* exhibit considerable variation, particularly in the number and orientation of ridges, and without a study of larger samples the definition of species is somewhat uncertain.

Hollinacea
Diceratobolbina diensti (Kummerow) n. gen., *D. gracilis* n. sp.

Beyrichiacea
Apatobolbina gutnica Martinsson, *A. tricuspidata* Martinsson, *A.* cf. *simplicidorsata* Martinsson, *A.?* sp. *a, Leptobolbina hypnodes* Martinsson, *Craspedobolbina (Craspedobolbina) mucronulata* Martinsson, *C. (C.) juguligera* Martinsson, *C. (C.) ornulata* Martinsson, *Craspedobolbina (Mitrobeyric-*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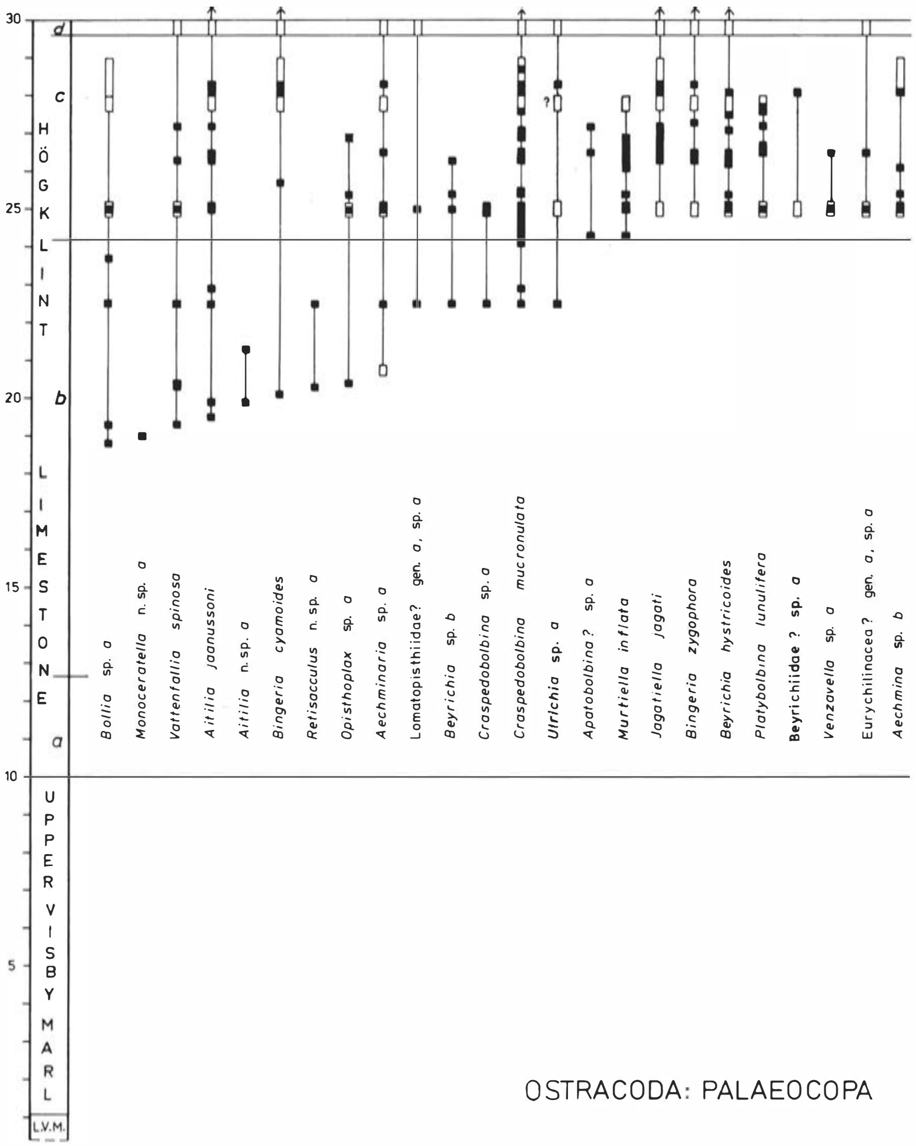
a
HÖGKLINT
LIMESTONE
UPPER VISBY MARL
L.V.M.
PALAEOCOPA
Leptobolbina hypnodes
Noviportia simpliciuscula
Apatobolbina cf. simplicidorsata
Barymetopon infantile
Neoprimitiella cf. litvaensis
Beyrichia halliana
Craspedobolbina unculifera
Craspedobolbina juguligera
Neoprimitiella versipella
Pseudoaparchites decoratus
Bollia amabilis
Apatobolbina tricuspidata
Apatobolbina gutnica
Ulrichia? palisadica
Beyrichia? n. sp. a
Paraprimitia? sp. a
Parahippa visbyensis
Beyrichia bicuspis
Venzavella germana
Aechmina sp. a
Diceratobolbina diensti
Clavofabella sp. a
Craspedobolbina ornulata
Craspedobolbinidae gen. a, n. sp. a
Diceratobolbina gracilis
Clintiella n. sp. a
Beyrichia echinodes
?

Fig. 41.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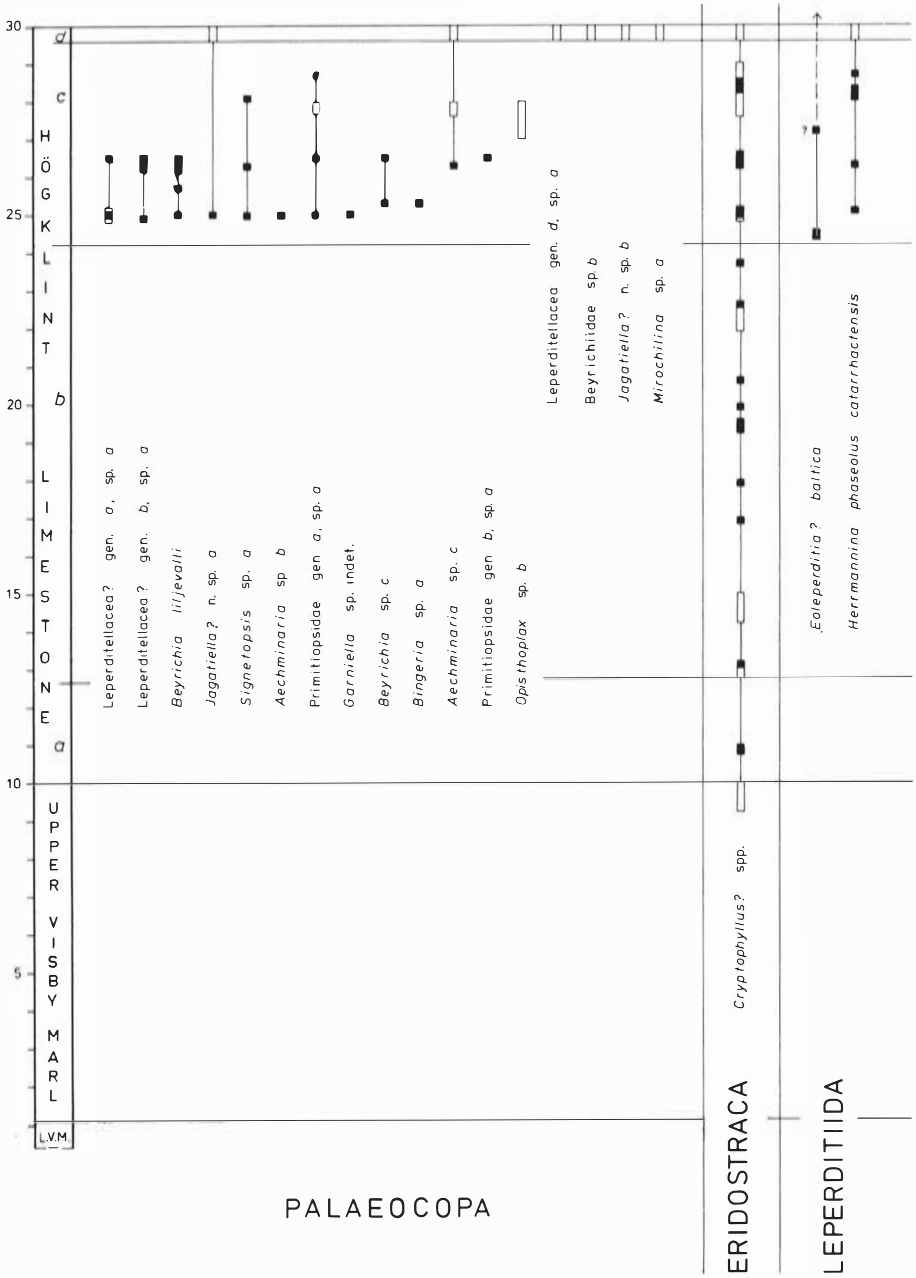
LIMESTONE
UPPER VISBY MARL
L.V.M.
Bollia sp. a
Monoceratella n. sp. a
Vattenfallia spinosa
Aitilia jaanussoni
Aitilia n. sp. a
Bingeria cyamoides
Retisacculus n. sp. a
Opisthoplax sp. a
Aechminaria sp. a
Lomatopisthiidae? gen. a, sp. a
Beyrichia sp. b
Craspedobolbina sp. a
Craspedobolbina mucronulata
Ulrichia sp. a
Apatobolbina? sp. a
Murtiella inflata
Jagatiella jagati
Bingeria zygophora
Beyrichia hystricoides
Platybolbina lunulifera
Beyrichiidae ? sp. a
Venzavella sp. a
Eurychilinacea ? gen. a, sp. a
Aechmina sp. b
?
OSTRACODA: PALAEOCOPA

Fig. 42.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HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
Leperditellacea? gen. a, sp. a
Leperditellacea? gen. b, sp. a
Beyrichia liljevalli
Jagatiella? n. sp. a
Signetopsis sp. a
Aechminaria sp b
Primitiopsidae gen a, sp. a
Garniella sp. indet.
Beyrichia sp. c
Bingeria sp. a
Aechminaria sp. c
Primitiopsidae gen b, sp. a
Opisthoplax sp. b
Leperditellacea gen. d, sp. a
Beyrichiidae sp. b
Jagatiella? n. sp. b
Mirochilina sp. a
Cryptophyllus? spp.
?
Eoleperditia? baltica
Herrmannina phaseolus catarrhactensis
PALAEOCOPA
ERIDOSTRACA
LEPERDITIIDA

Fig. 43.

hia) unculifera Martinsson, *C. (M.)* sp. *a* (4 tecnomorphs), *Aitilia jaanusson* n. sp., *A.* n. sp. *a, A.?* sp. *b* (19.80–19.85 m, a single tecnomorphic valve), *Clintiella* n. sp. *a*, *Barymetopon infantile* Martinsson, *Garniella* sp. indet. (two early tecnomorphs), *Retisacculus* n. sp. *a* (4 tecnomorphs), *Noviportia simpliciuscula* Martinsson, Craspedobolbinidae gen. *a,* n. sp. *a* (10 heteromorphs), *Beyrichia (Beyrichia) halliana* Martinsson, *B. (B.) bicuspis* Kiesow, *B. (B.)* sp. *b, Beyrichia (Simplicibeyrichia?)* sp. *c* (2 tecnomorphs), *Beyrichia* (inc. subgeneris) echinodes n. sp., *Beyrichia (Asperibyrichia) hystricoides* Martinsson, *B. (A.) liljevalli* n. sp., *B.?* n. sp. *a* (only tecnomorphs), *Bingeria zygophora* Martinsson, *B. cyamoides* Martinsson, *B.* sp. *a* (a heteromorphic valve), *Murtiella inflata* n. gen., n. sp., *Jagatiella jagati* n. gen., n. sp., *J.?* n. sp. *a*, *J.?* n. sp. *b,* Beyrichiidae? sp. *a* (2 tecnomorphs), Beyrichiidae sp. *b* (one heteromorphic and one tecnomorphic valve).

I consider *Craspedobolbina (C.) mucronulata* Martinsson, 1962 and *C. (C.) perornata* Martinsson, 1962 to be conspecific. The types of the species came from the same locality and horizon, and the material from Vattenfallet includes specimens that are morphologically intermediate (the crista on the syllobium only partially developed). For the species the name *C. (C.) mucronulata* is used here.

The differences between *C. (C.) juguligera* and *C. (C.) mucronulata* may lie at subspecies rather than at species level, but more material from different localities needs to be studied in order to solve this problem.

The Vattenfallet material includes a number of specimens with an anterodorsally pointed syllobium and pointed anterior lobe but which are otherwise similar to the contemporaneous *Craspedobolbina (Mitrobeyrichia) unculifera.* These specimens are believed to fall within the range of variation of *C. (M.) unculifera.*

Apatobolbina? sp. *a* has a reticulated surface and a distinct preadductorial boss.

Aitilia? sp. *b* (not entered in the log) has a prominent spine on the lateral surface of the valve, ventral of S2, instead of a spine or a spur on the velar ridge as in other species of *Aitilia.* For this reason the species is only tentatively included in *Aitilia.*

Beyrichia? sp. *a* has reticulated lobes, a dorsal spine on the syllobium, and some specimens are ornamented with a sparse tuberculation on the ventral side of the valve. Since no heteromorphs have been found, the species is difficult to define at present.

Questionable Palaeocopa
Paraprimitia? sp. *a,* Lomatopisthiidae? gen. *a,* sp. *a.*

In addition to the 71 palaeocope species listed above, the material includes specimens probably belonging to additional species, which for various reasons, such as fragmentary condition or poor state of preservation of the valves, were difficult to define. Most such specimens are from Högklint *d*.

Eridostraca

Eridoconchidae: *Cryptophyllus?* spp.

The taxonomy of eridostracans at the generic level is currently in a state of flux and for this reason the species recorded from Vattenfallet are included only conditionally in *Cryptophyllus*.

Discussion

Previous knowledge of palaeocope ostracodes from Gotland was based mostly on material found in marl samples (Martinsson 1962, 1967, etc.). The study of limestone samples has essentially complemented the previous data and resulted in extended ranges of many taxa, far too numerous to be listed individually. This is especially true with regards to Högklint *c* in which marly intercalations are almost totally absent and which therefore was poorly represented among Martinssons's samples. Moreover, at Vattenfallet this subdivision has far the greatest species frequency of palaeocope ostracodes (Fig. 76).

In the palaeocope faunas the boundary between the Lower and Upper Visby Marl is remarkably sharp at Vattenfallet, being marked by the disappearance of a distinctive assemblage comprising five species (Fig. 41). With the possible exception of *Apatobolbina gutnica* the palaeocope assemblage of the Upper Visby Marl does not include any moderate to high density species which appears in the division.

Martinsson (1967) distinguished within the Högklint Beds two palaeocope faunal assemblages: The *Apatobolbina gutnica* assemblage "in the lowermost member of the Högklint Beds" and the *Craspedobolbina ornulata* assemblage "in the massively reefy parts of the Högklint Beds". The overlying Tofta Beds were reported as containing the *Bingeria* assemblage. The Vattenfallet material shows that elements of Martinsson's (1967) *Bingeria* assemblage are already present in the uppermost Högklint *b (Bingeria cyamoides, Craspedobolbina mucronulata)* or at the base of Högklint *c (Bingeria zygophora)*. The pelletal limestone in these beds at Vattenfallet, especially in Högklint *c*, is similar to that of the Tofta Beds from which this assemblage was previously recorded. This suggests that the *Bingeria* assemblage had a preference for ecological conditions associated with deposition of bahamitic sediments. It is interesting to note that I have also found *Bingeria cyamoides* in the bedded inter-reef limestones of the Halla Beds at Hörsne Kanal, in a depositional environment that may not be very much different from that of Högklint *c*. *B. cyamoides* has been recorded also in the boring Marmorbrottet 1 (Hejdeby Parish) at the levels of 3.42–3.49, 7.62–7.67 (bahamitic limestone), and 8.77–8.80 m. The quarry of Marmorbrottet (Tjautet 1) is in the upper part of Slite *e* and lower part of Slite *g*.

The *Apatobolbina gutnica* assemblage occurs at Vattenfallet in Högklint *a* and *b* (see also quantitative data, Fig. 44). *Craspedobolbina ornulata* appears at the top of the Upper Visby Marl and ranges up to Högklint *d*; however, its relative frequency is low throughout its range. Martinsson's *C. ornulata* assemblage thus appears to be restricted mainly to the reef facies, and the possibility is not excluded that at Vattenfallet the material of the species includes reef-derived valves.

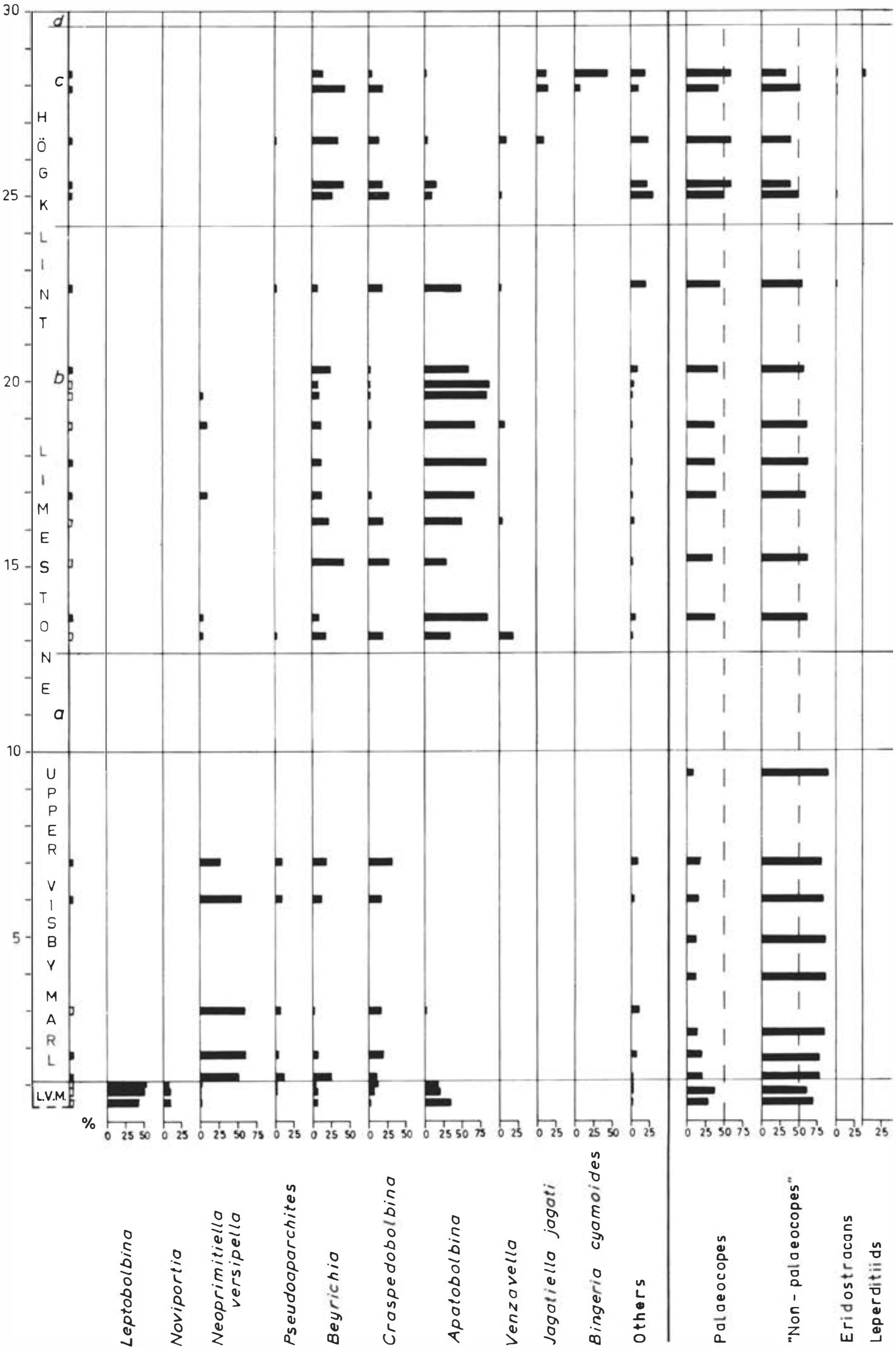
The quantitative distribution of various common palaeocope species, i.e. those which form at least ten per cent of the palaeocope valves in at least one of the samples, is shown in Fig. 44. The data were obtained by counting all palaeocope valves in a sample, and only samples that yielded more than 50 valves are recorded in Fig. 44. In several samples from the Upper Visby Marl palaeocope ostracodes were so rare that I did not succeed in finding the required minimum number of the valves. The total number of counted valves was about 6400.

In the Lower Visby Marl *Leptobolbina hypnodes* is dominant and *Apatobolbina* also occurs in high relative frequencies. The change in quantitative composition of the palaeocopes is very sharp at the boundary between the Lower and Upper Visby Marl.

In the Upper Visby Marl, where the proportion of palaeocopes among ostracodes is low, the small species *Neoprimitiella versipella* dominates. The relative frequency of this ostracode among ostracodes in general is not very much higher there than in some samples from Högklint *b*, but its importance among palaeocopes is high because of the low relative frequencies of other palaeocopes. The relative frequency of *Apatobolbina* is low.

From Högklint *a* none of the available samples yielded the minimum number of palaeocope specimens. Throughout Högklint *b Apatobolbina gutnica* is dominant but its importance in Högklint *c* is low. In the upper part of Högklint *c Bingeria cyamoides* is the dominant species. In addition to the levels recorded in the log (Fig. 44), it is also the commonest palaeocope at 28.0–28.2 m (c. 40–45 per cent; this was not entered in the log because the total number of the counted valves in the sample was somewhat less than 50).

In *Beyrichia* and *Craspedobolbina* early instars are difficult to identify at species level and therefore only genera are recorded in Fig. 44. However, the material examined indicates that in the Upper Visby Marl the dominant *Craspedobolbina* species are *C. juguligera* and *C. unculifera* whereas in Högklint *c C. mucronulata* dominates.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Leptobolbina
Noviportia
Neoprimitiella versipella
Pseudoaparchites
Beyrichia
Craspedobolbina
Apatobolbina
Venzavella
Jagatiella jagati
Bingeria cyamoides
Others
Palaeocopes
"Non - palaeocopes"
Eridostracans
Leperditiids

Samples from Högklint *d* were not analysed quantitatively. However, rough estimates indicate that *Aitilia jaanussoni* is one of the commonest species. *Apatobolbina gutnica* and *Venzavella* were not found at all. In these beds the composition of the palaeocope fauna resembles to some extent that of the Přidoli Formation in Bohemia. The genera in common include *Parahippa, Mirochilina, Aechmina, Eurychilinacea?* gen. *a,* and *Clintiella* (personal observations and M. Krůta, personal communication).

Description of new taxa

Superfamily Leperditellacea

Parahippa n. gen.

Type species. – Parahippa visbyensis n. sp.

Diagnosis. – A non-sulcate to faintly unisulcate genus with a sulcal depression to a faint S2 some distance in front of the midheight of the valve, and a row of seven to nine prominent spines adventrally. Acroidal processes well developed.

Remarks. – The generic name *Hippa* Barrande, 1872 is a junior homonym replaced by Přibly (1949) with *Trubinella* (type species *Hippa latens* Barrande, 1872). Examination of the types of *T. latens* in the National Museum, Praha, revealed that this Ordovician species is probably close to *Oecematobolbina* and is generically distinct from the second (Silurian) species, *H. rediviva* Barrande, 1872, originally included in *Hippa* by Barrande (1872). For the latter species, as well as for a congeneric species from Vattenfallet, the new genus *Parahippa* is proposed here. By its diagnostic characters *Parahippa* is clearly distinguished from the other related ostracodes. The genus is a member of the Leperditellacea (or Aparchitacea if this group is distinguished) but the familial classification is at present uncertain.

Parahippa visbyensis n. sp.

Fig. 45A–F

Holotype. – A right valve, SGU Type 37 (Fig. 45A–B) from Högklint *d* at Vattenfallet.

Diagnosis. – Valves with a faint, straight sulcal depression dorsal of a distinct, small, rounded adductorial muscle scar.

Fig. 44. Percentage frequencies of palaeocope ostracodes (left), and of all ostracodes (right). Data on palaeocope ostracodes have been obtained by Sethi by counting at least 50 valves per sample. Only those species or genera are recorded which form at least ten per cent of the palaeocopes in at least one sample. Black rectangles along the stratigraphical column show the location of limestone samples and open rectangles the marl samples. The quantitative composition of all ostracodes has been obtained by counting at least 100 valves, up to 19 m by Jaanusson and in the upper part of the section by Sethi; only limestone samples were used.

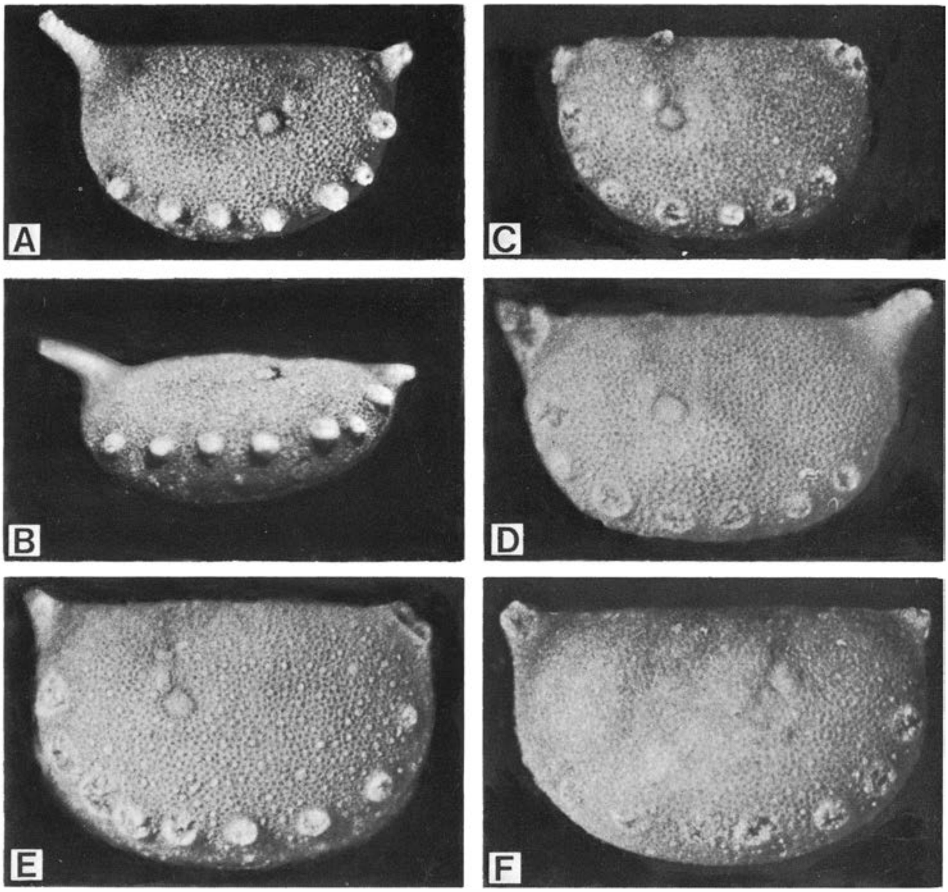


Fig. 45. *Parahippa visbyensis* n. sp. A–B. Holotype, a right valve, in lateral and lateroventral view; SGU Type 37. C. Left valve in lateral view showing the base of a spine at the dorsal margin above the adductorial muscle spot; SGU Type 38. D. Left valve in lateral view; SGU Type 39. E. Left valve with 9 spines in lateral view; SGU Type 40. F. Right valve in lateral view; SGU Type 41. All specimens are from Högklint *d* at Vattenfallet, ×50. Photograph D. Sethi.

Description. – The material examined consists of 46 valves, all except two from Högklint *d*. The species is at present known only from the type locality. The small, rounded adductorial scar is distinctly defined in all specimens. The distance between the dorsal margin of the scar and the dorsal margin of the valve equals about three times the diameter of the scar; the distance between the posterior margin of the scar and the mid-length of the valve is slightly less than twice the diameter of the scar. A faint, rounded preadductorial node is developed anterodorsal of the scar (Fig. 45F). The sulcal depression varies: it is straight and fairly well-defined in some specimens but scarcely traceable in others. The valves have a long acroidal process at both the anterior and posterior cardinal corner. The number of adventral spines varies from 7 to 9. One specimen (Fig. 45C) shows the base of a spine at the dorsal margin of the valve at the level of the adductorial scar. Surface of the valves very finely reticulate with scattered small granules.

Dimensions. – Maximum lenght–maximum height in mm: 0.80–0.49 (holotype), 1.01–0.66, 0.97–0.60, 0.94–0.66, 0.91–0.60, 0.83–0.53, 0.80–0.51.

Remarks. – *Parahippa visbyensis* differs from *P. rediviva* (Barrande) from Bohemia in the presence of a distinct adductorial scar on the lateral surface of the valve, and by having a sulcal depression instead of a faint, narrow sulcus.

Family Bolliidae

Ulrichia? palisadica n. sp.

Fig. 46A–D

Holotype. – A carapace, SGU Type 42 (Fig. 46A–D) from the Upper Visby Marl (9.2–10.0 m) at Vattenfallet.

Diagnosis. – An *Ulrichia*-like species with the posterior node only very slightly behind the mid-length of the valve, forming the dorsal termination of a crest which extends in a broad curve anteriorly and turns in front of the anterior node posterodorsally, almost reaching the dorsal margin of the valve.

Description. – The available material consists of 5 carapaces and 8 valves. The lateral surface of the valve is bordered by a crest-like carina along the whole free margin; subcarinal field slightly concave. The dorsal terminations of the nodes project somewhat beyond the dorsal margin. The posterior node is elongate, distinctly narrower than the anterior node. The crest is narrow, distinct, turns in front of the anterior node postero-dorsally and becomes obsolete slightly before reaching the dorsal margin of the valve. Lateral surface of the valve coarsely reticulate. The holotype is 0.46 mm long and has a maximum height of 0.31 mm.

Remarks. – *U.? palisadica* belongs to a group of species, including *Ulrichia* (*U.*) *verticalis* (Copeland 1974, Pl. 12:29–31) and *U.* (*U*). *macgilvrayensis* (Copeland 1974, Pl. 12:37–41) in which the posterior node is narrow and continues anteroventrally in a ridge of crest. The relationship of this group to the true *Ulrichia* is uncertain. *U.? palisadica* differs from the other representatives of the group by the development and anterior extent of the crest.

Family Aechminellidae

Vattenfallia n. gen.

Type species. – *Vattenfallia spinosa* n. sp.

Diagnosis. – A trilobate genus with L1 extending almost to the anterior margin of the valve, L2 very small and L3 reaching posteriorly to about the mid-length of the valve; L1 and L3 produced dorsally into long spines. Adductorial pit shallow but distinct.

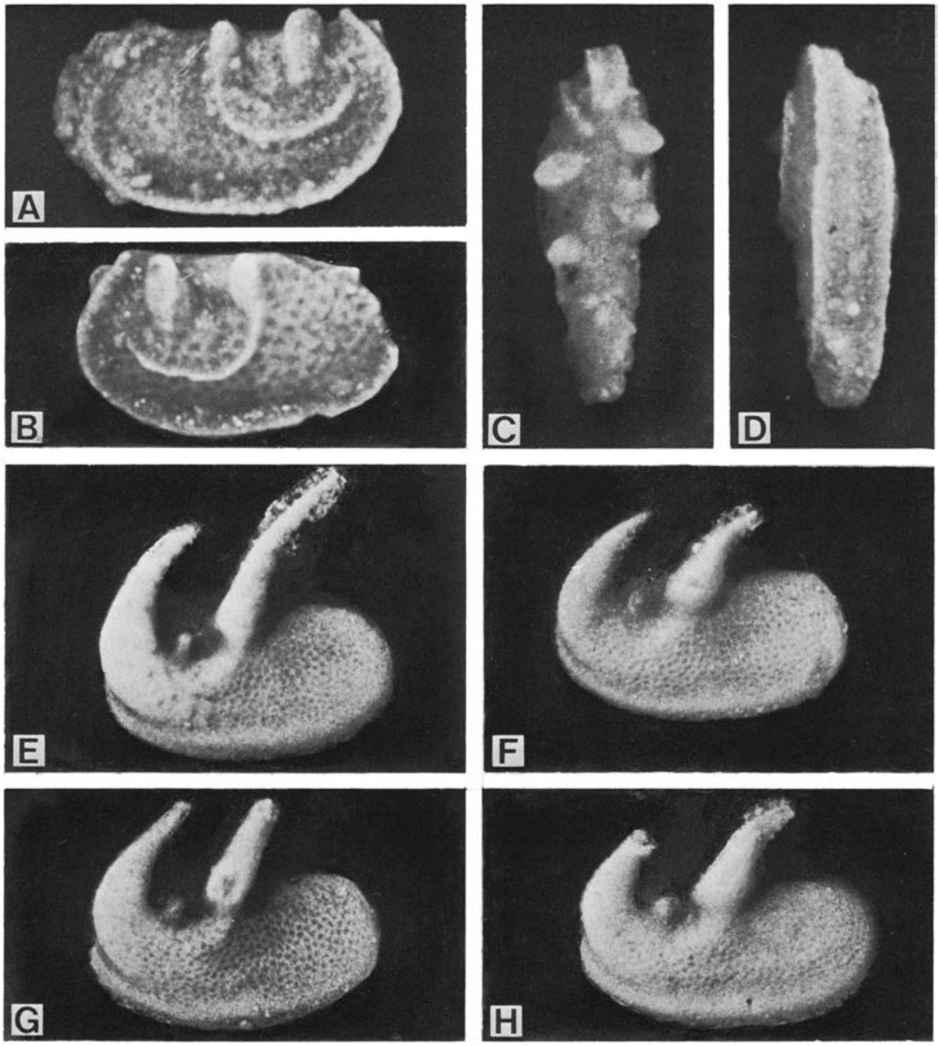


Fig. 46. A–D. *Ulrichia? palisadica* n. sp., holotype, SGU Type 42, carapace in four different views, ×70; Vattenfallet, Upper Visby Marl, 9.20–10.0 m. E–H. *Vattenfallia spinosa* n. gen., n. sp., ×50; Vattenfallet, Högklint Limestone. E. Holotype, left valve; 27.13–27.26 m, SGU Type 43. F. Left valve; 20.30 m, SGU Type 44. G. Left valve; 20.30 m, SGU Type 45. H. Left valve; 19.25 m, SGU Type 46. Photograph D. Sethi.

Remarks. – *Vattenfallia* is apparently a member of the aechminellids and this extends the range of the family down to the Lower Wenlockian. It differs from the other aechminellids most distinctly by the long, flattened post-lobate area which comprises almost half the length of the valve. The genus is at present monotypic.

Vattenfallia spinosa n. sp.

Fig. 46E–H

Holotype. – A left valve, SGU Type 43 (Fig. 46 E) from Högklint *c* (27.13–27.26 m) at Vattenfallet.

Description. – The material examined comprises 25 valves. The lobate area is confined to the anterior half of the valve. L1 strongly curved, extending anteriorly almost to the level of the anterior free margin of the valve or even protruding beyond it; L2 is formed as a minute lobe; L3 is mostly constricted proximally but the amount of constriction varies and in some specimens (Fig. 46E) it is scarcely noticeable. A small, shallow, distinct adductorial pit is developed between the bases of L2 and L3. No adventral structures, but marginal spines have been observed in some specimens. In some specimens the distal part of L3 has been observed to carry a row of small spines both anteriorly and posteriorly, giving the lobe a serrate contour in lateral view. The lateral surface of the valve is finely reticulated. The reticulation extends also to the proximal part of L1 but the rest of the spine-like lobes appear to be smooth.

Dimensions. – Maximum length–maximum height in mm: 0.70–0.37 (holotype), 0.69–0.31, 0.66–0.37, 0.63–0.34, 0.60–0.34.

Occurrence. – Upper part of Högklint *b*, Högklint *c* and Högklint *d* at Vattenfallet Fig. 42); Boring Marmorbrottet 1 (Hejdeby Parish), 36.34–36.42 m and boring Rosendal 1(Follingbo Parish), 50.70–50.80.

Superfamily Hollinacea

Diceratobolbina Jaanusson and Sethi n. gen.

Type species. – *Ctenobolbina diensti* Kummerow, 1924.

Diagnosis. – Valves unisulcate, S2 long, geniculate. Tecnomorphs with a pair of long, curved spurs on either valve, fringed and dorsally partly connected by a thin adventral flange. Heteromorphs with a broad dolon which terminates abruptly posteriorly; inner part of the dolon interiorly with four distinct locular pits and exteriorly with corresponding rounded inflations.

Discussion. – The type species (Fig. 47E–F; Kummerow 1924, Pl. 21:8; for a photograph of the holotype, see Kummerow 1943, Pl. 47:13) is represented in the Vattenfallet material by 7 heteromorphs and 51 tecnomorphs. An additional species, *D. gracilis* n. sp., is described below.

Diceratobolbina is very close to *Grammolomatella* Jaanusson, 1957 and differs from it mainly by the distinctly loculate dolon. A pair of the tecnomorphic spurs and a loculate dolon is present also in *Semibolbina* but in that genus the posterior spur is situated somewhat higher on the lateral surface of the valve and is not incorporated in the dolon.

In addition to the Lower Wenlockian of Gotland (Upper Visby Marl and Högklint Beds), *Diceratobolbina* is known also in the Wenlockian of the Oslo Region and the Upper Llandoverian of Shropshire (recorded as *Ctenobolbina* or *Parabolbina diensti;* for references see Henningsmoen (1954:58).

Diceratobolbina gracilis Sethi n. sp.

Fig. 47A–D.

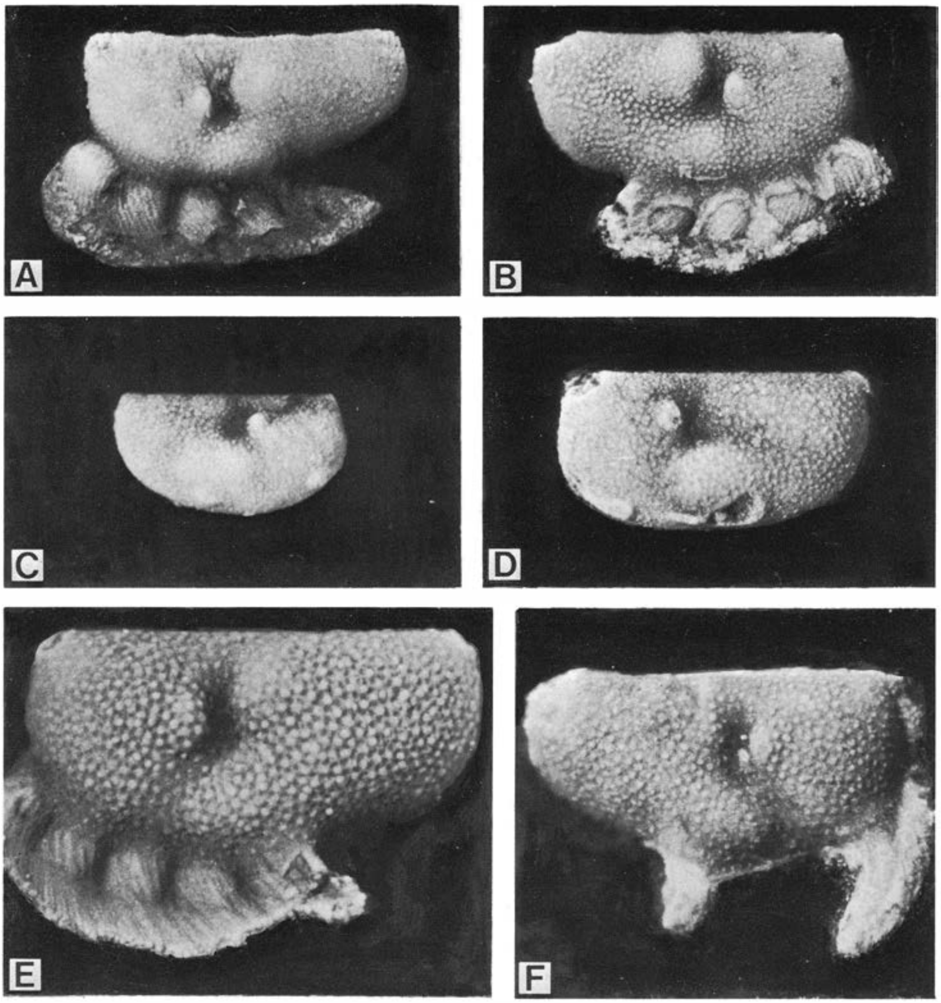


Fig. 47. A–D. *Diceratobolbina gracilis* n. sp. A. Left heteromorphic valve; 13.55 m, SGU Type 47. B. Holotype, right heteromorphic valve; SGU Type 48. 24.80–25.20 m. C. Right valve of an early instar; SGU Type 49, 25.0 m. D. Left tecnomorphic valve; SGU Type 50, 24.80–25.20 m. E–F. *Diceratobolbina diensti* (Kummerow) n. gen. E. Left heteromorphic valve; SGU Type 51, Högklint *d*. F. Right tecnomorphic valve; SGU Type 52. Högklint *d*. All specimens are from the Högklint Limestone at Vattenfallet, ×50. Photograph D. Sethi.

Holotype. – Right heteromorphic valve, SGU Type 48 (Fig. 47B), from Högklint *c* (24.80–25.20 m) at Vattenfallet.

Diagnosis. – A *Diceratobolbina* species with a faint S2 ventral of the geniculum. Valves with inflations behind the dorsal and ventral part of S2.

Description. – The material comprises 2 heteromorphic and 2 tecnomorphic valves, all from the Högklint Beds at Vattenfallet. The adult valves are much smaller and more elongate than in *D. diensti*. The spurs are broken off in the figured tecnomorphs. A thin flange appears to be developed between the bases of the spurs but details are unclear; also in *D. diensti* the exact configuration of the flange is not known because the structure is very thin and easily broken off. The dorsal part of S2 is deep, the ventral part shallow and poorly defined behind a hump-like ventral inflation of the valve; the development of the ventral hump varies: in heteromorphs it is mostly distinct whereas in tecnomorphs it may be poorly defined. Another inflation is located behind the anterior part of the sulcus: in the holotype it is well-defined and resembles both in shape and location the bulbous L3 of many post-Silurian hollinids, but in other heteromorphs the inflation is less distinctly developed and in tecnomorphs it is poorly defined. Dolon as in *D. diensti;* the locular inflations on the lateral surface of the dolon are obliquely striated. Surface of the valve otherwise densely granulate.

Discussion. – *D. gracilis* differs from *D. diensti* in its smaller adult size, poor development of the ventral part of S2, development of inflations behind S2, and a much more finely granulose surface.

Dimensions. – Heteromorphs 1 and 2 (holotype): maximum length (1) 0.77 mm, (2) 0.74 mm; height of the lateral surface (1) 0.37 mm, (2) 0.34 mm; maximum height (including dolon) (1) 0.75 mm, (2) 0.63 mm.

Superfamily Beyrichiacea

Beyrichia (Asperibeyrichia) liljevalli n. sp.

Fig. 48A–D

Holotype. – A right female valve, SGU Type 53 (Fig. 48A–B) from Högklint *c* (26.19–26.37 m) at Vattenfallet.

Diagnosis. – A species of *B. (Asperibeyrichia)* without cusps or spines on the cuspidal parts of the lobes; L1 almost completely obsolete. No lobule between the crumina and L2.

Description. – The material comprises one heteromorphic and 11 tecnomorphic valves, all from Högklint *c*. The species has not yet been found outside the type locality. Valves subamplete with almost obsolete L1. In tecnomorphs S1 very poorly developed, in several specimens obsolete; L2 thus anteriorly with an indistinct boundary, in several specimens almost completely fused with L1. The cuspidal part of the syllobium is rounded, not protruding beyond the hinge line. None of the specimens show a tendency to form any cusps or spines on the cuspidal part of the lobes. There is no syllobial groove or any tendency for the development of a calcarine spine. Early tecnomorphs provided with a short zygal ridge. The velum is developed as a low, rounded ridge. The heteromorphic valve has a shallow S1 anteroventrally. Crumina very large, reaching anteriorly to S2. Lateral surface of the valves ornamented with a coarse, sparse tuberculation; the lateral surface of the crumina is smooth but a narrow strip of the ventral cruminal surface has sparse tubercles along the velar ridge. Hinge length of the holotype 1.29 mm, height along S2 1.03 mm.

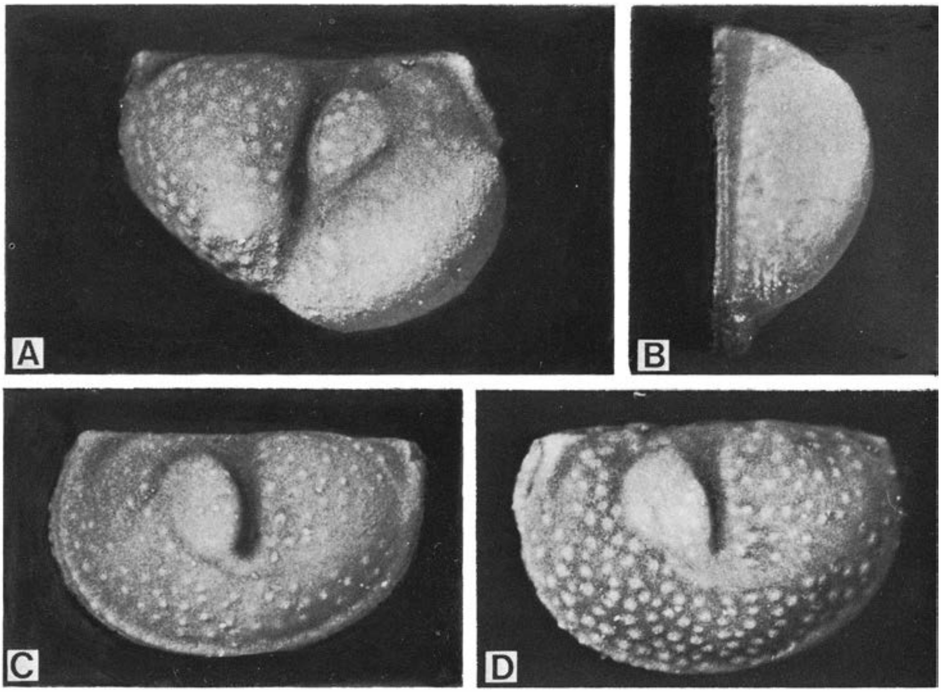


Fig. 48. *Beyrichia (Asperibeyrichia) liljevalli* n. sp. A. Holotype, right female valve; SGU Type 53, 26.19–26.37 m. B. Ventral view of the holotype (posterior end upwards). C. Left tecnomorphic valve; SGU Type 54, 25.0 m. D. Left tecnomorphic valve; SGU Type 55, 25.60–25.80 m. All specimens are from Högklint *c* at Vattenfallet, ×40. Photograph D. Sethi.

Remarks.—This species combines characteristics of two different subgenera. It shares with *Beyrichia (Simplicibeyrichia)* the marked tendency towards obsolescence of L1 and S1 and the lack of lobial cusps. On the other hand the poor differentiation of the crumina from L1 resembles that of *Beyrichia (Asperibeyrichia)*. The closest described species appears to be *B. (A.) hystricoides* Martinsson which differs clearly in having a spinous anterior lobe, and in the presence of a lobule between the crumina and S2.

Beyrichia (incerti subgeneris) echinodes n. sp.

Fig. 49A–F

Holotype.—A right female valve, SGU Type 58 (Fig. 49C) from Högklint *c* (28.60–28.80 m) at Vattenfallet.

Diagnosis.—*Beyrichia* with spinose dorsal margin in adult specimens; L1 obsolete. S2 very shallow and narrow, adductorial muscle spot well defined externally.

Description.—The number of valves examined exceeds 60. L1 not differentiated as a lobe; L2 of varying convexity, very low and indistinctly defined in some specimens. S2 narrow, very shallow, terminating ventrally in a distinct ovate muscle spot which is mostly well defined externally; the latter feature makes it easy to identify even small

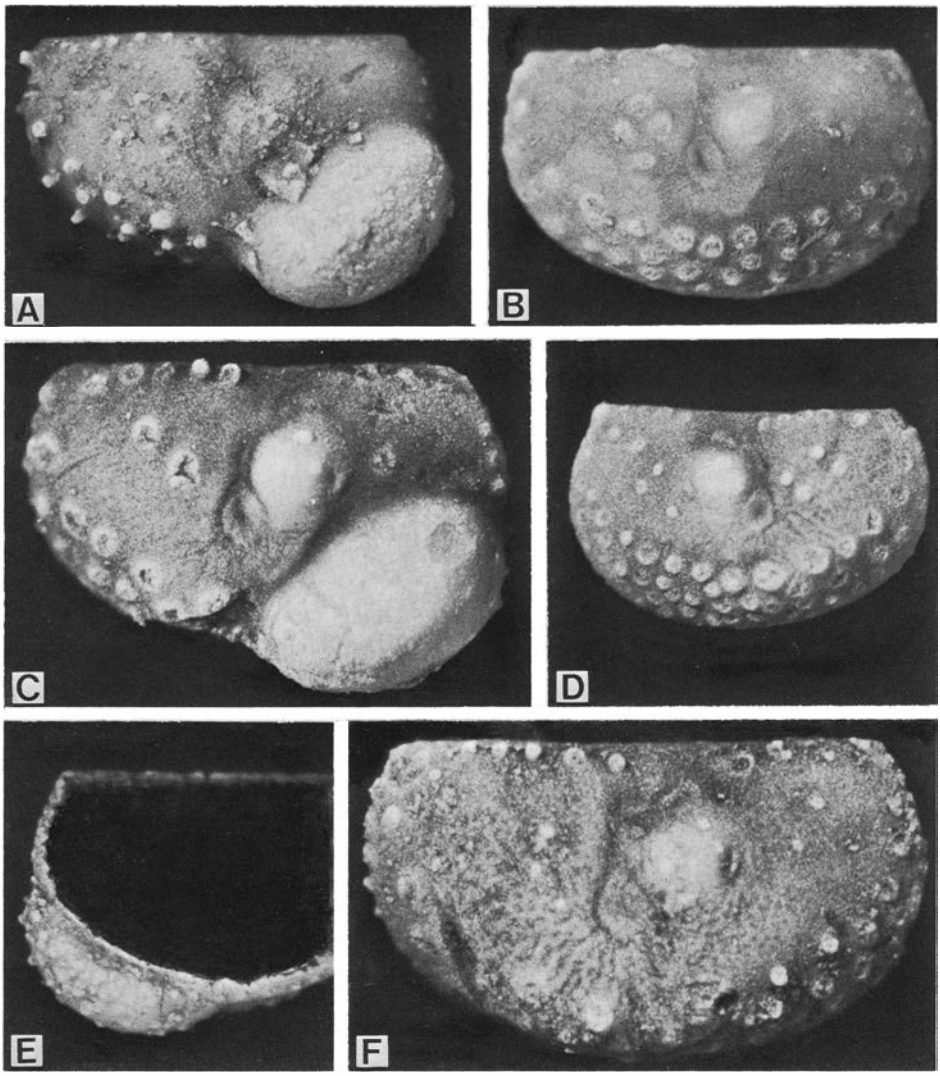


Fig. 49. *Beyrichia* (inc. subgen.) *echinodes* n. sp. A. Right female valve; SGU Type 56, 19.80–19.85 m. B. Right tecnomorphic valve; SGU Type 57, 26.64–26.73 m. C. Holotype, right female valve; SGU Type 58, 28.0–29.0 m. D. Left tecnomorphic valve; SGU Type 59, 26.28–26.37 m. E. Ventral view of the crumina of a right female valve; SGU Type 60, 19.80–19.85 m. F. Right adult tecnomorphic valve showing anastomosing "vascular" markings; SGU Type 61, 20.10–20.15 m. All specimens are from the Högklint Limestone at Vattenfallet; A–E ×40, F ×60. Photograph D. Sethi.

instars or fragmentary specimens of the species. Velar structure formed by a low, rounded ridge. Crumina strongly inflated, without striated field ventrally; the velar ridge can be traced on the ventral side of the crumina as a bend with a row of tubercles. Several specimens show traces of anastomosing "vascular" markings (Fig. 49F), recently discussed by Sohn (1974). Ornamentation consists of short spines which are normally broken off. The spines are sparsely spaced and concentrated in a row along the dorsal margin and on the ventral part of the valve; lateral surface of syllobium has two to five spines, L2 frequently has three, and the lateral surface in front of L2 has a few spines.

Remarks.–Beyrichia echinodes resembles *B. erinacea* Martinsson in having spines dorsally along the cuspidal part of the lobes. The similarity is also hinted at by the name of the species (both the Latin *erinacea* and the Greek *echinodes* mean hedgehog). It differs from *B. erinacea* in having a narrow and shallow S2 and by the obsolete L1 (*B. erinacea* has a low spinose ridge in the cuspidal part of L1).

*Dimensions.–*Hinge length-Sulcal height of female valves in mm. Vattenfallet specimens: 0.91–0.80, 1.06–0.77, 1.17–0.89 (holotype), 1.22–0.89, 1.31–1.00. Annelund 1 specimens: 1.29–0.91, 1.26–0.87, 1.23–0.87, 1.20–0.86. The average size of the female valves tends to increase from Högklint *b* to *d*.

*Occurrence.–*Högklint *b, c* and *d* at Vattenfallet (Fig. 41); Annelund 1, loose block, Högklint *c* or lowermost Tofta Limestone; Hejdeby Parish, boring Marmorbrottet 1 7.62–7.67, 24.80–24.90 and 28.70–28.79 mm and boring Katrinelund 1 3.81–3.86 and 11.60–11.64 m.

Murtiella n. gen.

Type species.–Murtiella inflata n. sp.

*Diagnosis.–*A small trilobate Beyrichiidae with strongly inflated large crumina which merges anterodorsally and posteriorly into the lobate area without any distinct boundary; smooth ventrally without traces of dolonal scar or ridges. Velar structure represented by a velar bend or low velar ridge; a smooth canaliculus developed in both tecnomorphs and heteromorphs.

*Remarks.–*The genus is at present monotypic. It is one of the smallest beyrichiaceans known. *Murtiella* has some resemblance to *Frostiella* and *Kloedenia* which also have a well-developed heteromorphic canaliculus. However, otherwise it differs from these genera in a number of characters. The name is derived from the Hindi *murti,* as beautiful as a statue.

Murtiella inflata n. sp.

Fig. 50A–G

*Holotype.–*A left female valve, SGU Type 62 (Fig. 50A) from Högklint *c* (25.20–26.00 m) at Vattenfallet.

*Description.–*The material comprises 7 heteromorphic and 25 tecnomorphic valves, all from Högklint *c*; the species has not been found outside the type locality. Tecnomorphs are distinctly trilobate. L1 strongly curved, in some specimens (Fig. 50F) separated posteroventrally from the rest of the lobate area by a depression or shallow groove; dorsal termination of L1 somewhat pointed or rounded. L2 relatively large, prominent;

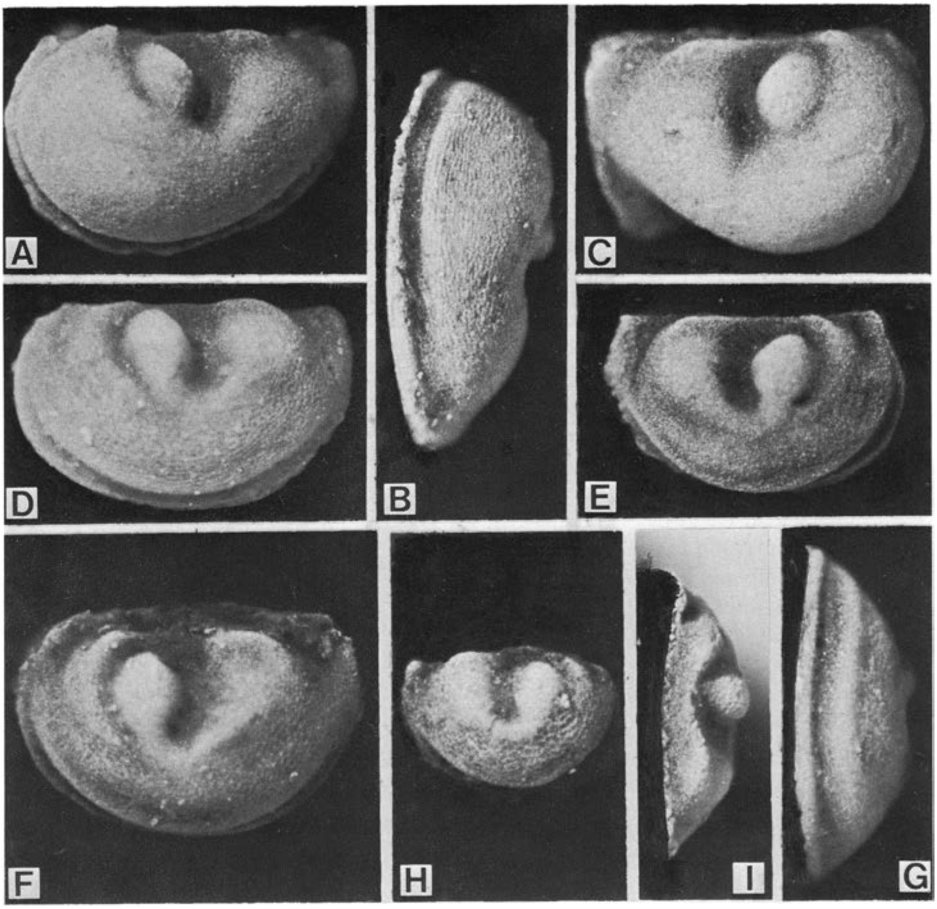


Fig. 50. *Murtiella inflata* n. gen., n. sp. A. Holotype, left female valve; SGU Type 62, 25.20–26.0 m. B. Left female valve in ventral view; SGU Type 63, 26.28–26.37 m. C. Right female valve; SGU Type 64, 25.10–25.20 m. D. Left tecnomorphic valve; SGU Type 65, 26.28–26.37 m. E. Right tecnomorphic valve; SGU Type 66, 26.46–26.55 m. F–G. Left tecnomorphic valve in lateral and ventral view; SGU Type 67, 26.91–27.0 m. H. Right valve of an early instar; SGU Type 68, 26.28–26.37 m. I. Dorsal view of a tecnomorphic valve; SGU Type 69, 25.33 m. All specimens are from Högklint *c* at Vattenfallet, ×50. Photograph D. Sethi.

shape of the syllobium variable, mostly with poorly defined ventral and posterior boundary. Dorsal boundary of the syllobium is formed by a low crest to sharp edge; the edge defines the lateral margin of a vertical, fairly high dorsum which extends from L1 to the syllobium. Cruminal inflation involves L1, except its dorsal tip, and the whole anteroventral part of the lateral surface; the inflation has no distinct boundaries on the lateral surface of the valve. Because of the inflation, S1 is much shorter and shallower than in tecnomorphs. S2 is wide, deep, and well defined. The velar structure is developed as a distinct bend or a low, rounded ridge which laterally defines a narrow, smooth canaliculus. In most specimens the lateral surface of the valve appears to be smooth but in some specimens a very fine, fingerprint-like irregular lineation is distinguishable.

Dimensions. – Hinge length – maximum height in mm; tecnomorphs: 0.83–0.60, 0.80–0.54, 0.71–0.54, 0.69–0.57, 0.63–0.46, 0.60–0.43; heteromorphs: 0.86–0.60, 0.80–0.60, 0.75–0.54 (holotype), 0.74–0.57, 0.74–0.54.

Jagatiella n. gen.

Type species. – *Jagatiella jagati* n. sp.

Diagnosis. – Smooth to finely punctate non-lobate Beyrichiidae with a distinct, large, ovate muscle spot at the mid-height of the valve and a faint sulcal depression or a narrow, straight, fissure-like sulcus extending from the muscle spot to the dorsal margin of the valve. In heteromorphs the domicilium is considerably inflated anteroventrally and ventrally; dorsally the inflated area merges into the lateral surface of the valve without a distinct boundary. The velar structure is represented by a low velar ridge.

Remarks. – In addition to the type species, the Vattenfallet material includes two further species, here referred to as *Jagatiella?* n. sp. *a* and *J.?* n. sp. *b,* which might belong to the genus. For their correct generic assignment more material is needed. A possible further species of *Jagatiella* is *Kiltsiella sarvi* (Copeland 1974, Pl.IV:1–19) from Anticosti, although it appears to lack a distinct adductorial muscle spot and seems to possess a relatively high dorsum. In this species the development of the crumina is very similar to that in *Jagatiella* whereas *Kiltsiella* has an exteriorly well-defined cruminal pouch (Sarv 1968, Pl. 3:8).

The development of the crumina in *Jagatiella* resembles that in *Noviportia* (Martinsson 1962, Fig. 138A, C), but the latter genus lacks a sulcus or a distinct sulcal depression and has a shallow adductorial pit, a high dorsal plica and a clearly different ventral morphology of the crumina.

The name is derived from the Hindi *Jagat,* earth, alluding to the rounded shape of the carapace.

Jagatiella jagati n. sp.

Fig. 51A–I

Holotype. – A right female valve, SGU Type 70 (Fig. 51A) from Högklint *c* (28.0–29.0 m) at Vattenfallet.

Description. – The material comprises more than 100 valves from Högklint *c* and *d* at Vattenfallet, some valves from a loose block at Annelund 1 (Högklint *c* or Tofta Beds) and from Katrinelund 1 boring 2.90–2.92 and 12.50–12.60 m. The sulcal structure varies from a very narrow, fissure-like straight sulcus to a very faint sulcal depression. Adductorial muscle spot relatively large, in some heteromorphic valves surrounded by a narrow depression. Only one articulated tecnomorphic carapace has been available; it shows that the right valve overlaps the left valve along the free margin but the amount of overlap is not great. The velar structure forms a rounded ridge along the whole free margin. The cruminal inflation occupies the anteroventral and ventral part of the female valve and merges dorsally into the lateral surface of the valve without a distinct

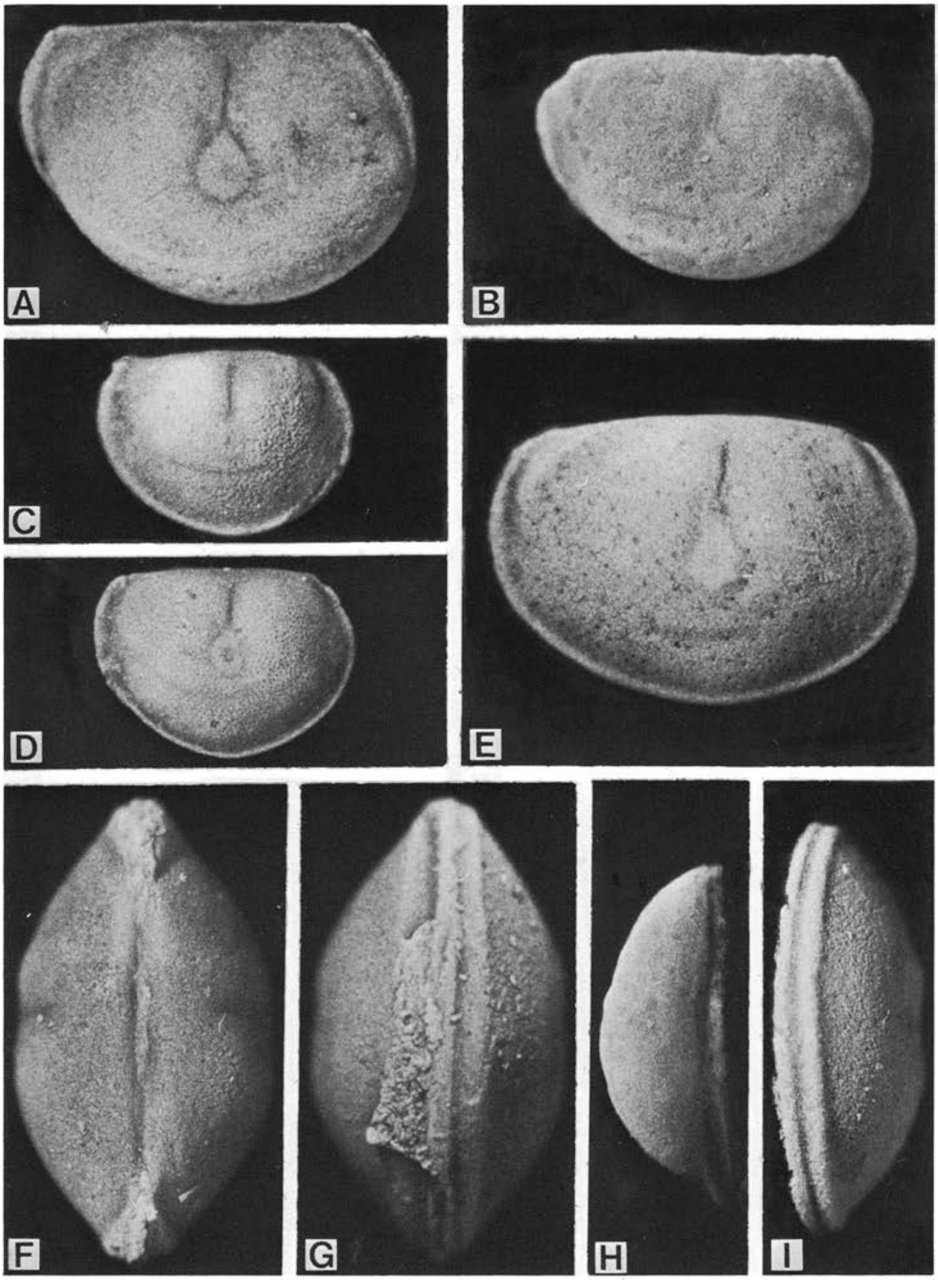
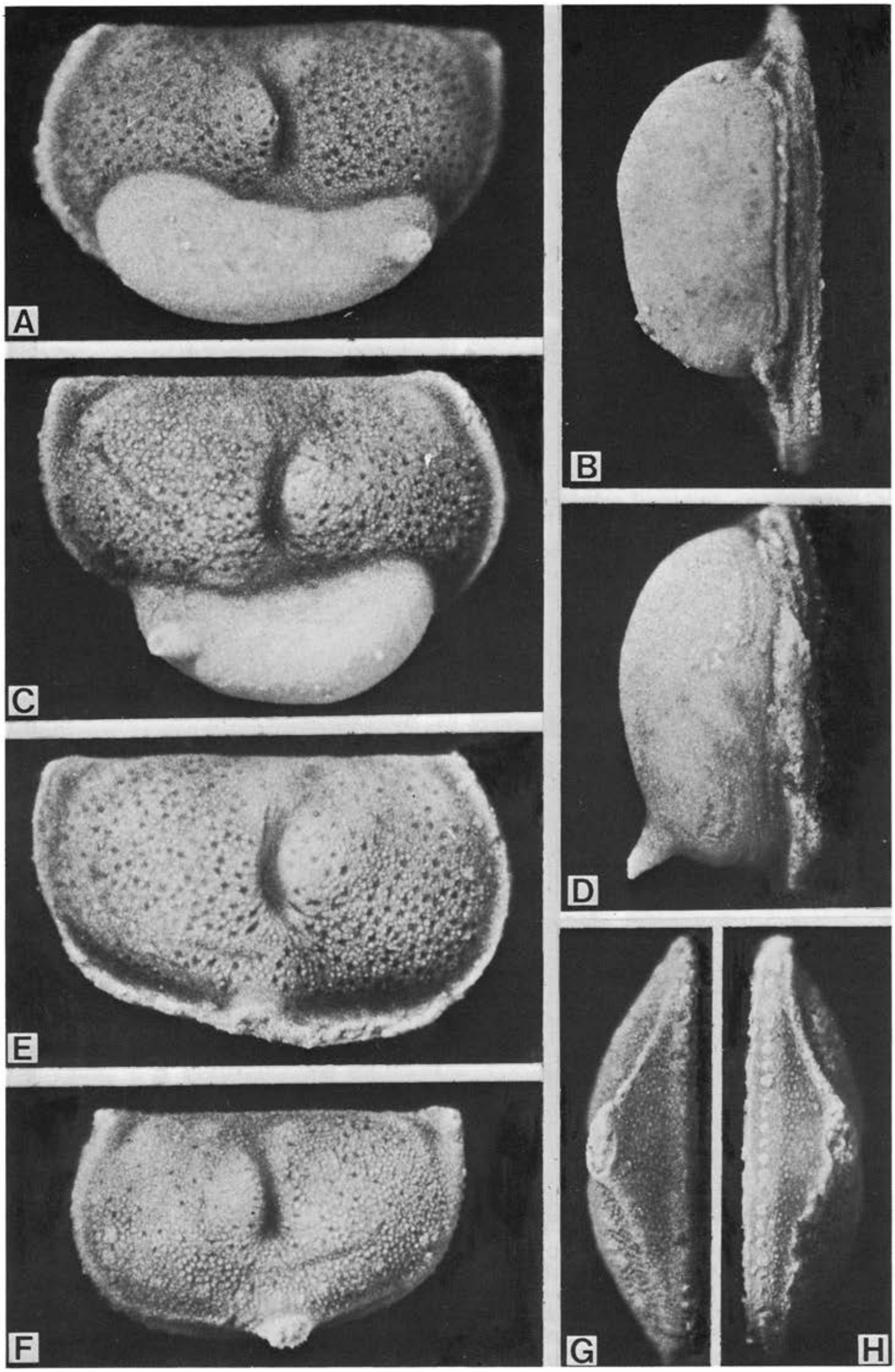


Fig. 51. *Jagatiella jagati* n. gen., n. sp. A. Holotype, right female valve; SGU Type 70, 28.0–29.0 m. B. Right female valve; SGU Type 71, 26.46–26.55 m. C. Right tecnomorphic valve; SGU Type 72, 27.65–28.00 m. D. Right tecnomorphic valve; SGU Type 73, 27.65–28.00 m. E. Right adult tecnomorphic valve; Annelund 1, Högklint *c* or lowermost Tofta Limestone; SGU Type 74. F–G. Dorsal and ventral view of a tecnomorphic carapace; SGU Type 75, 27.65–28.00 m. H. Right female valve in ventral view; SGU Type 76, 26.46–26.55 m. I. Tecnomorphic valve in ventral view; Annelund 1, Högklint *c* or lowermost Tofta Limestone; SGU Type 77. All specimens, except E and I, are from Högklint *c* at Vattenfallet. Magnification ×40. Photograph D. Sethi.


A
B
C
D
E
F
G
H

boundary or a clear change in curvature. The velar structure continues on the ventral side of the crumina as a poorly defined ridge. In many specimens the surface appears to be smooth but some show distinct scattered small pits (Fig. 51E). Several tecnomorphic valves exhibit a concentric groove parallel to the free margin, obviously forming a mark of the valve of the preceding instar (Fig. 51C).

Dimensions. – Hinge length – maximum height in females in mm. Vattenfallet: 0.94–0.89 (holotype), 0.97–0.89, 0.97–0.89, 0.86–0.77, 0.86–0.71. Annelund 1: 1.00–1.00, 0.89–0.86. Largest available specimen (Vattenfallet, measurements partly based on extrapolation of broken cardinal corner): 1.29–1.17.

Aitilia jaanussoni n. sp.

Fig. 52A–H

Holotype. – A right female valve, Riksmuseum Ar.51085 (Fig. 52C) from the *"Pterygotus"* Beds (Högklint *d*) at Vattenfallet.

Diagnosis. – *Aitilia* species with a velar ridge in heteromorphs and a velar flange on either side of the calcarine spine in tecnomorphs. Tecnomorphs with a syllobial groove and a long calcarine spine which points laterally and is situated at about the level of S2. Crumina long, with a concave contour dorsally and a calcarine spine close to the posterior end.

Description. – The material comprises more than 100 valves from Högklint *b, c* and *d* of Vattenfallet and some valves from a loose block at Annelund 1 (Högklint *c* or Tofta Beds) and from Katrinelund boring 20.45–20.47 m. Tecnomorphs with a long calcarine spine (broken off in the figured specimens) at about the level of S2; it is incorporated in the velar structure which widens considerably towards the spine and forms a triangular flange on either side of the spine (the peripheral margin of the flange is broken off in the figured specimens). In ventral view the subvelar field forms a high triangular field with the calcarine spine at its apex (Fig. 52G–H). Syllobial groove distinct, oriented roughly parallel to the free margin. Heteromorphs with a smooth sausage-shaped crumina, widest anteriorly and with a concave dorsal contour. The ventral morphology of the crumina is shown in Fig. 52B. The velar structure terminates on either end of the crumina at a laterally directed fold. A conspicuous feature is a distinct furrow (Martinsson's "dolonoid scar") parallel to the free margin. The ornamentation of the lateral surface of the valves consists of densely spaced fine granulae and scattered pits.

Dimensions. – Hinge length – maximum height (including crumina) in female valves in mm: 1.29–0.94, 1.17–0.91, 1.11–0.89, 1.09–0.89, 1.07–0.87, 1.06–0.97, 1.06–0.89, 1.03–0.79, 1.01–0.89 (holotype), 0.91–0.80.

Fig. 52. *Aitilia jaanussoni* n. sp. A. Left female valve; RM Ar. 51086. B. Ventral view of the crumina with the calcarine spine broken off; RM Ar. 51092. C. Holotype, right female valve; RM Ar. 51085. D. Ventral view of a right valve showing the calcarine spine; RM Ar. 51087. E. Right tecnomorphic valve, the calcarine spine and part of the peripheral margin of the velar flange broken off; RM Ar. 51088. F. Left tecnomorphic valve; RM Ar. 51089. G. Tecnomorphic valve in ventral view; RM Ar. 51090. H. Tecnomorphic valve in ventral view; RM Ar. 51089. In the specimens G and H the calcarine spine is broken off. All specimens are from Högklint *d* at Vattenfallet, × 50. Photograph D. Sethi.

Discussion. – This is the earliest *Aitilia* species recorded from Gotland; other species are known from the uppermost Slite, Halla, Hemse, and Eke Beds (Martinsson 1962). *A. jaanussoni* can be easily distinguished from *A. calcarulata* Martinsson and *A. hyrsinicola* Martinsson by the shape and morphology of the crumina, the relative width of the velum and the position of the calcarine spine.

Acknowledgements. – I am very much indebted to Professor G. Henningsmoen, Paleontologisk Museum, Oslo, and Professor H. Jaeger, Museum für Naturkunde, Berlin, for the loan of the types of *Platybolina lunulifera* Henningsmoen and *Diceratobolbina diensti* (Kummerow), respectively. Dr. Rudolf J. Prokop, Národni Museum, Praha, kindly allowed access to the collections of Národni Museum, Praha, and loaned topotype specimens of *Parahippa rediviva, Mirochilina jarovensis* and *Aechmina cuspidata*. Dr. M. Krůta, Institute of Geology, Czechoslovakian Academy of Sciences, has generously shown me his unpublished material from the Pridolian of Bohemia. Professor V. Jaanusson revised my manuscript.

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Metacope, platycope and podocope ostracodes

ROBERT F. LUNDIN

The metacope, platycope and podocope ostracodes (subsequently referred to loosely as "nonpalaeocope" ostracodes) form a large and diversified fauna in the Silurian rocks of Gotland. Since the work of Jones (1888, 1889), studies of these ostracodes have been limited to detailed morphological analyses of a few interesting species (e.g. Martinsson 1956; Adamczak 1966a, b). In fact, no comprehensive faunal analysis of Gotland "nonpalaeocopes" has ever been done. For that reason the author is now engaged in this long term project. A monographic publication of this study is anticipated. Accordingly, open nomenclature is commonly used herein for species reported from the section at Vattenfallet. For the same reason no species are described or illustrated herein. Familial classification of many "nonpalaeocope" genera is in question. Therefore, in the faunal list only those genera whose familial placement is reasonably stable are referred to familial categories among the Metacopa, Podocopa and Platycopa. Others are listed as "family uncertain". For a few species morphological analysis is so inadequate that subordinal classification is provisional. Accordingly, when detailed morphological analysis is complete the suprageneric (and for that matter, the generic) classification of some of the species listed here will be changed.

The data presented in the log are based upon two different kinds of material: marls from which specimens have been washed, and limestone chips in which ostracodes are embedded. Ostracodes had been removed from the marl samples by G. Liljevall who also had sorted out many of the limestone chips with "nonpalaeocope" ostracodes. Additional marl samples were prepared for "nonpalaeocopes" by Mrs. Meit Lindell at the Department of Palaeobiology in Uppsala. Many of the remaining limestone chips were assembled by Dalip Sethi. Virtually all of the specimens from the washed marls could be identified (a few were too poorly preserved for identification). Relatively large numbers of the specimens embedded in the limestones could not be identified because they were too poorly exposed for verification of critical morphological features. This problem is not considered significant because, (1) less than 10 % of the specimens on the rock chips were unidentifiable, (2) the total number of specimens on the rock chips was small compared to the total number of all specimens identified and (3) the ostracodes in the limestone chips are not apparently different from those in the washed marls. Therefore, it is doubtful that more complete identification of the specimens in the limestone chips would significantly alter the log showing the stratigraphical occurrences of "nonpalaeocope" ostracodes at Vattenfallet.

Annotated faunal list

Metacopa

Thlipsuridae
Longiscella oblonga (Jones), *Silenis longus* Abushik, *S. mawii* (Jones), *S. divergens* (Jones), *S.* cf. *proteus* Pranskevicius, *Thlipsura* cf. *jonesii* Krandijevsky, *T.* n. sp. *a*, Thlipsuridae n. gen. *a*, n. sp. *a*.

Family uncertain
"Bythocypris" cf. *phaseolus* Jones, *"B." elongatus* Jones, *"B."* n. sp. *a*, *Healdianella* cf. *decliva* Pranskevicius, *Longiscula? smithii* (Jones), *L?* sp. *a*, *Steusloffina* sp. *a*.

Podocopa

Beecherellidae
Medianella? sp. *a*, *Pseudorayella* cf. *scala* Neckaja, *P.* cf. *arta* Abushik, *P.* sp. *a*, *Scaphina* sp. *a*, *S.* sp. *b*.

Bairdiidae
Bairdiacypris cf. *venustus* Abushik.

Pachydomellidae
The Silurian rocks of Gotland including those exposed at Vattenfallet contain a large complex of pachydomellid and pachydomellid-like ostracodes. Monographic study of the entire complex is necessary to sort out and understand the various taxa which are included. Therefore, on the log showing the stratigraphic occurrences of "nonpalaeocope" ostracodes, this complex of species has been lumped under Pachydomellidae spp. It can be said that species which have traditionally been placed in *Tubulibairdia* and *Microcheilinella* are included in this group. These species are very poorly defined in the literature, but the section at Vattenfallet contains at least four species.

Family uncertain
Daleiella sp. *a*, *Cadmea* cf. *inexplorata* Pranskevicius, Podocopa gen. *b*, sp. *a*.

Platycopa

Cytherellidae
Birdsallella cornuta Neckaja, *Gotlandella martinssoni* Adamczak.

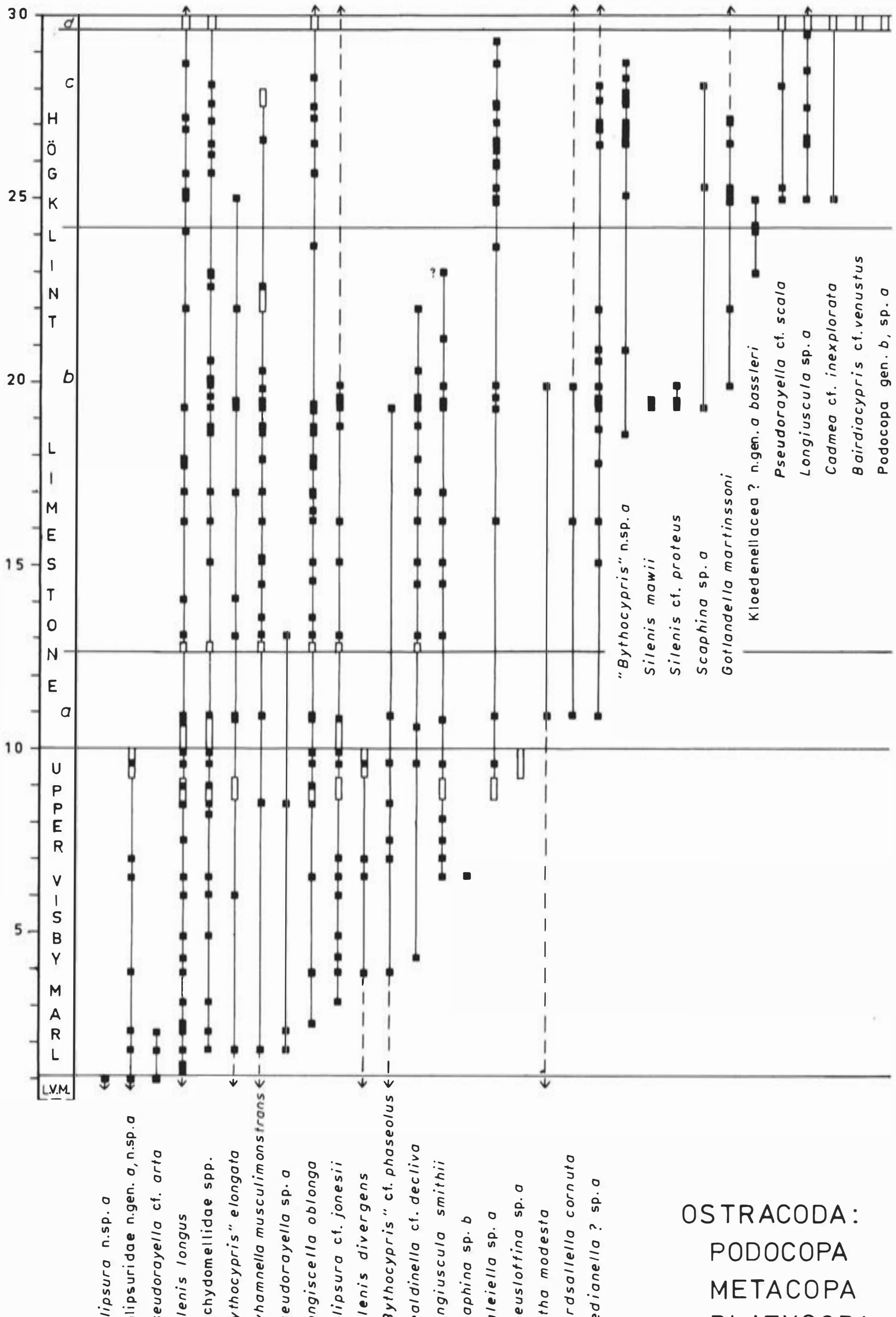
30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
Thlipsura n.sp. a
Thlipsuridae n.gen. a, n.sp. a
Pseudorayella cf. arta
Silenis longus
Pachydomellidae spp.
"Bythocypris" elongata
Nyhamnella musculimonstrans
Pseudorayella sp. a
Longiscella oblonga
Thlipsura cf. jonesii
Silenis divergens
"Bythocypris" cf. phaseolus
Healdinella cf. decliva
Longiscula smithii
Scaphina sp. b
Daleiella sp. a
Steusloffina sp. a
Altha modesta
Birdsallella cornuta
Medianella ? sp. a
"Bythocypris" n.sp. a
Silenis mawii
Silenis cf. proteus
Scaphina sp. a
Gotlandella martinssoni
Kloedenellacea ? n.gen. a bassleri
Pseudorayella cf. scala
Longiscula sp. a
Cadmea cf. inexplorata
Bairdiacypris cf. venustus
Podocopa gen. b, sp. a
OSTRACODA:
PODOCOPA
METACOPA
PLATYCOPA

Fig. 53.

Kloedenellidae
Nyhamnella musculimonstrans Adamczak.

Family uncertain
Altha modesta Neckaja, Kloedenellacea? n. gen. *a bassleri* (Kummerow).

The species here referred to as Kloedenellacea? n. gen. *a bassleri* (Kummerow) has been examined by Valdar Jaanusson. According to him, in this unisulcate species a curved dorsal margin appears to be associated with a long but relatively narrow anterior stragulum on the left valve, but details are unclear because all available specimens are separate valves in the rock. In the heteromorphs the domicilium is distinctly inflated posteroventrally. Both dimorphs have a prominent velar ridge. The particular combination of characters is unique, and the species is therefore difficult to classify; morphology of the hinge-line seems to indicate kloedenellacean affinities. Kummerow's (1924) syntypes (Paläontologisches Museum, Berlin) have been available for comparison.

Taxonomic remarks

The identification and classification of the "nonpalaeocopes" from Vattenfallet is complicated by the following:

(1) Ontogeny is poorly known for many species. Although this is not a serious problem for some species for which juveniles are distinctive, the recognition of immature specimens of some species is difficult.

(2) Dimorphism has not been adequately analysed for the thlipsuracean ostracodes. I doubt that this has caused problems in identification of the Vattenfallet ostracodes but the possibility of "splitting" dimorphs of one species exists.

(3) Recognition of many "nonpalaeocope" species is based upon a clear understanding and evaluation of valve relationships and hinge and contact margin structures. Ideally this requires well preserved, clean isolated valves as well as complete carapaces. All Vattenfallet specimens and species are not represented by this kind of material. Accordingly, identifications of some specimens have been based on characteristics of secondary significance.

(4) Many Vattenfallet species are known previously only from the eastern Baltic Silurian. Some of these are inadequately illustrated and described. Furthermore, satisfactory comparative material has not been available for all of these species.

(5) Many of Jones' (1888, 1889) species and varieties are based upon deformed specimens. It has been difficult in some cases to relate these types to the material from Vattenfallet.

These problems further justify the use of open and questioned nomenclature shown on the log (Fig. 53). More intensive study of these and related species will stabilize and clarify the taxonomy of the Vattenfallet species.

"Nonpalaeocope" succession

The log of stratigraphical occurrences (Fig. 53) shows a more or less continuous appearance (eight species are known to occur in the Lower Visby Beds) and disappearance (seven species occur in beds younger than those analysed at Vattenfallet) of "nonpalaeocope" species. Primary faunal changes occur within the Upper Visby Beds and within the Högklint Beds, especially between 19 and 20 m above seal-level. The latter change is perhaps in part a reflection of the availability of large collections in this interval.

Abundance of "nonpalaeocope" ostracodes is highly variable in the samples analysed. For example, a marl sample from level 19.25 m contains many more specimens than any other sample. Likewise, that sample contains almost 50 % of all species which are listed in the log. In short, the statistical significance of the appearance and disappearance of species at Vattenfallet as indicated by the log is subject to question. I believe, however, that the log presents a good general picture of the "nonpalaeocope" faunal succession at Vattenfallet within thè limits of restrictions posed by general taxonomic problems (discussed above).

The thlipsurids strongly dominate the "nonpalaeocope" fauna especially in the lower part of the section (Upper Visby Beds). *Silenis longus, Longiscella oblonga* and *Thlipsura* cf. *jonesii* are especially common. Pachydomellids, particularly species of *Tubulibairdia,* are common throughout the section. Platycopes, especially *Nyhamnella musculimonstrans* and *Gotlandella martinssoni* are more common in the upper part (Högklint *b* and *c*) than in the lower part of the section, although the former species is known to occur commonly in the Lower Visby Beds at Nyhamn. *Medianella*? sp. *a* is a common species in the upper parts of the Högklint Beds.

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Bryozoans

KRISTER BROOD

The first serious attempt to monograph Silurian bryozoans from Gotland was by Hennig (1905, 1906, 1908). Some additions and revisions have subsequently been published by Borg (1965) and Brood (1968). A new monographic study of Gotland bryozoans, excluding the trepostomes, has been started by the present author, and the first part, comprising Cyclostomata, has been published (Brood 1975), whereas the second part, dealing with Cryptostomata and some cystoporates, although completed serveral years ago, is still unpublished. In the present contribution it has been advantageous to use my manuscript names for two new species (referred to as Brood MS in the faunal list) instead of applying an open nomenclature. The trepostomes and the bulk of cystoporates from Gotland still require modern revison. The cryptostomates of the Silurian of Estonia, including some species from Podolia, have recently been described by Kopaevich (1975) and many of the species occur also on Gotland. Some Silurian trepostomates of Estonia have been described by Astrova (1970).

In the fauna from Vattenfallet bryozoans form one of the most abundant groups. The available material comprises about 2300 specimens that can be classified as macrofossils (0.5 cm long or larger), and innumerable small specimens. In addition, many species could be identified in thin sections or dry peels prepared from rock samples.

With respect to the way in which material was collected, five categories can be distinguished. (1) Specimens picked up or extracted from the rock in the field by Liljevall during his systematic collecting from the section in 1908. In this collection small species are clearly under-represented. (2) From some levels rich in fossils, slabs of varying size were brought home by Liljevall and on these slabs the bedding surfaces mostly abound in bryozoans of varying size. (3) Liljevall also collected a number of marl samples from which bryozoans and other fossils were extracted in the laboratory. In order to complement this material, I collected an additional series of marl samples in 1976 from the lower half of Högklint *b,* and similar samples were obtained by S. Lindbom from the Lower Visby Marl. (4) Many corals and stromatoporoids, as well as occasional other large fossils, are encrusted by numerous bryozoans, especially on the lower side of colonies (see also Spjeldnaes 1975). Most such fossils were examined for encrusting bryozoans. (5) Most bryozoans can be identified in thin sections or dry peels from rock samples. For this reason all thin sections used for lithological study were examined for bryozoans, and dry peels were prepared from all available rock samples. The identifications based on sections or peels are entered in the log as open circles (Figs. 54–55).

From the upper part of Högklint *b* (above 20.5 m) no marl samples were available, and Högklint *c* lacks marly intercalations. In these beds the coverage of bryozoans is less complete than lower down in the section. However, the quantitative data indicate that bryozoans are relatively less abundant in these beds than in the rest of the section, and the low taxonomic diversity there is therefore probably real.

Annotated faunal list

Cyclostomata

Clonopora gotlandica Brood, *Sagenella consimilis* (Lonsdale), *Corynotrypa hennigi* Brood, *C. dissimilis* (Vine), *C.* n. sp. *a*, *Diploclema regulare* (Vine).

Corynotrypa n. sp. *a* (RM By23689) differs from other Silurian species of the genus in having much smaller zooecial dimensions (length of zooecium 0.3 mm, width of aperture 0.04 mm).

Cryptostomata

Helopora lindstroemi (Ulrich), *Nematopora visbyensis* Brood MS, *Phaenopora lindstroemi* Ulrich, *Ptilodictya lanceolata* (Goldfuss), *P. triangularis* Hennig, *P. flabellatiformis* Kopaevich, *Hemipachydictya holmi* (Hennig), *H. macropora* (Hennig), *Saffordotaxis gotlandicus* Brood, *Glauconomella disticha* (Goldfuss), *Thamniscus toernquisti* Hennig, *Archaeofenestella rigidula* (M'Coy), *Fenestella subantiqua* D'Orbigny, *Reteporina reticulata* (Hisinger), *Isotrypa gotlandica* Ulrich, *Semicoscinum clavatum* Kopaevich, *Sphragiopora silurica* Hennig.

Cystoporata

Crepipora lunariata Hennig, *Fistulipora pusilla* Brood MS, *"F."* sp. *a*, *Ceramoporella lindstroemi* (Hennig), *Ceramopora armata* Hennig, *Fistuliporella* sp. *a* (9.8 m).

Trepostomata

Asperopora asperum (Hall), *A. multiporum* (Bassler), *A. ramosum* (Owen), *A.? claviformis* (Hennig), *Monotrypa gotlandica* Hennig, *Bythopora ulrichi* Hennig, *Mesotrypa suprasilurica* Hennig, *Eridotrypa densipora* Hennig, *E.* n. sp. *a*, *Eridotrypella sepizensis* Astrova, *Hallopora elegantula* (Hall), *H. bassleri* Hennig, *Cyphotrypa* cf. *juruensis* Astrova. The trepostomes suffer from lack of recent monographic study and the identifications of species not reported earlier from Gotland should be regarded as tentative.

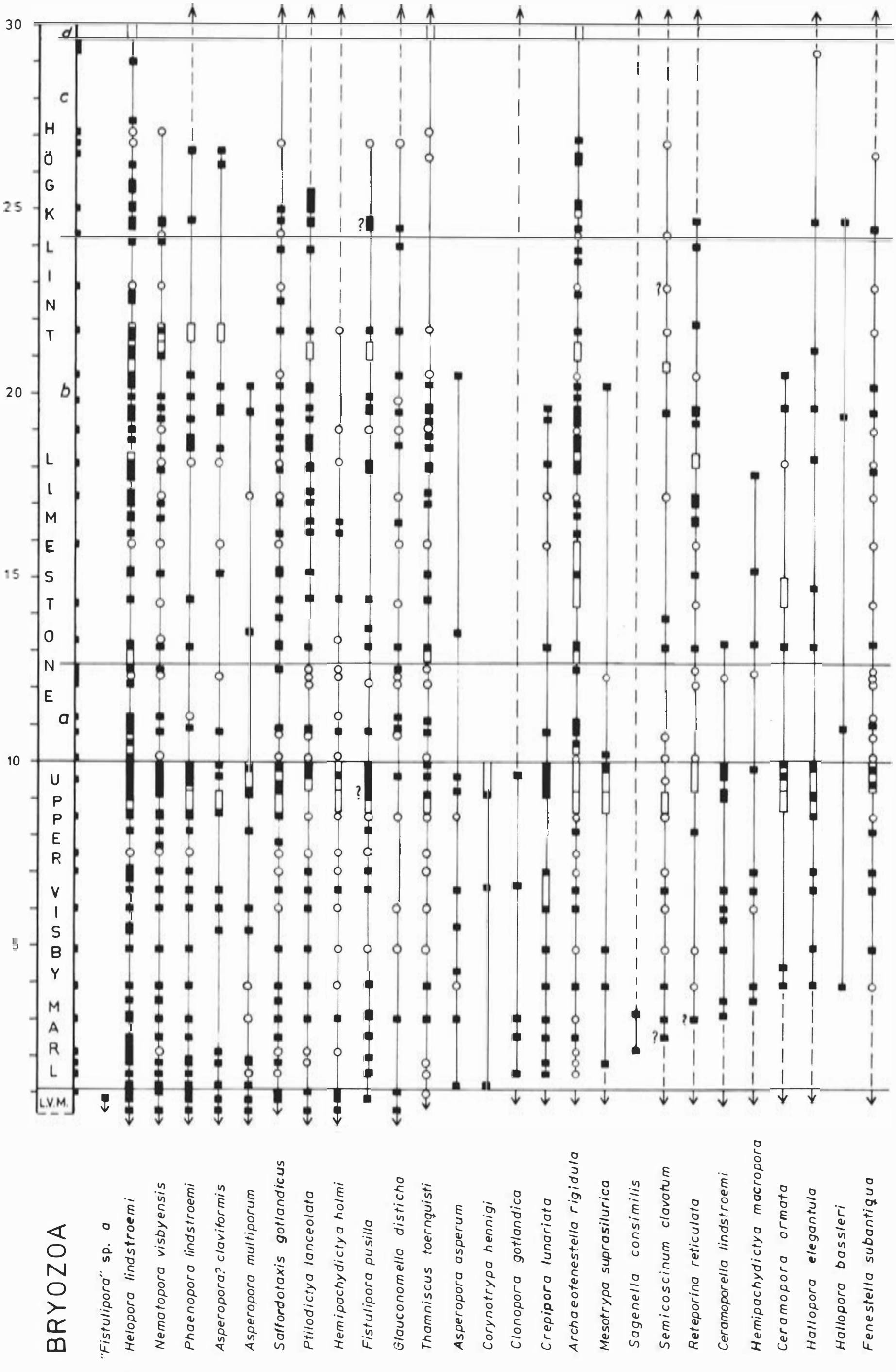
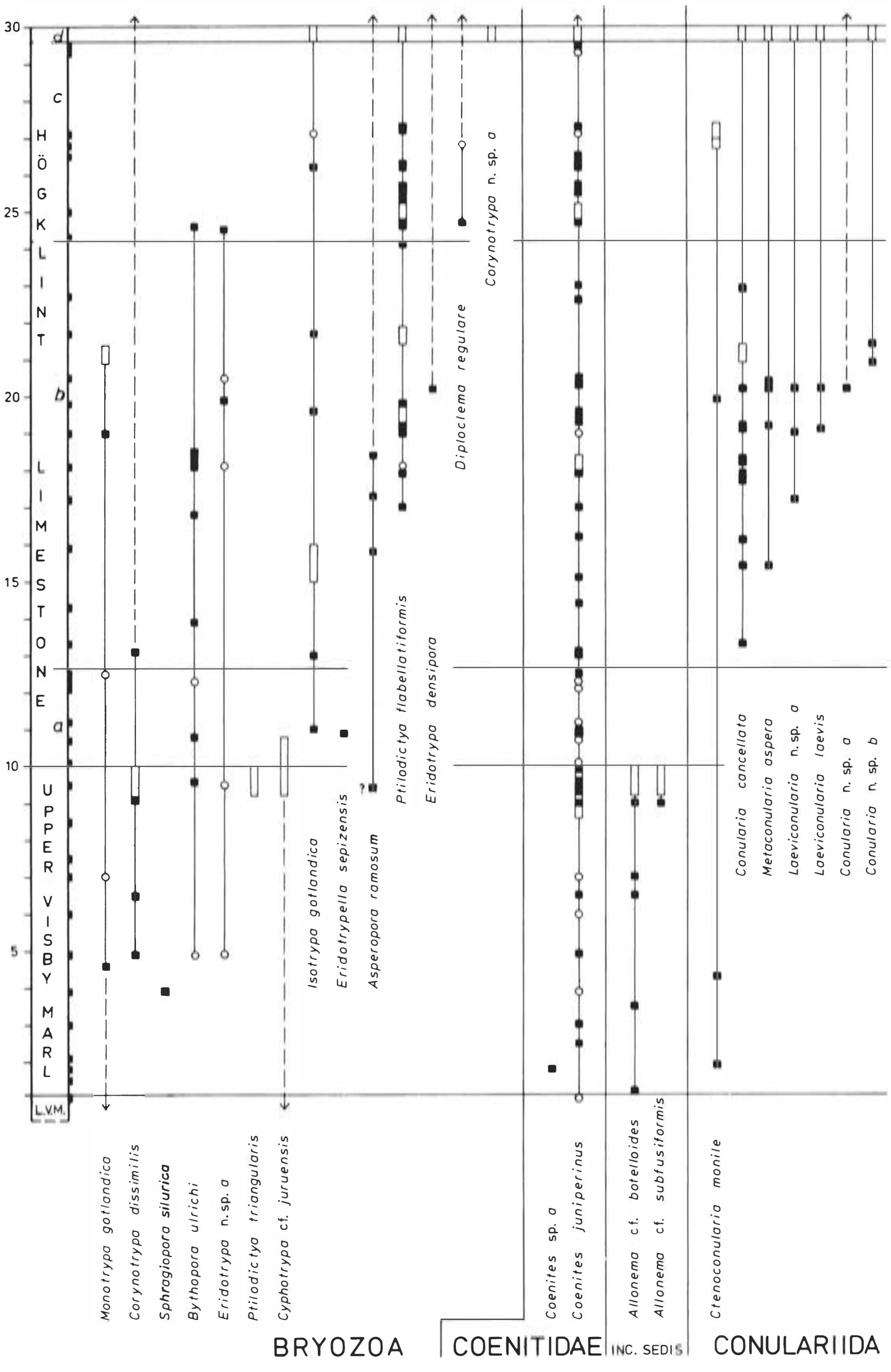


Fig. 54. Distribution of bryozoans in the Vattenfallet section. Continued on Fig. 55. Black rectangles along the stratigraphic column show the levels of thin sections and peels examined for bryozoans and coenitids. The levels in which a species has been recorded only in a thin section or peel are given in the log as open circles.


30
25
20
15
10
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d
c
HÖGKLINT LIMESTONE
b
a
UPPER VISBY MARL
L.V.M.
Monotrypa gotlandica
Corynotrypa dissimilis
Sphragiopora silurica
Bythopora ulrichi
Eridotrypa n.sp. a
Ptilodictya triangularis
Cyphotrypa cf. juruensis
Isotrypa gotlandica
Eridotrypella sepizensis
?
Asperopora ramosum
Ptilodictya flabellatiformis
Eridotrypa densipora
Diploclema regulare
Corynotrypa n. sp. a
Coenites sp. a
Coenites juniperinus
Allonema cf. botelloides
Allonema cf. subfusiformis
Ctenoconularia monile
Conularia cancellata
Metaconularia aspera
Laeviconularia n. sp. a
Laeviconularia laevis
Conularia n. sp. a
Conularia n. sp. b
BRYOZOA
COENITIDAE
INC. SEDIS
CONULARIIDA

Fig. 55.

Stratigraphical distribution

I have noted elsewhere (Brood 1975 and in press) that in the bryozoan fauna there is little qualitative difference between the Upper Visby Marl and the Högklint Limestone. Most species in these beds range from the upper part of the Lower Visby Marl to the upper part of the Högklint Limestone. Among the 17 cryptostomatous species found in the section, 14 occur both in the Upper Visby Marl and the Högklint Beds. *Sphragiopora silurica,* recorded from the Upper Visby Marl of the section has elsewhere been found in the Högklint Beds. *Ptilodictya triangularis* occurs in the section only in the upper part of the Upper Visby Marl, but it is a rare species and is known from the Högklint Limestone on Fårö.

Two species, *Isotrypa gotlandica* and *Ptilodictya flabellatiformis,* are restricted to the Högklint Limestone. Both are comparatively rare. *I. gotlandica* is normally a reef dwelling species whereas *P. flabellatiformis* is characteristic of high energy, shallow water environments.

Of the six cyclostomatous species recorded, three have been found only in the Visby marls. *Clonopora gotlandica* and *Corynotrypa dissimilis* also occur in higher beds elsewhere on Gotland and their restricted occurrence in the section is probably due to chance. *Corynotrypa hennigi* may be restricted to the Upper Visby Marl. *Diploclema regulare* has been found only in the Högklint Limestone, but it is very rare on Gotland and may have a wider distribution.

The trepostomes are represented in the section by 13 species, of which nine occur both in the Upper Visby Marl and the Högklint Limestone. Because of the lack of a monographic study, ranges on Gotland of several species are uncertain.

The cystoporates are represented in the section by four species all of which have been found both in the Upper Visby Marl and the Högklint Limestone.

Ecological considerations

Bryozoans form an important constituent in the skeletal material at Vattenfallet. The bryozoan content in the rocks is on average about two to three per cent, a value agreeing closely with data from other parts of Gotland (Brood 1976).

It is difficult to obtain representative quantitative data on bryozoans based on macrofossils, that is, specimens that are 0.5 cm or larger. Apart from encrusting and massive colonies, the zoaria are extensively fragmented and this makes it impossible to estimate the frequency in terms of individual colonies. Liljevall's material was assembled by a non-specialist and many bryozoans were probably overlooked. This also affects the faunal log (Figs. 54, 55) in which coverage is obviously less complete for bryozoans than for brachiopods or trilobites. Rough estimations based on the available bryozoan "macrofauna" shows that it is strongly dominated by the articulated cryptostome *Helopora lindstroemi,* which is abundant throughout the section. In the Upper Visby Marl the bifoliate cryptostome *Phaenopora lindstroemi* is common whereas in Högklint *b* the fenestrate *Archaeofenestella rigidula,* bifoliate *Ptilodictya lanceolata,* and the articulated *Saffordotaxis gotlandicus* form a subdominant element. In Högklint *c* the comparatively large bifoliate cryptostome *Ptilodictya flabellatiformis* is a dominant species in several beds.

As noted above, bryozoans can easily be identified in thin sections or peels, mostly down to species level. Through point counting the importance of various species in the sequence can be determined by volume. For this purpose dry peels were prepared of 31 rocks samples. Peels were used because a far larger sample surface could easily be produced for counting than on conventional thin sections. When point counting, the grain bulk definition was applied for defining the area of cross-sections of bryozoans to be counted, that is, the whole area, including the cavities, of the bryozoan particle. The results are given on Figs. 56–57, excluding samples in which the total number of bryozoan counts was less than 100. The latter data were considered to be unreliable. Some of the variation in the plotted data is obviously due to chance, particularly with respect to whether or not large colonies of encrusting forms or massive trepostomes happened to be included within the peel area. In order to significantly decrease the effect of chance, the area counted had to be increased beyond what was practically possible to count within the time available for the present study. Nevertheless, the data obtained provide fairly good indications of the quantitative importance of the commonest bryozoan species.

Helopora lindstroemi dominates in most samples also by volume. Bifoliate cryptostomes. such as *Phaenopora lindstroemi, Ptilodictya lanceolata* and *Hemipachydictya holmi* are, on average, far more common in the Upper Visby Marl than in Högklint Limestone. These forms, as well as the erect articulated cryptostomes *Helopora lindstroemi* and *Nematopora visbyensis,* require only small firm substrates for attachment. The quantitative data indicate that massive trepostomes are more common in the Upper Visby Marl than in the Högklint Beds. Also encrusters, such as the cystoporates *Ceramoporella lindstroemi, Ceramopora armata* and *Fistulipora pusilla* and trepostomes *Asperopora multiporum* and *A.? claviformis,* are more abundant in the Upper Visby Marl than in the bedded Högklint limestones. This probably correlates with the relative abundance of colonial organisms in the Upper Visby Beds (see Klaamann and Nestor, this volume) which formed a suitable substrate for many encrusting bryozoans. It is noteworthy thant these encrusting forms are particularly abundant on the lower side of the colonies of stromatoporoids,

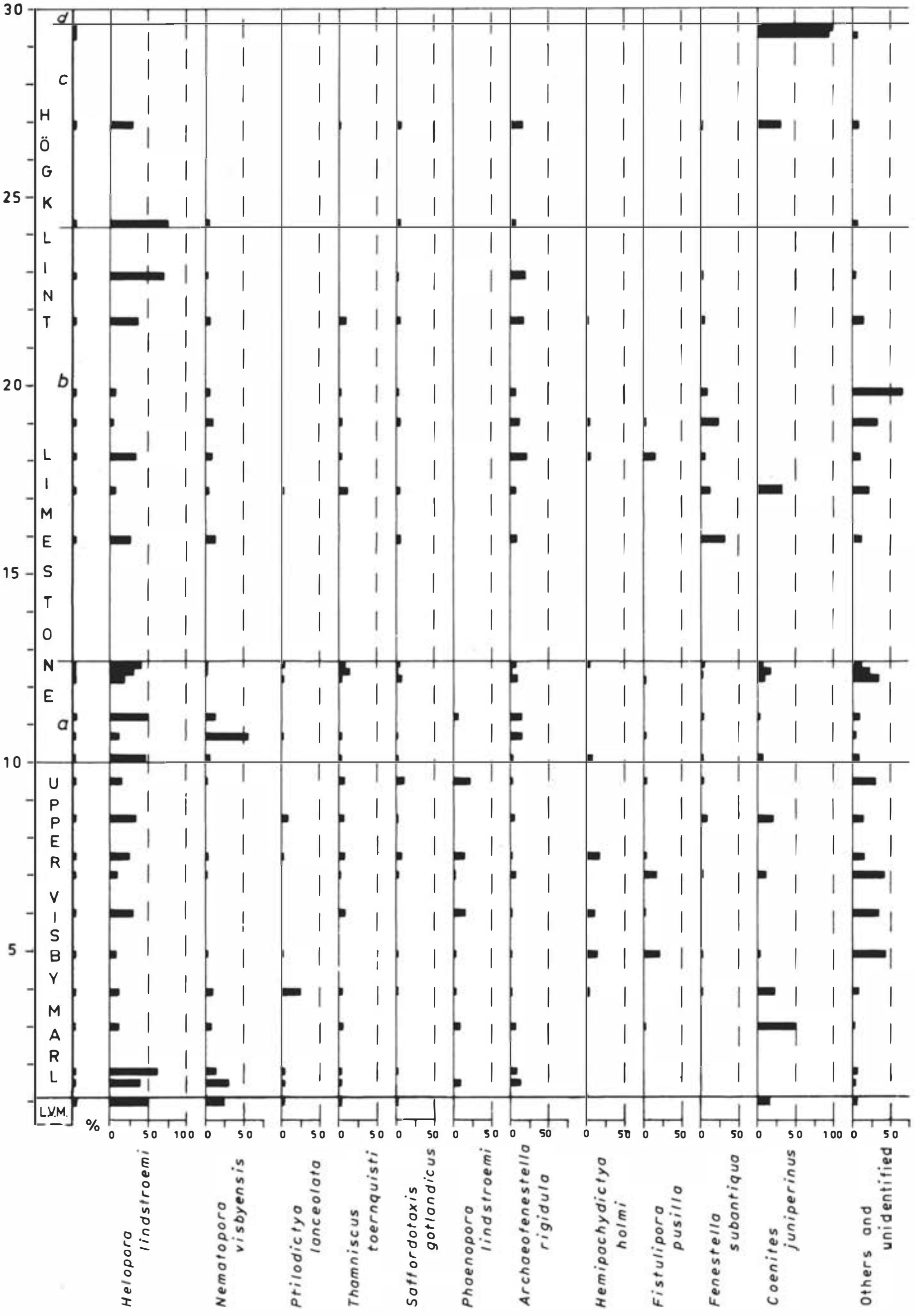

Fig. 56. Quantitative composition of the bryozoan and coenitid fauna by percentage grain-bulk volume, determined on dry peels by point counting. Only those levels are included which yielded a total of at least 100 hits for bryozoans and coenitids together. Only those species are recorded which formed at least ten per cent of the total bryozoan and coenitid volume in at least one sample. The levels of the samples are indicated by black rectangles along the stratigraphical column.

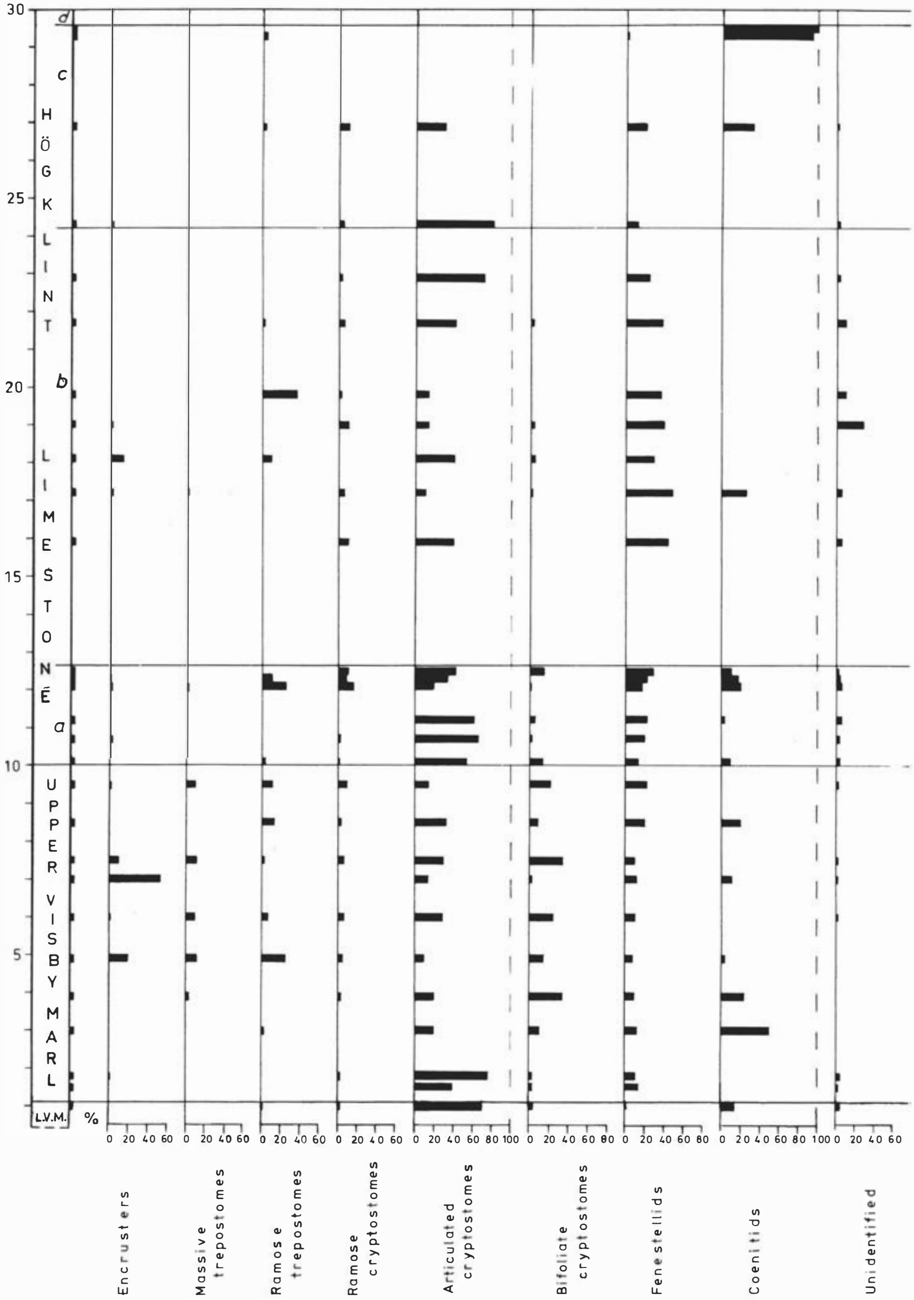

Fig. 57. Quantitative composition of the bryozoan and coenitid fauna by percentage grain-bulk volume according to growth types. The base data are the same as in Fig. 56.

tabulates and heliolitids. Several loose encrusting zoaria were also found in which the substrate had probably consisted of some firm-bodied organism that has perished without trace.

In the winnowed calcarenites of Högklint *a* many bryozoans are probably transported and the quantitative composition of the fauna may not reflect biotic conditions.

The content of skeletal sand in the lower, calcilutitic part of Högklint *b* is low and quantitative data on bryozoans from these beds are unreliable. Higher in the sequence, in the middle and upper part of Högklint *b*, fenestrate bryozoans are significantly more abundant than in the Upper Visby beds. On Gotland, the abundance of fenestellids characterizes reef environments where they form up to 40 or 50 per cent of the bryozoans by volume (Brood 1976). It is possible that these forms were transported from nearby reefs into the relatively quiet water depositional environment in which the bedded, partly pelletal limestones of the middle and upper Högklint *b* were formed.

The content of bryozoans in the pelletal, moderately high energy limestones of Högklint *c* is relatively low and from the available quantitative data no safe conclusions are possible. The large bifoliate cryptostome *Ptilodictya flabellatiformis,* which is not uncommon as a macrofossil in these beds, has not been recorded from the peels or thin sections. This indicates that its contribution by volume to the sediment was low.

In the fine-grained *"Pterygotus"* Beds (Högklint *d*) the bryozoan content is generally very low. This environment was clearly unsuitable for this group.

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Coenitids

KRISTER BROOD

There is doubt as to the true taxonomic position of the coenitids (see Brood 1970, 1976a) since some authors refer them to corals and others to bryozoans. For this reason the family is not assigned here to a phylum.

In the Vattenfallet collections coenitids are represented by *Coenites juniperinus* Eichwald and *C.* sp. *a.* The material comprises about 300 fragments of colonies that can be regarded as macrofossils, together with a great number of small fragments. The distribution is shown in Fig. 55.

Branched colonies of *Coenites* from the Wenlockian of Gotland have previously been generally identified as *C. repens* (Wahlenberg) (Hennig 1906; Brood 1970, etc.). However, the status of *C. repens* is doubtful because no types exist and the type locality is unknown. Klaamann (1964) revised *Coenites juniperinus,* the type species of the genus, and stabilised the concept of the species by designating a neotype from the Jaagarahu Stage of Estonia. The specimens from Vattenfallet compare closely with *C. juniperinus* both in structure and dimensions. No attempt is made here to distinguish the growth forms of the species described by Hennig (1906) because they appear have no taxonomic value. Colonies of *Coenites* sp. *a* have a laminar growth.

The volumetric importance of *Coenites* relative to bryozoans is shown on Figs. 56–57. The genus is particularly common in some beds at the top of Högklint *c*, but the fragments there are rounded and frequently encrusted by algae. The material was probably transported. Colonies of *Coenites* lived with a holdfast attached to, or encrusting a hard substrate. On Gotland the genus is especially common in reef environments (Brood 1976b), and particularly in basal portions of reef bodies.

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Allonema

KRISTER BROOD

The genus *Allonema* has traditionally been considered to be a bryozoan (Ulrich & Bassler 1903; Bassler 1953), but this view is not accepted here because the "zooids" lack any trace of an aperture. The true taxonomic position of this enigmatic organism currently remains unknown. Ulrich & Bassler (1903) described several *Allonema* species from Gotland but without information on exact localities. Without re-examination of their material a definite identification of the Vattenfallet specimens is difficult. However, the genus is represented by two species, here identified tentatively as *Allonema* cf. *botelloides* Ulrich and Bassler and *A.* cf. *subfusiformis* Ulrich and Bassler. The material comprises 10 specimens whose distribution is shown on Fig. 55.

Allonema is an encrusting organism, common on the lower side of tabulate corals and stromatoporoids. Its distribution in the section mainly reflects the availability of such large colonies.

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Conulariids

KRISTER BROOD

In the Vattenfallet material conulariids are represented by 80 specimens, as well as numerous fragments obtained mostly from residues of samples processed by Jeppsson for conodonts. The bulk of the specimens are from two beds, the *"Pterygotus"* Marl (Högklint *d*; 61 specimens) and a marly bed at 20.20–20.25 m of Högklint *b* (6 specimens). In the latter bed the conulariids are also associated with eurypterid remains. Most material from the rest of the section is greatly fragmented but since conulariids can generally be identified from characters of the ornamentation, the fragmentary nature of the specimens does not always cause serious taxonomic problems.

Conulariids from Gotland were described monographically by Lindström (1886; refigured by Holm 1893). In this contribution a narrower species concept is used compared with that applied by Lindström. For example, in the Vattenfallet material three different species are distinguished which all fall into Lindström's concept of *Conularia cancellata,* and two species which Lindström included in *Conularia laevis*. The generic classification is revised after Sinclair (1952) and Moore & Harrington (1956).

Faunal list

Conulariida (see Fig. 55)
Conularia cancellata Sandberger, *C.* n. sp. *a, C.* n. sp. *b, Ctenoconularia monile* (Lindström), *Metaconularia aspera* (Lindström), *Laeviconularia laevis* (Lindström), *L.* n.sp. *a*.

In addition, unidentifiable small fragments of conulariids were recorded from the following levels: 8.9 m, 12.8 m, 14.4 m, 17.45 m, and 23.7 m.

Discussion

Conulariids have a thin-walled and fragile test that is rarely preserved intact in high energy environments. It is therefore significant that in the Vattenfallet section the rich fauna of conulariids is mainly from the *"Pterygotus"* Marl (Högklint *d*), which was deposited in tranquil, shallow-water conditions and where no bioturbation has taken place in the sediment. There the material is dominated by species with very thin walls, such as *Metaconularia aspera* (41 specimens) and *Laeviconularia* n. sp. *a* (18 specimens). A somewhat similar rock at 20.20–20.25 m again contains the same species. Otherwise the conulariids found on Gotland mostly belong to the relatively robust genus *Conularia*. In the Silurian fauna of Gotland conulariids were probably not so rare as they appear to be from collections of macroscopic specimens. In the acid resistant residues from limestone samples they frequently form a significant component (Lennart Jeppsson, personal communication).

The mode of life of conulariids has been the subject of divergent opinions. Many authors concluded that they were sessile animals (Slater 1907; Kozłowski 1968), whereas others have considered a free-swimming mode of life probable (Kiderlen 1937; Moore & Harrington 1956). Since the conulariid skeleton is hydrodynamically unsuitable for a free-swimming mode of life, and since several have been found with their proximal end attached to foreign objects (Slater 1907, among others), it appears probable that they were sessile.

It has been assumed that the conulariids were carnivorous and fed by means of tentacles projecting from the aperture (Kiderlen 1937; Moore & Harrington 1956; Werner 1966). All these reconstructions were based on the assumption that the conulariids were related to cnidarians. However, this relationship is far from certain and in the conulariids the presence of tentacles around the apertural rim in a coelenterate fashion is difficult to visualise. It is far more likely that the conulariids were filter feeders, with water entering through the aperture into a kind of mantle cavity via a filtering apparatus possibly similar in function to a lophophore.

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Brachiopods

MICHAEL G. BASSETT

The recent summary review of taxonomy and stratigraphical distribution of Gotland brachiopods by Bassett & Cocks (1974) is restricted to the articulates; the only attempt to survey the complete brachiopod fauna was made by Lindström (1861), who, in addition to the articulates, at that time recognised just 6 species of inarticulates. Since then the inarticulate fauna has been relatively neglected, with the notable exception of a few important studies of the Trimerellacea. Lindström (1868) briefly discussed the internal structure of *Trimerella,* following which Davidson & King (1872, 1874) used Gotland material in part of a broader study dealing with classification and description of the group. The only other systematic study to include any Gotland inarticulates of any group is that by Huene (1899) on the Craniacea, in which he described (p. 303) a single new species from the Eke Beds (as *Philhedra gracilis);* in the same paper Huene classified *Craniops* (as *Pholidops)* with the Craniacea and reported (p. 280) *C. implicatus* from probable Mulde and younger Wenlock beds on the island. Other records of Gotland inarticulates are restricted mainly to faunal lists in various stratigraphical papers. The complete inarticulate fauna is very much in need of taxonomic study. I am currently investigating Craniacea, Discinacea and Acrotretacea from throughout the full Gotland sequence.

For the articulate brachiopods Bassett & Cocks (1974) summarised the state of knowledge of the fauna at that time and brought the nomenclature up to date. Since 1974 there has been very little further taxonomic revision, with only three papers giving any systematic descriptions. Walmsley & Boucot (1975) deal with Isorthinae from the full sequence, Copper (1977) has revised *Atrypoidea (=Atrypella) prunum* from the Hemse Beds in a comparative study of the genus, and Rubel & Rozman (1977) include six Gotland species in a study of Estonian and Gotland rhynchonellids. Other recent work on Gotland brachiopods has concentrated instead on aspects of palaeoecology and functional morphology (e.g. Hurst 1974, 1975a, b; Watkins 1975); much of this work is still in progress, and some comments are included later in this account. A great deal of taxonomic work is still necessary on the Gotland articulate fauna, and in this respect the Bassett & Cocks (1974) review was not only intended to up-date the nomenclature, but also to draw attention to those groups requiring further study. Dr. P. Copper (Sudbury, Canada) is currently revising the Atrypidina, and I am working on the Rhychonellida and some Pentamerida; of the remaining material, some of the Strophomenida in particular would repay detailed investigation.

The identified brachiopod material from Vattenfallet comprised in excess of 5000 specimens (see also numerical analysis below).

Annotated faunal list

Taxa are listed here in Superfamily groups for both the articulates and inarticulates. Material listed under open nomenclature is generally either too fragmentary or too poorly preserved to allow firm comparison with, or assignment to, known species, but where possible some comparative remarks are given to indicate possible relationships. For the articulates such comparative comments are given for named species only where their interpretation differs from that in Bassett & Cocks (1974).

Inarticulata

Lingulacea
"Lingula" sp. *a* is a small, suboval form with distinctive growth lines, somewhat similar to the British Silurian *"L." lewisii* J. de C. Sowerby. *"L."* sp. *b* is larger with subparallel margins, evenly curved posterior margins and fine growth lines, all features which may suggest affinity with the approximately contemporaneous *"L." brodiei* Davidson from the Woolhope Limestone Formation of the Welsh Borderland. The two Vattenfallet "species" are separated here mainly on the basis of size and shape. though larger collections might eventually show that there is continuous variation between them. Two additional indeterminate lingulid valves (not included in log), from "near 10 m" and 15–16 m in the section respectively, may belong to either "species". I consider it unlikely that any Silurian material belongs to the Recent genus *Lingula*. *Craniops* aff. *implicatus* (J. de C. Sowerby) probably belongs entirely to that species, but it has not yet been possible to compare the wide range of variation in the Vattenfallet material with that in British type populations.

Trimerellacea
Dinobolus aff. *davidsoni* (Salter).

Acrotretacea
Acrotretidae n. gen. *a,* n. sp. *a* is known only from 3 samples digested for conodonts by L. Jeppsson, and its records in the log probably do not indicate its full range. It has a high, slender conical pedicle valve with pitted protegular ornament typical of the subfamily Torynelasmatinae. The brachial valve is subcircular, with an apparently simple septum, in this respect differing from the Ordovician genus *Torynelasma* which bears a concave septal plate.

Discinacea

Schizocrania sp. *a* is subcircular to oval, with fine ribbing similar to *S. striata* (J. de C. Sowerby) from the British Ludlow. *S.* sp. *b* is a larger form with more widely separated costellae; it may be related to *S. verneuilii* (Davidson) from the Much Wenlock Limestone Formation of Britain, which I have identified elsewhere on Gotland in younger beds. Discinacea n. gen. *a*, n. sp. *a* is subcircular with subcentric dorsal and ventral beaks, a flat to gently subconical brachial valve, and a flat to depressed pedicle valve with a long, parallel sided pedicle notch open at the posterior margin; this latter feature distinguishes it from most other Palaeozoic discinaceans apart from *Oehlertella,* but that genus is biconvex with a submarginal dorsal beak. *Schizotreta?* sp. *a* may be an extreme variant of the new genus, but the single brachial valve included here is separated on the basis of having an elongate oval outline and a beak placed well towards the posterior margin. *Orbiculoidea* sp. *a* has a subconical pedicle valve and subcentral beak, with a lanceolate notch confined to the posterior slope. A single, additional probable discinacean (not entered in log) from 20.15–20.29 m has polygonal, pitted ornament and may be related to the Ordovician genus *Trematis*.

Craniacea

Petrocrania sp. *a* is assigned to this genus on the basis of its slightly conical brachial valve which is essentially smooth apart from irregular concentric growth lines. Craniacea indet. *a* lacks these growth lines. Craniacea n. gen. *a*, n. sp. *a* is a tiny, ribbed form somewhat similar to *"Philhedra" grayii* (Davidson) from the Much Wenlock Limestone Formation of Britain.

Articulata

Orthacea

Platystrophia jaaniensis Rubel, *Skenidioides lewisii* (Davidson). A few specimens from the Upper Visby and lower part of the Högklint Beds are identified as *Skenidioides*? spp. indet. on the basis of their external morphology, but in each case the internal structures have not been available to confirm the generic assignment; they can, however, all be distinguished from *S. lewisii* by their external features; some specimens possibly belong to the poorly known species *S. acutum* (Lindström), particularly those at 13.1 m, but the variation in morphology suggests that more than one species is present.

Enteletacea

Dicoelosia verneuiliana (Beecher), *Visbyella visbyensis* (Lindström), *Linoporella punctata* (de Verneuil), *Resserella basalis* (Dalman), *Levenea loveni* (Lindström) (assigned to this genus following Walmsley & Boucot 1975), *Isorthis* sp. *a, Salopina* sp. *a, Dalejina* spp.

Virtually all the specimens of *Dicoelosia* identified from Vattenfallet can be identified confidently as *D. verneuiliana,* but the few specimens available from the Lower Visby Marl are immature individuals which could possibly belong to a different species (see also Bassett & Cocks 1974:11). Specimens assigned to *Isorthis* sp. *a* and *Salopina* sp. *a* are separated mainly on the basis of differences in ribbing patterns; some shells show internal features to confirm the generic identifications, but in general do not allow comparison with other species of these genera that occur elsewhere on Gotland; some *Salopina,* however, show possible affinities with *S. conservatrix* (McLearn). *Dalejina* spp. include shells with a wide range of sizes and variation in gross external form, but there are virtually no interiors available to allow any assessment to be made of specific differentiation; more than one species is fairly certainly present, including *D. hybrida* (J. de C. Sowerby) which occurs elsewhere on Gotland (see Bassett & Cocks 1974:11 for comments on variation in this species); rare large specimens from the upper half of Högklint *b* (e.g. 19.25 m and 20.20–20.25 m) may belong to *D. phaseola* (Rubel) which is known elsewhere on Gotland only from the Lower and Upper Visby Marl.

Other Orthida (not entered in log)
In addition to the orthaceans and enteletaceans noted above, numerous samples from throughout the complete Vattenfallet section contain small indeterminate orthids. Some few hundred specimens are probably involved in this category, with most of them close to or below 5 mm in any maximum dimension. Most of these small orthids probably represent immature growth stages of taxa named above, but the problems of identifying very early growth forms of orthids are such that it is impossible to separate them at present, some even at the superfamily level. The problem of identification is particularly acute with immature enteletaceans, and highlights the need for ontogenetic studies to be made in order to relate early growth stages to the named Gotland taxa, which are based almost entirely on mature shells. However, in addition to these early growth forms, some samples do include distinctive small shells which may represent naturally small (and probably new) taxa. Material in this latter category, some possibly related to *Hesperorthis* and some to *Glyptorthis,* occurs particularly in samples high in the Upper Visby Marl, while there is also a tiny distinctive alate orthacean at about the 6.5 m level; all this material requires further investigation from larger samples.

Triplesiacea
Plectotreta lindstroemi Ulrich & Cooper.

Eichwaldiacea
Dictyonella capewellii (Davidson).

Plectambonitacea
Eoplectodonta transversalis (Wahlenberg), *E. duvalii* (Davidson).

Strophomenacea
Megastrophia/*Brachyprion* spp., *Pentlandina loveni* (de Verneuil), *Leptaena rhomboidalis* (Wahlenberg), *L.* sp. *a*, *L.* sp. *b*, *L.* sp. indet., *Liljevallia gotlandica* Hedström, *Scamnomena rugata* (Lindström) (see Bassett 1977:134 for generic assigment), *Katastrophomena* sp. *a*, *Leptostrophia* spp., *Brachyprion* sp. *a*.

I have discussed elsewhere (Bassett 1977:138) the difficulties involved in differentiating Silurian *Megastrophia*, *Brachyprion* and *Leptostrophia* because of the wide variation in some features considered to be diagnostic of each genus. Vattenfallet material listed as *Megastrophia*/*Brachyprion* shows considerable variation in curvature and it is likely that more than one species is involved, although much of the material is too fragmentary to allow more meaningful assessment here. *Brachyprion* sp. *a* from the *"Pterygotus"* Beds has moderate curvature and can be distinguished from *Megastrophia*/*Brachyprion* spp. by its more distinctive, unequally parvicostellate ornament. *Leptostrophia* spp. are almost biplanate shells, the one specimen from 10.7–10.8 m having a sharply triangular ventral muscle field which allows a fairly positive assignment to this genus; none of the specimens have the fine, equally parvicostellate ornament of *L. filosa* (J. de C. Sowerby) which Bassett & Cocks (1974:15) have reported from contemporaneous levels on Gotland.

Katastrophomena sp. *a* is too poorly preserved to discuss its affinities. *Leptaena* sp. *a* differs from *L. rhomboidalis* in having finer costellae and more shallow, closely spaced rugae; it lacks the lobed trail typical of *L. depressa* (J. de C. Sowerby). *L.* sp. *b* has a fairly convex pedicle valve with a distinct protegular node and strong growth fila which produce a reticulate ornament; the rugae are lower and finer than in *L. rhomboidalis*. *L.* sp. indet. at 1.7–1.9 m is poorly preserved but can not be readily included in any of the other taxa listed here.

Davidsoniacea
Coolinia pecten (Linnaeus), *Valdaria testudo* Bassett & Cocks, *Morinorhynchus* sp. *a*. A sample from "about 6–8 m" contains a single pedicle valve of *C. pecten* to extend its range in the section below that indicated in the log. The presence of *Morinorhynchus* is confirmed by specimens having a large pseudodeltidium; the Vattenfallet material differs from the two known, younger Gotland species, *M. crispus* (Lindström) and *M. adnatus* (Hedström), in having a distinctly orthocline ventral interarea and stout, stubby teeth. *M.* sp. *a* is probably a new species.

Chonetacea

Strophochonetes piptis n. sp. (see description below), Chonetidae indet. *a*. The absence of spines precludes identification of the single pedicle valve listed as Chonetidae indet. *a,* but it is more strongly convex, smaller and more ovate than *S. piptis,* suggesting possible affinities with *Protochonetes minimus* (J. de C. Sowerby).

Pentameracea

Clorinda rotunda (Lindström), *Gypidula?* sp. *a*. A further single specimen of *Clorinda* (not in log) from 9.2–10.0 m appears to differ from *C. rotunda* in having a stronger fold and sulcus, a more convex brachial valve, and parallel brachial plates. *C. rotunda* typically has distinctly divergent brachial plates. *Gypidula?* sp. *a,* based on a single pedicle valve, has a low anterior fold and shows the trace of a septum, which together suggest possible assignment to the genus.

Rhynchonellacea

Sphaerirhynchia sp. *a, Estonirhynchia?* sp. *a, Stegerhynchus* sp. *a, S. diodontus* (Dalman), *Rhynchotreta* sp. *a, Microsphaeridiorhynchus* sp. *a, Eocoelia angelini* (Lindström), Rhynchonellacea n. gen. *a,* n. sp. *a*. Specimens identified as *Estonirhynchia?* sp. *a* are small, globose forms with ungrooved ribs confined to the anterior half of the shell, and with long, slender dental plates; confirmation of the generic assignment, and possible relationships with *E. estonica* Schmidt from the Jaani Stage of Estonia, require further investigation. *Sphaerirhynchia* sp. *a* also includes small, globose forms, but the material differs from that included in *Estonirhynchia?* in appearing to have greatly reduced dental plates, a higher anterior tongue and groove, and grooved ribs. The common Silurian species *S. wilsoni* (J. Sowerby), known from both Britain and Gotland, is less globose than the Vattenfallet material. *Stegerhynchus* sp. *a* is probably conspecific with material described recently from Estonia as *S. estonicus* Rubel (in Rubel & Rozman 1977), but the species name is not used here since there is some nomenclatorial confusion in this group with regard to the correct identity of *S. borealis* (von Buch) that requires further clarification. Similarly, *Rhynchotreta* sp. *a* should probably be included entirely within *R. gracilis* Rubel, but further investigation of possible variation in the Gotland material is necessary.

In common with other species of the genus, *Eocoelia angelini* has commonly been regarded in the past as a member of one of the spire-bearing groups, but I agree with Cocks (1978:149) that it should be placed within the Rhynchonellida. *Microsphaeridiorhynchus* sp. possibly includes more than one species, but until relationships can be clarified in detail the material is here grouped together; serial grinding of some specimens has confirmed the presence of a posterior cover plate on the septalium, which is one of the diagnostic criteria for the genus, but the external morphology is somewhat variable, with some closely resembling material described by Rubel from Estonia as *Hemitoechia undvaensis*. This latter genus, however, typically has an open septalium throughout its growth. Rhynchonellacea n. gen. *a*, n. sp. *a* is a finely costellate form externally resembling the Bohemian genus *Decoropugnax*, from which it differs, however, in having long, slender, dental plates.

Atrypacea

Atrypa sp., *Eospinatrypa?* sp. *a*, *Spinatrypina tubulosa* Bassett & Cocks, *Plectatrypa lamellosa* (Lindström), *P.* sp. *a*, *"Zygospira" exigua* (Lindström), *Glassia obovata* (J. de C. Sowerby), *Septatrypa subaequalis* n. sp. (see description below).

Generic identification of some of the Vattenfallet atrypaceans should be regarded for the present as no more than tentative, since in very few are details known of the internal morphology. *Atrypa* sp. includes forms with a range of ribbing patterns, some approaching *Desquamatia* as recorded by Bassett & Cocks (1974:29), but most have the typical imbricate ornament recognised for the genus by Copper (1967). *Eospinatrypa?* sp. *a* has the more undulose, interrupted and frilled ribs decribed by Copper (1973:496) in his diagnosis of this genus, but I consider that these variations in ribbing patterns may not necessarily be as important as considered by Copper since some populations of Vattenfallet material tend to exhibit different styles in detail, particularly when parts of the shell are exfoliated. *Plectatrypa* sp. *a* lacks the distinctly frilled ornament of *P. lamellosa* and has a higher fold and sulcus more reminiscent of *P. imbricata* (J. de C. Sowerby). *"Zygospira" exigua* has been regarded in the past as a rhynchonellacean (e.g. Bassett & Cocks 1974:40), but re-investigation now indicates that it is an atrypid, although fairly certainly it does not belong to *Zygospira* s.s.

Athyridacea

Whitfieldella sp. *a*, *Nucleospira pisum* (J. de C. Sowerby). All specimens identified as *Whitfieldella* have a distinct dorsal septum to confirm the generic assignment. It is probable that other material of this genus is also included within Athyridacea indet., which embraces numerous exteriors of smooth shells lacking any diagnostic features, from throughout the section.

Cyrtiacea

Eospirifer radiatus (J. de C. Sowerby), *Striispirifer plicatellus* (Linnaeus). Some fragments of eospiriferid ribbing could possibly belong to *Cyrtia*, but since in all the reasonably complete material examined there is no evidence of that genus it is all included here in *Eospirifer*.

Spiriferacea

Howellella elegans (Muir-Wood), Kozlowskiellininae? sp. indet *a.* Most specimens of *H. elegans* are small, with one or two lateral plications typical of the species, though a few larger forms with three to four plications do occur (e.g. 21.95–22.75 m), somewhat resembling *H. anglica* (Lamont & Gilbert) from the Llandovery of the Welsh Borderland. The single small spiriferacean from about 13.1 m is extremely alate with a large delthyrium and no deltidium, and has incipient frilly ornament suggesting affinities with the Kozlowskiellininae; it may be a new species.

Stratigraphical remarks

From the point of view of correlation the most significant brachiopod element in the Vattenfallet section is *Eocoelia angelini,* the end-member of the *Eocoelia* evolutionary lineage (Bassett & Cocks 1974:32–33). The extension of this lineage into the early Wenlock (Sheinwoodian) was first demonstrated at Vattenfallet and in the immediately neighbouring area to the south, where it was shown to overlie beds containing *Cyrtograptus* and to occur in intimate association with *riccartonensis* Zone graptolites (Bassett & Cocks 1974:5; Skoglund, this volume). A Sheinwoodian age for *E. angelini* has also been confirmed in the Oslo district (Bassett & Rickards 1971) and in southern Wales (Walmsley & Bassett 1976), and more recently Rubel (1977:218) has described it from the Ninase Member of the upper part of the Jaani Stage (J1N) of Estonia, which on other grounds is also known to be early Wenlock. At Vattenfallet *E. angelini* is now known to occur also below the Högklint Limestone, with well preserved specimens present in argillaceous facies of the uppermost Upper Visby Marl. I have also collected specimens of *E. angelini* from the topmost Upper Visby Marl at Ygne, south of Visby, to confirm its occurrence at Vattenfallet.

The range of many of the Vattenfallet brachiopods through other parts of the Gotland sequence can be noted by a comparison of the logs (Figs. 58–60) with Table 1 of Bassett & Cocks (1974:42–44). One amendment worthy of note is that the type specimens of *Valdaria testudo* are from the Högklint Limestone at Vattenfallet, and not from the Upper Visby Marl as stated by Bassett & Cocks (1974:19), and the logs indicate that this species is known only from the uppermost part of the Högklint.

Numerical and ecological analysis

A total of 5318 separate brachiopod specimens from Vattenfallet has been examined for this study as the basis for the logs (Figs. 58–60), comprising 1941 pedicle valves (36 %), 1201 brachial valves (23 %), 1026 conjoined valves (19 %), and 1150 (22 %) indeterminate valves; the last category includes either specimens buried partly in rock or large fragments of shell with distinctive ribbing patterns etc., but in every case they are generically or specifically identifiable from the material available. These figures do not include the majority of specimens observed when counting brachiopod valves in rock samples used in an attempt to illustrate the quantitative composition of the articulate brachiopod fauna throughout the section (Fig. 61). In Fig. 61 the levels of these additional rock samples are indicated along the margin of the stratigraphical column by black rectangles. The diagram as a whole illustrates the relative frequencies of individual valves of those articulate brachiopods which form at least 15 per cent of the total number of valves in at least one sample; all conjoined specimens were counted as two valves for this compilation. For the Upper Visby and Högklint *a* rock samples the data are based on a minimum number of 50 valves per sample; similar counts were also possible on large limestone slabs from 19.5–19.6 m and in a rock sample from 25.1 m. The remaining data for Högklint *b* and *c* are based on Liljevall's collections, with a minimum sample size of 30 valves and from within a stratigraphical interval of 20 cm or less, but these may not always be fully representative because of some degree of selective collecting (e.g. large and spectacular forms may be over-represented, juvenile individuals under-represented, and Liljevall may not have collected fragmentary specimens such as those of *V. testudo* which occur commonly in Högklint *c*).

No lower limit for the size of specimens has been applied, and in the Upper Visby Marl in particular the abundant indeterminate juvenile enteletaceans (grouped together as 'others') may mask the presence of additional dominant or subdominant species. The term dominant is used here for any species that forms more than 25 % of the total assemblage at any one level; subdominant taxa are those forming between 15 % and 25 % of an assemblage. All taxa not reaching at least 15 % at any single level are grouped as 'others'. Where two or more taxa each comprise more than 25 % they can be regarded as subequally dominant, although it is notable that this rarely happens; in most cases there is either one clearly dominant species, or there are a number of subdominants.

Fig. 61 shows that *Dicoelosia verneuiliana* is the dominant species in the section throughout the Upper Visby Marl and lower Högklint *a*. *Atrypa* sp. is the only other common brachiopod in the Upper Visby. *Visbyella visbyensis* occurs in almost every sample but not in excess of 15 %, although this is one case in which the true values may be masked by the inclusion of juveniles among unidentified material.

Throughout the Upper Visby Marl the quantitative composition of the articulates appears to be fairly uniform from sample to sample. In contrast, the relative frequencies in the Högklint Limestone fluctuate considerably from

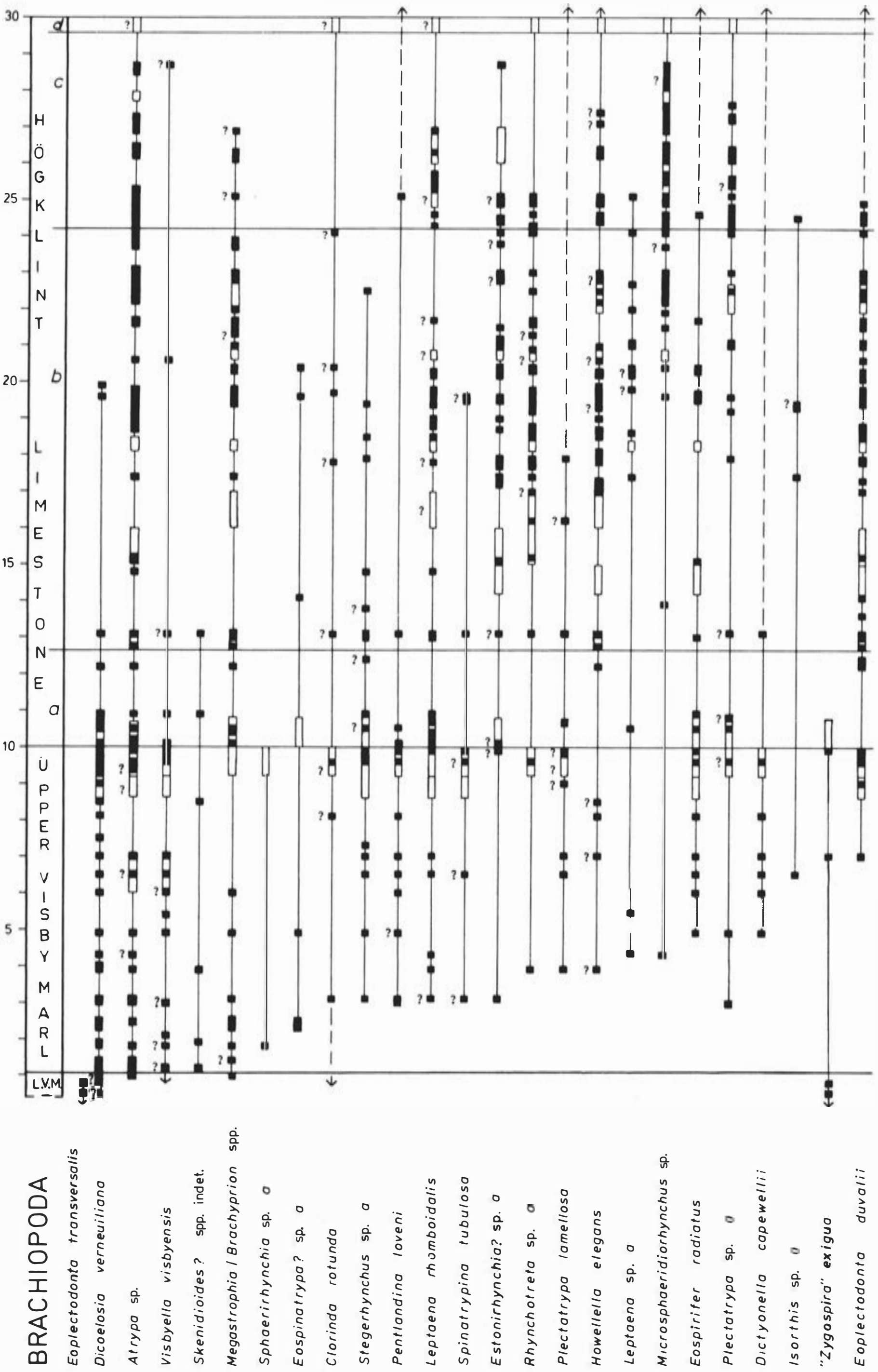
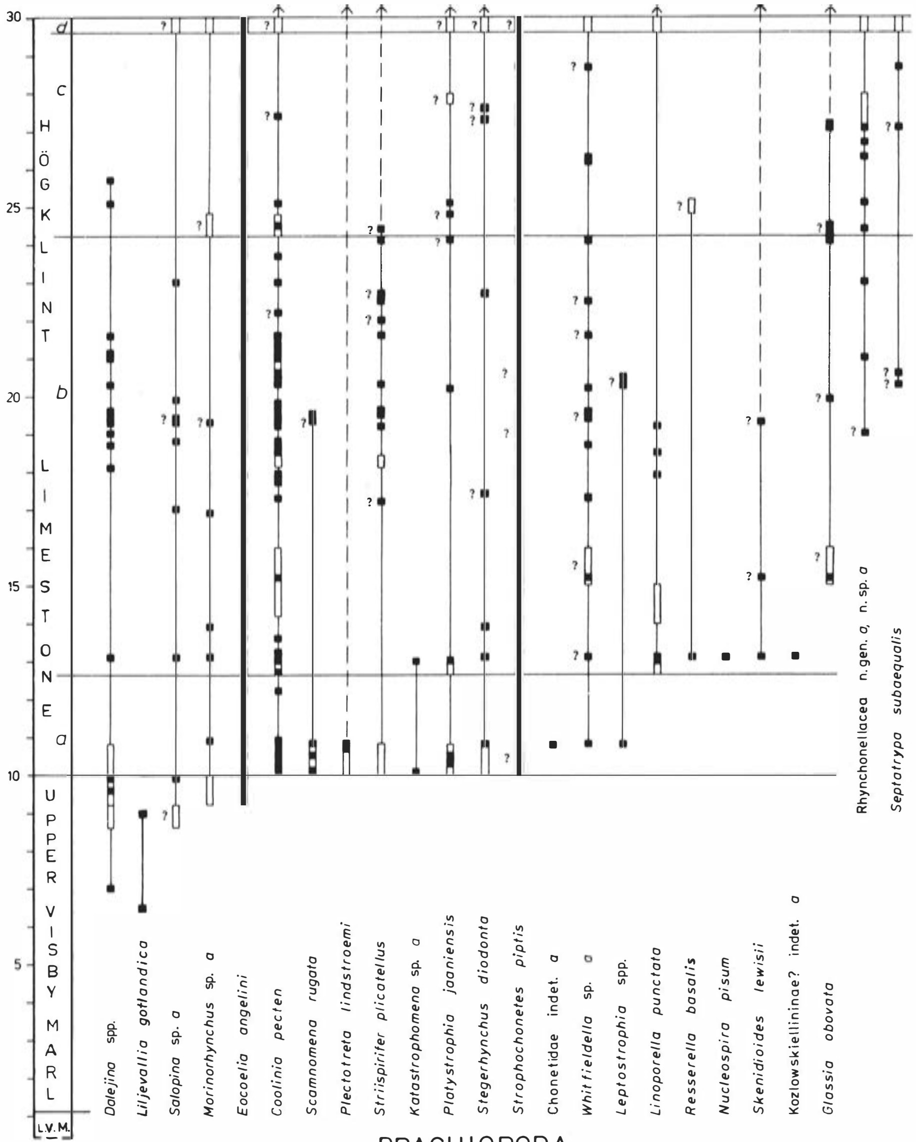

30
25
20
15
10
5
d
c
b
a
HÖGKLINT
LIMESTONE
UPPER VISBY MARL
L.V.M.
?
BRACHIOPODA
Eoplectodonta transversalis
Dicoelosia verneuiliana
Atrypa sp.
Visbyella visbyensis
Skenidioides ? spp. indet.
Megastrophia / Brachyprion spp.
Sphaerirhynchia sp. a
Eospinatrypa? sp. a
Clorinda rotunda
Stegerhynchus sp. a
Pentlandina loveni
Leptaena rhomboidalis
Spinatrypina tubulosa
Estonirhynchia? sp. a
Rhynchotreta sp. a
Plectatrypa lamellosa
Howellella elegans
Leptaena sp. a
Microsphaeridiorhynchus sp.
Eospirifer radiatus
Plectatrypa sp. β
Dictyonella capewellii
Isorthis sp. β
"Zygospira" exigua
Eoplectodonta duvalii

Fig. 58.


30
25
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5
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
a
b
c
d
Dalejina spp.
Liljevallia gotlandica
Salopina sp. a
Morinorhynchus sp. a
Eocoelia angelini
Coolinia pecten
Scamnomena rugata
Plectotreta lindstroemi
Striispirifer plicatellus
Katastrophomena sp. a
Platystrophia jaaniensis
Stegerhynchus diodonta
Strophochonetes piptis
Chonetidae indet. a
Whitfieldella sp. a
Leptostrophia spp.
Linoporella punctata
Resserella basalis
Nucleospira pisum
Skenidioides lewisii
Kozlowskiellininae? indet. a
Glassia obovata
Rhynchonellacea n. gen. a, n. sp. a
Septatrypa subaequalis
BRACHIOPODA
?

Fig. 59.

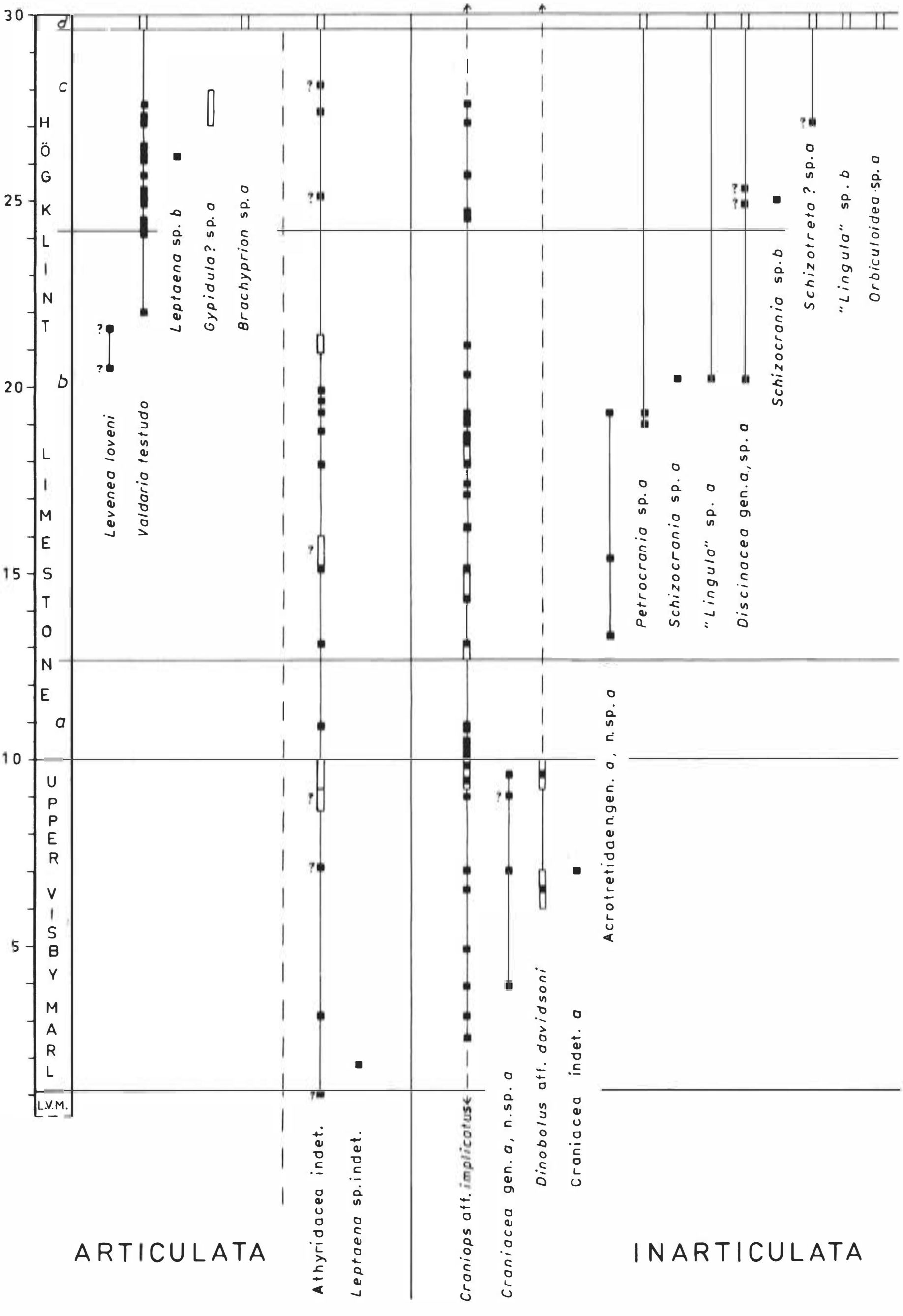

30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
Levenea loveni
Valdaria testudo
Leptaena sp. b
Gypidula? sp. a
Brachyprion sp. a
Athyridacea indet.
Leptaena sp. indet.
Craniops aff. implicatus
Craniacea gen. a, n. sp. a
Dinobolus aff. davidsoni
Craniacea indet. a
Acrotretidae n. gen. a, n. sp. a
Petrocrania sp. a
Schizocrania sp. a
"Lingula" sp. a
Discinacea gen. a, sp. a
Schizocrania sp. b
Schizotreta ? sp. a
"Lingula" sp. b
Orbiculoidea sp. a
?
ARTICULATA
INARTICULATA

Fig. 60.

level to level, and a far greater number of species attain dominance or subdominance in at least one or a few samples. *Eocoelia angelini* is quantitatively important in most samples throughout the Högklint, but at some levels a single other species occurs in great abundance, often crowding a bed. Examples are *Eoplectodonta duvalii* at 12.35 m, *Estonirhynchia?* sp. *a* at 17.9 m, *Atrypa* sp. at 24.1–24.2 m, and *Microsphaeridiorhynchus* sp. at 27.6–27.7 m. There is also a notable shift in quantitative importance of various species from Högklint *b* to Högklint *c*, with *E. duvalii, Rhynchotreta* sp. *a* and *Howellella elegans* forming important constituents of the lower subdivision, but being substituted by *Valdaria testudo, Microsphaeridiorhynchus* sp. and *Plectatrypa* sp. *a* in Högklint *c*. This shift is probably associated with a decrease in water depth.

Some data on the quantitative composition of articulate brachiopods from Högklint *d* have been obtained by counting valves on large limestone blocks and slabs collected by G. Lindström and others, but these data are not included in Fig. 61 since the material is from several unspecified levels which cannot be tied down with sufficient stratigraphical accuracy. On several large slabs which are clearly from the same level, *V. testudo* is a strongly dominant element, forming up to 76 % of the assemblages (n=290), and no other species reach 15 %. On limestone blocks from another level *Septatrypa subaequalis* (24 %) and Rhynchonellacea n. gen. *a*, n. sp. *a* (21 %) are subequally dominant (n=164). In the soft pelletal marl known to come from the base of Högklint *d* Discinacea n. gen. *a*, n. sp. *a* is the only common species and was probably dominant at this level, although exact counts have not been possible with the material available. The mode of life of this discinacean is an interesting factor, since pedunculate forms generally favour a hard substrate, but the pelletal marl must have formed a very soft bottom; the large, open pedicle groove of the species indicates that it was truly pedunculate, but it may have been that in this case the distal end of the pedicle was split into fine rootlets to give a rhizosessile mode of attachment on the fine-grained soft pellets; the few Recent brachiopod species known to attach in this way have very thin shells, and this is true for the Vattenfallet species.

In general terms the *Dicoelosia*-dominated Upper Visby faunas fit closely within Benthic Assemblage 4 of Boucot (1975:14; see also for general description of communities). The continued dominance of *Dicoelosia* into the lower part of the winnowed skeletal sand of Högklint *a* may be a reflection of a high proportion of transported shells in this high energy environment. The upward change to beds in which *Eocoelia* becomes quantitatively important superficially suggests a shift to Boucot's Benthic Assemblage 2, but in detail the assemblages from the higher levels are difficult to fit into Boucot's model, since at Vattenfallet beds with abundant *Eocoelia* also have a high taxonomic diversity and in part represent a low energy environment (lower part of Högklint *b*; see Jaanusson, this volume).

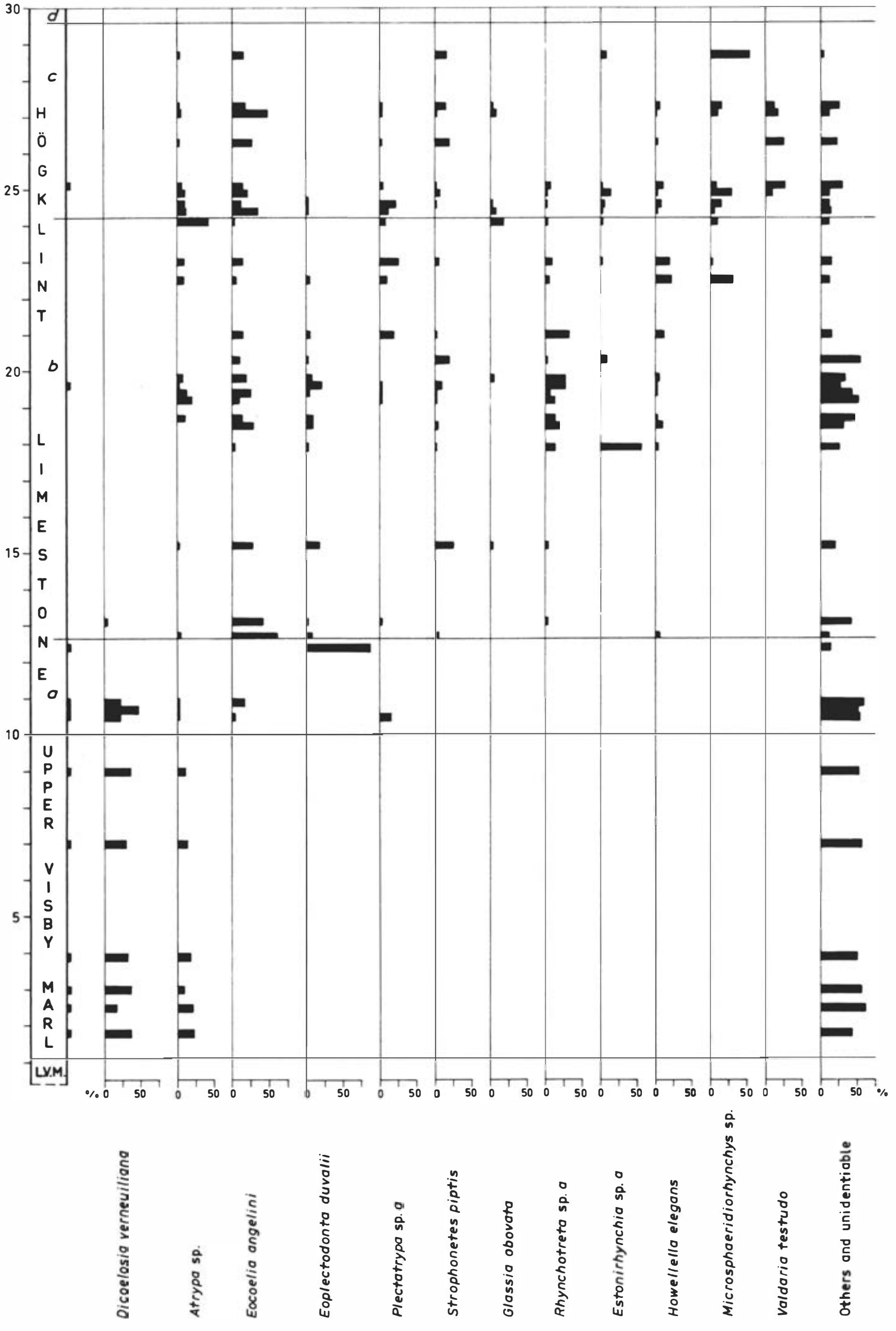


Fig. 61. Percentage frequencies of those articulate brachiopod species which form at least 15 per cent of the total articulate brachiopod fauna in at least one sample. See text for full explanation.

As a final comment on ecology it is relevant to mention that two of the samples analysed by Hurst (1975b) give quantitative data on macrofossils at Vattenfallet from adjacent beds in the Högklint Limestone. Information given by Hurst to Jaanusson suggests that the samples were from the 12 to 13 m interval, and in detail this can be confirmed since Hurst's (1975b, Table 1) sample G–65.2 compares very closely with material plotted on Fig. 61 at 12.35 m, particularly because of the dominance in both analyses of *E. duvalii;* this level has been checked in the field and can be confirmed as the only horizon at which *E. duvalii* becomes dominant. In his diary Liljevall also drew attention to this distinctive level at 12.4 m as being rich in "*Leptaena transversalis*" (=*E. duvalii* herein). It is important to note the unique nature of the *E. duvalii* dominated level at 12.35 m, since it is atypical of the Vattenfallet section as a whole, and indicates that Hurst's data are not fully representative of the overall quantitative composition. This factor is also supported by the differences noted by Hurst (1975b:253) in his own samples from Vattenfallet, and emphasises the need for bed by bed collection as a basis for palaeocommunity analysis.

Systematic descriptions of new taxa

As noted above in the annotated faunal list, some of the new taxa require further investigation before a full systematic account can be given, but two of the new species are represented by abundant and well preserved material and are thus described here. Figured specimens are in the Riksmuseum (RM) and Sveriges Geologiska Undersökning (SGU), Uppsala.

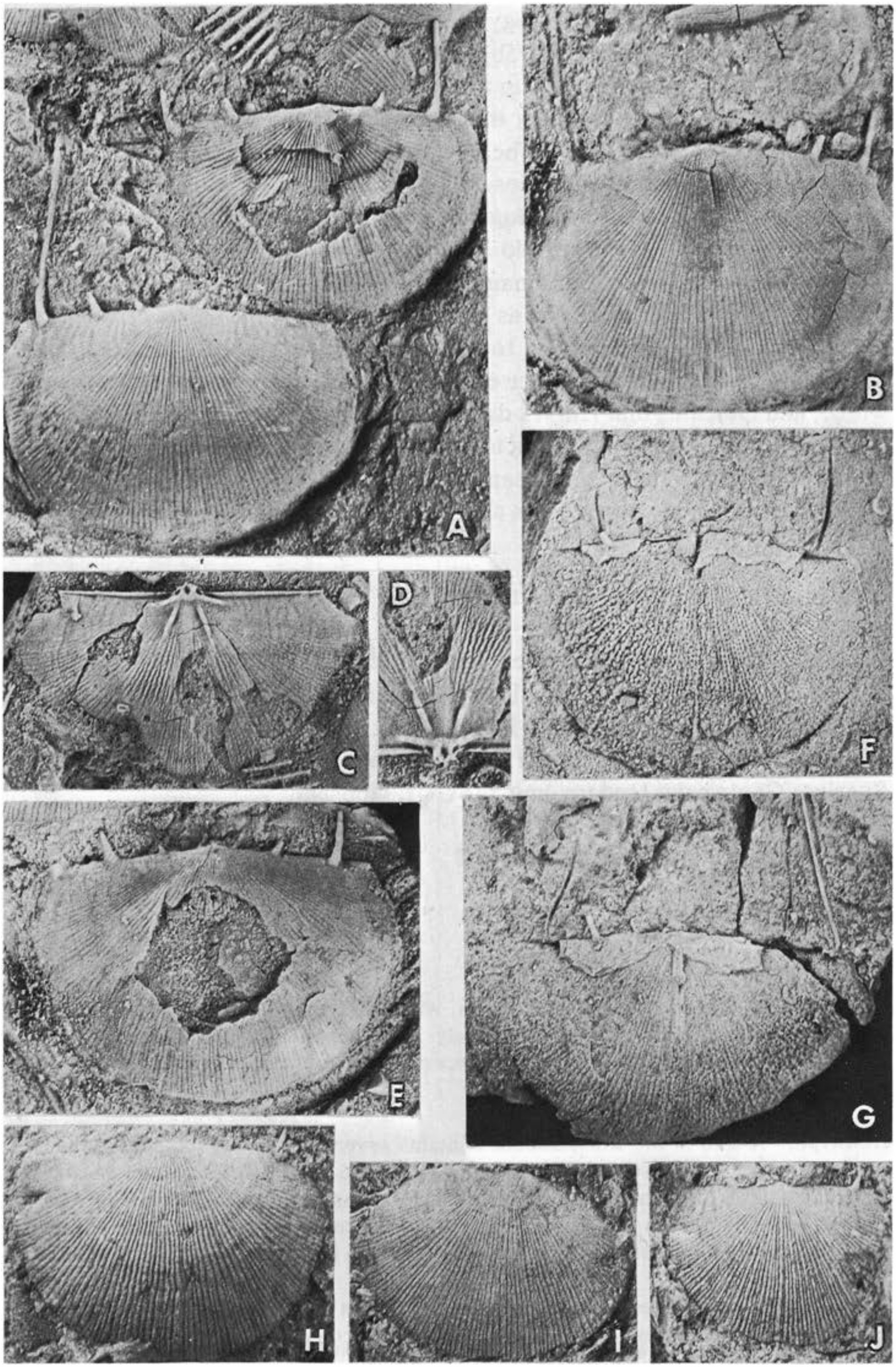
Superfamily: Chonetacea Bronn, 1892

Strophochonetes piptis n. sp.
Fig. 62

Diagnosis. – Relatively large for the genus, with long spines. Ventral septum short and stout, non-bifurcating. Anderidia relatively long, separated by a low ridge. Socket ridges widely divergent, long; cardinal process lobes stout. Ventral median capilla may or may not be thickened.

Holotype. – A slab in the Riksmuseum contains seven well preserved specimens of *S. piptis;* the slab bears two numbers, Br106494–106495. Four of the specimens are here designated as Br106495a–d, and the remaining three as Br106494a–c, of which 106495a, pedicle valve figured on Fig. 62A (lower fig.) is designated as the holotype. The slab is from the Högklint Limestone at Vattenfallet, but from an uncertain level in the section.

Paratypes. – Four of the remaining six specimens on Br106495–106494 are figured on Fig. 62. Other paratypes are all in the Vattenfallet collection at SGU. The species is known so far only from Vattenfallet.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Derivation of name. – From the Greek word *pipto* meaning fall, alluding to the Vattenfallet section.

Description. – Semi-circular to suboval, with a straight hinge and maximum width close to the mid-length; cardinal angles obtusely rounded, lateral and anterior margins smoothly and evenly curved. Weakly to moderately concavo-convex, evenly curved throughout growth. Umbones low to obsolescent, ventral beak barely protruding posterior to the hinge. Ventral interarea apsacline, short, delthyrium apparently open, delthyrial angle about 90°; dorsal interarea linear, notothyrium not observed. Spines confined to the ventral cardinal margin, normally three on either side of the umbo, initially divergent at about 70 to 80° to the hinge, but curving after about 1 mm to an approximately normal alignment; the spine bases are stout, with the spines tapering slightly distally, straight to gently curved and long (maximum observed length 9 mm). Spacing of the spines is uneven, but numbers 3 and 3^1 are commonly set medial of the cardinal angles. Ornament capillate with 4 to 5 low, rounded capillae at the 5 mm growth stage of the pedicle valve; the median ventral capilla is generally, but not always, thickened. Faint concentric rugae may be present around the ventral umbo (e.g. Fig. 62A). Fine concentric growth fila may produce a reticulate ornament across the capillae in places. Rib increase is mainly by insertion, with some subsidiary branching.

Teeth small, elongated laterally along the hinge. A short, simple ventral septum thickens posteriorly and occupies up to 1/6 of the length of the valve. Ventral muscles long and narrow, occupying about 1/9 of the valve width, elongated alongside a very low, faint median ridge which extends anteriorly from the septum to about the mid-length of the valve; the muscle scars extend slightly beyond the distal end of the ridge. Cardinalia well developed (Fig. 62C–D); cardinal process bilobed and stout, with each lobe directed posteroventrally as a grooved ridge to produce a quadrilobed myophore. Socket ridges divergent at about 150° to one another, fused medially with the base of the cardinal process. The posterior face of the cardinal process is covered by curved chilidial plates which extend down into the sockets. Anderidia strong and rounded, divergent at about 50–60° to one another. Median septum not developed, but a low, broad, rounded swelling forms a low median ridge extending anteriorly slightly beyond the margins of the anderidia. Dorsal musculature not preserved.

Fig. 62. A–J. *Strophochonetes piptis* n. sp. A. Holotype (lower figure) RM Br106495a and Paratype RM Br106495b, two pedicle valve exteriors showing long spines. B. Paratype, exterior of pedicle valve RM Br106494a. C–D. Paratype, interior of brachial valve in dorsal and posterodorsal views; note the long anderidia, low median ridge, divergent socket ridges, quadrilobed myophore, and delicate chilidial plates extending down into the sockets. RM Br106495c. E. Paratype, exterior of pedicle valve. RM Br106494b. F. Paratype, internal mould of pedicle valve showing simple septum. SGU Type 78. G. Paratype (on same slab as F), partially exfoliated pedicle valve. SGU Type 79. H. Paratype, exterior of pedicle valve. SGU Type 80. I. Paratype, exterior of pedicle valve. SGU Type 81. J. Paratype, exterior of pedicle valve. SGU Type 82.

D ×4; all others ×3. All specimens from Högklint Limestone at Vattenfallet; A–E from uncertain level; F–G from 20.20–20–25 m; H from 20.15–20.20 m; I from 26.19–26.37 m; J from 26.0–27.0 m.

Dimensions of figured specimens (in mm). –

	Length	Maximum width	Hinge width	Spines preserved
RM Br106495a (Holotype)	10.9	16.1	14.9	$3^1 2^1 1^1 13$
RM Br106495b	9.5	14.0	13.0	$3^1 2^1 23$
RM Br106494a	11.5	16.0	14.6	$2^1 3$
RM Br106494b	11.7	16.5	14.6	$3^1 2^1 1^1 123$
RM Br106495c	9.3	15.6	–	–
SGU Type 78	11.8	16.5	15.0	$2^1 3$
SGU Type 79	10.3	18.9	16.1	$3^1 2^1 1^1 23$
SGU Type 81	9.6	–	–	–
SGU Type 82	7.4	–	9.8	$1^1 12$
SGU Type 80	9.9	–	–	$2^1 1^1 123$

Comparison. – This species has all the criteria used by Racheboeuf (1976:48, text-fig. 4) to define *Strophochonetes (Strophochonetes),* and clearly belongs within that subgenus. The closest described species to *S. piptis* is the type species *S. cingulatus* from younger Wenlock beds on Gotland, but while the two are similar in general external morphology, *cingulatus* differs in having a more slender ventral septum, shorter and more slender anderidia, and more delicate cardinal process lobes.

Superfamily: Atrypacea Gill, 1871

Septatrypa subaequalis n. sp.

Figs. 63–64

Diagnosis. – Subequally biconvex *Septatrypa* with a stout septum and slender walled, deep septalium, the depth approximately equal to the septal height.

Holotype. RM Br 62772, conjoined valves (Fig. 64A–D) from the "*Pterygotus* Beds" (Högklint *d*) at Vattenfallet.

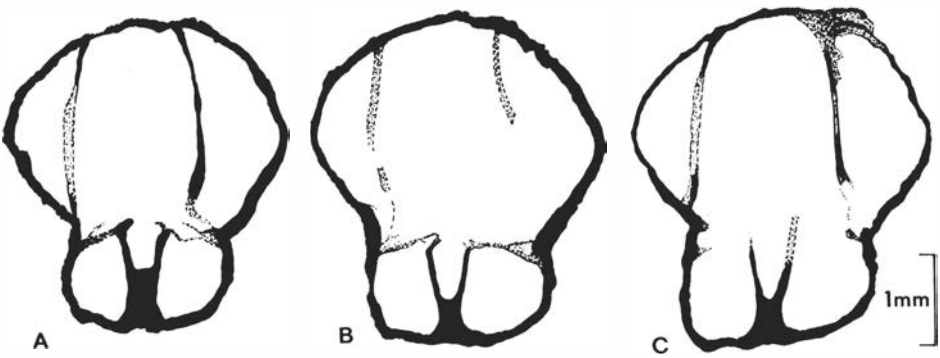


Fig. 63. Serial sections (peels) of *Septatrypa subaequalis* n. sp. RM Br62773. See Fig. 64 P–Q for illustration of complete shell. A=3.0 mm from posterior tip of pedicle valve, B=3.5 mm, C=4.0 mm. Note the slender dental plates, deep lateral cavities, stout dorsal septum, and slender-walled, deep septalium.

Paratypes. – RM Br 62773–77, Br106487–89, Br106508–18, all conjoined valves from the "*Pterygotus* Beds" at Vattenfallet, form the main basis for interpretation of the species, which is most common at this level. Other paratypes, both from this horizon and slightly lower levels in the Högklint, are in the Riksmuseum and SGU. *S. subaequalis* is known so far only from the upper part of the Högklint Limestone in this section.

Derivation of name. – Referring both to the subequal convexity of the valves and to the subequal height of the dorsal septum and walls of the septalium.

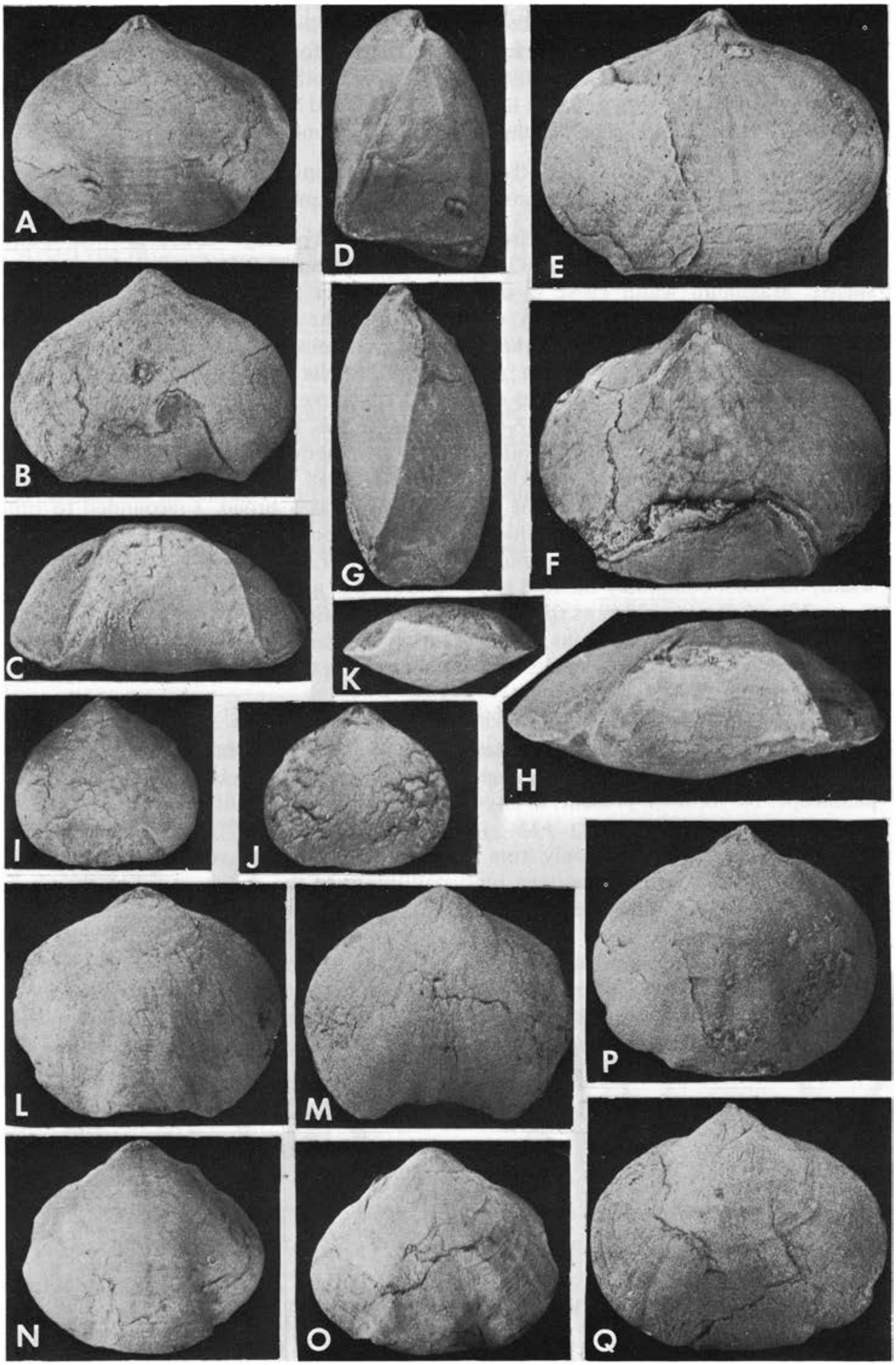
Description. – Outline initially subcircular, becoming subpentagonal with growth. Width commonly about 90 % of length (O.R. 78–101 %, mean 89.2 % in 19 well preserved shells). Maximum width close to or slightly anterior to mid-length. Posterolateral margins gently curved and widely divergent from the beak, lateral margins evenly curved or with a slight shoulder at the point of maximum width; anterior margin initially gently curved, becoming straight at maturity. Shells moderately and subequally biconvex, never globose, sometimes slightly dorsibiconvex at maturity. Thickness close to 60 % of maximum width (O.R. 42–67 %, mean 57.2 %, n= 19). Pedicle valve typically most convex at the umbo, flattening slightly peripherally. Commissures sharp and smooth, anterior commissure weakly uniplicate in small shells, becoming broadly and deeply uniplicate with growth. The brachial valve has a broad, subrounded to subquadrate fold in its anterior half, which originates at about 6 to 8 mm; the pedicle valve has a complementary sulcus. The tongue at the anterior margin is of variable height and width, but most commonly the fold is 60–70 % as high as wide (O.R. 55–75 %, mean 64 %, n=19). In some specimens the sulcus bears very faint, low, flat undulations (1 to 3 observed) as incipient plications, and there may be a faint groove along the mid-length of the fold. Otherwise the complete shell is smooth with the exception of well developed growth fila.

Hinge curved, merging smoothly with posterolateral margins. True interareas lacking, palintropes curved but mainly masked below beaks. Umbones low, ventral beak suberect but not curved over the hinge, dorsal beak blunt and curved against ventral palintrope. No foramen present, delthyrial and notothyrial structures masked by curvature of beaks.

Internal structures known only from serial sections, which show limited detail in the material studied because of coarse recrystallisation of the sediment filling the shell. However there is sufficient detail to confirm some features (see Fig. 63) of generic importance. Teeth are small and pointed. Dental plates long and slender, with deep lateral cavities. Inner hinge plates lacking, septalium supported throughout its length on a relatively stout dorsal septum. The septalium has slender lateral walls and is relatively deep, the depth approximately equalling the height of the septum. The dental plates, septum and septalium may extend to about the mid-length of the shell. Spiralia not observed.

Dimensions of figured specimens (in mm). –

	Length	Maximum width	Thickness	Width of fold	Height of fold
RM Br 62772 (Holotype)	10.5	12.4	6.2	8.9	5.8
RM Br 106487	12.8	15.4	6.6	10.0	4.0
RM Br 106515	11.0	11.7	7.7	7.3	5.0
RM Br 106508	8.5	8.8	5.5	6.6	4.2
RM Br 106489	10.5	11.8	8.0	7.4	5.7
RM Br 62773	11.6	12.9	7.5	7.3	3.8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Comparison.—This is the first record of *Septatrypa* from Gotland, but the general external morphology, dental plates, septalium, and septum confirm the generic identification. Within the Baltic basin the only other records of the genus have been made by Rybnikova (1967:205–207) from boreholes through the Silurian of Latvia. She identifies *S. secreta,* the type species, from beds of early Ludlow age (*scanicus* Zone), but her limited illustrations and absence of internal detail prevent a detailed comparison with the Gotland material. However, Kozłowski's (1929:177, text-fig. 8, Pl. 1.9, figs. 18–24) original description of *S. secreta* from Podolia indicates that it can be easily separated from *S. subaequalis* by its very shallow septalium and high septum which are together restricted to about 1/4 of the length of the valve. Rybnikova (1967:206) also described a species from the Wenlock of Latvia as *Septatrypa*(?) *subanaloga,* but her description and illustration (fig. 34) indicate that this species lacks dental plates, and on these grounds it can be excluded from *Septatrypa.* I consider that her species is not an atrypacean, but is probably a rhynchonellacean and may belong to *Plagiorhyncha* (see also Kaljo 1970:143, table 15).

Plodowski (1971) has recently revised a number of late Silurian *Septatrypa* from Central Europe. Of these, *S. sappho* (Barrande) is closest to *S. subaequalis* externally, but it has a wider fold and sulcus that occupy almost the whole width of the shell at the anterior margin; internally *S. sappho* has shorter dental plates, a shorter septum, and shallow septalium. *S. harpyia* (Barrande) has a deeper and more narrowly elongated fold and sulcus than *S. subaequalis,* and from Plodowski's (1971) limited description also appears to lack the distinctive internal structures of the Gotland species.

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Fig. 64. A–Q. *Septatrypa subaequalis* n. sp. A–D. Holotype, dorsal, ventral, anterior, and posterior views. RM Br62772. E–H. Paratype, dorsal, ventral, lateral, and anterior views. RM Br106487. I–K. Paratype, dorsal, ventral and anterior views. RM Br106508. L–M. Paratype, dorsal and ventral views. RM Br106489. N–O. Paratype, dorsal and ventral views. RM Br106515. P–Q. Paratype, dorsal and ventral views. See also Fig. 63 for sections of this specimen. RM Br62773.

All ×3; all from *"Pterygotus"* Beds (Högklint *d*), Vattenfallet.

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Tentaculitoids

KENT LARSSON

The tentaculitoid fauna of Gotland is fairly rich and diverse but has not previously been described. I have recently completed a study of the whole fauna, and the names used here (referred to as Larsson MS) will be published in a forthcoming monograph. The material from Vattenfallet comprises about 100 specimens. For ranges in the section see Fig. 65.

Annotated faunal list

Tentaculites limatulus Larsson MS, *Seretites? exilis* Larsson MS, *S.? cataractae* Larsson MS, *Gotlandellites areolatus* Larsson MS, *G. visbyensis* Larsson MS, *Alternatus?* spp.

Tentaculitidae gen. et sp. indet. have also been recorded at 17.9 and 28.60–28.80 m. The genus *Alternatus?* is represented by fragmentary specimens which are difficult to identify at species level, but appear to comprise at least two different species.

Remarks

Tentaculitoids are best preserved and easiest to collect in marls and on bedding surfaces of argillaceous limestones. The low species diversity in uppermost Högklint *b* and in Högklint *c* of the section is probably due to the nature of the hard rock rather than to the rarity of the group in these beds. This is also indicated by the fact that the greatest number of indeterminate specimens, mostly preserved as internal moulds, is from Högklint *c*.

The mode of life of tentaculitoids remains a matter of discussion. All representatives of this group from Gotland are thick-walled and it is therefore very unlikely that any were planktic or nectoplanktic. For benthic forms Blind (1969, 1970) suggested a twofold mode of life: a larval, free-living stage followed by an adult, sessile stage in which the conch was in a vertical position largely embedded in the sediment, apex downward. My studies on morphology and microstructure of the conch support Blinds's hypothesis. Thus adult tentaculitoids most probably had a semi-infaunal mode of life, although their posture was not always necessarily vertical, and they were probably suspension feeders, possibly by means of some kind of tentacle apparatus.

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Cornulitids

KENT LARSSON

It is difficult to make a satisfactory assessment of the cornulitid fauna of Vattenfallet because it is completely undescribed. Cornulitids are poorly known, and not only the material from Gotland but also the group as a whole is badly in need of monographic study. There are many cases of misinterpretation. For example, it is doubtful if *Cornulites serpularius,* the type species of the genus, has ever been identified correctly since Schlotheim (1820) described the species. It has become mostly associated with a very stout, unattached conical conch with a characteristic cellular wall structure, similar to the species figured as *C. serpularius* by Sowerby (in Murchison 1839, Pl. 26:6–9), but there is very little agreement between this conch and the specimen figured by Schlotheim (1820, Pl. 29:7). This taxonomic disorder is difficult to resolve because Schlotheim's type specimen cannot be located (Hermann Jaeger, personal communication).

The material from Vattenfallet comprises about 40 specimens. For ranges in the section see Fig. 65.

Annotated faunal list

Cornulites? cf. *scalariformis* Vine, *C.?* sp. *a, Conchiolites* sp. *a*, Cornulitidae gen. *a*, sp. *a,* Cornulitidae gen. *b,* sp. *a,* Cornulitidae gen. *c,* sp. *a,* Cornulitidae gen. *d,* sp. *a* (3.0 m). Unidentifiable cornulitids have been recorded also at 0.75, 1.0, 1.75, and 4.9 m.

A conch which is very similar to *Cornulites? scalariformis* occurs in Högklint *d*, and a specimen has also been found in the road-cut at Palisadvägen (Högklint *c*, c. 26.5–27.5 m, not entered in the log). Before a definite identification of the specimens can be made, examination of Vine's (1882) type specimen is necessary. *Cornulites?* sp. *a* resembles *C.? scalariformis* but differs in having a clearly curved conch.

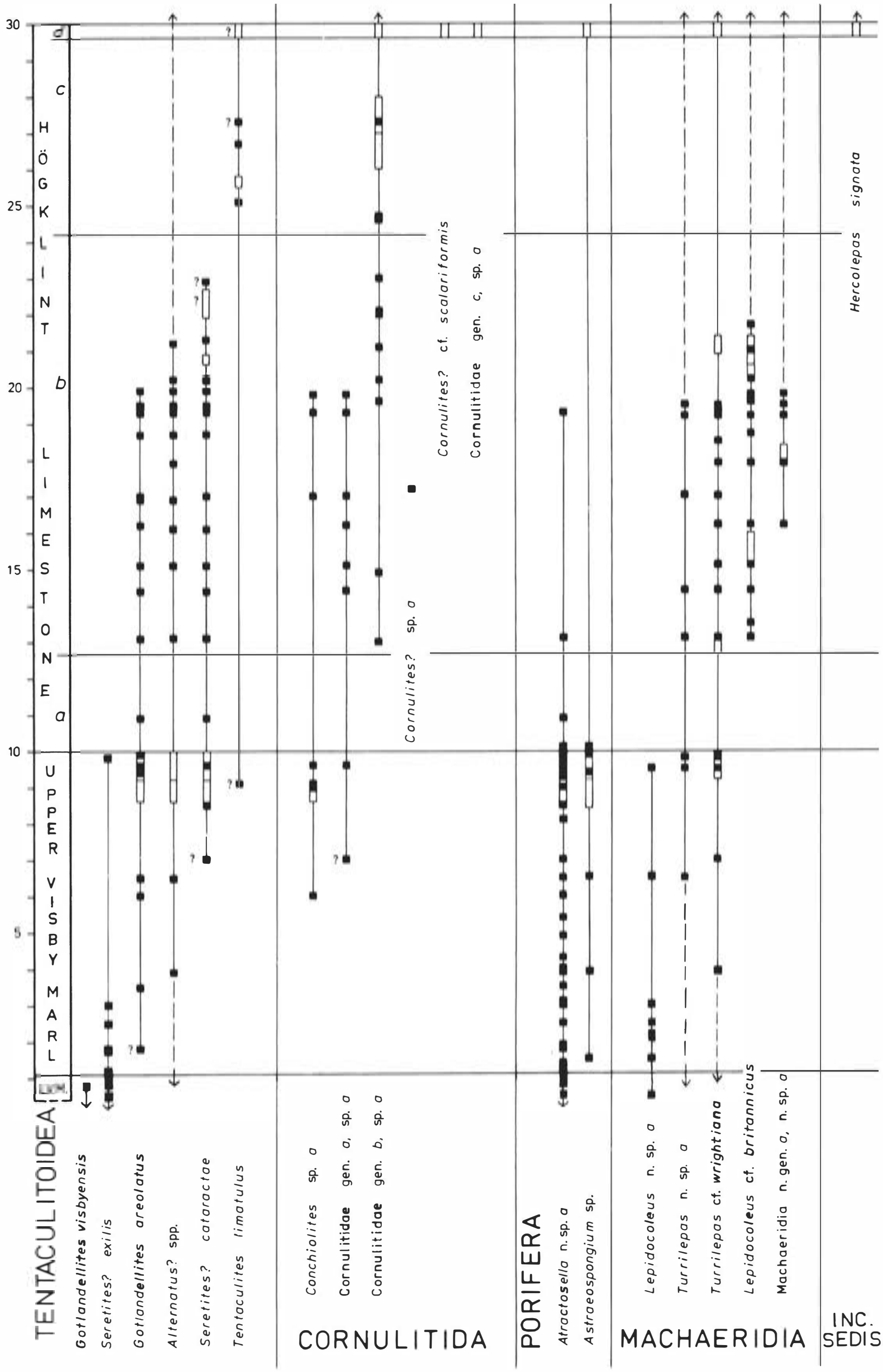
30
25
20
15
10
5
HÖGKLINT LIMESTONE
a
b
c
d
UPPER VISBY MARL
?
TENTACULITOIDEA
Gotlandellites visbyensis
Seretites? exilis
Gotlandellites areolatus
Alternatus? spp.
Seretites? cataractae
Tentaculites limatulus
CORNULITIDA
Conchiolites sp. a
Cornulitidae gen. a, sp. a
Cornulitidae gen. b, sp. a
Cornulites? sp. a
Cornulites? cf. scalariformis
Cornulitidae gen. c, sp. a
PORIFERA
Atractosella n. sp. a
Astraeospongium sp.
MACHAERIDIA
Lepidocoleus n. sp. a
Turrilepas n. sp. a
Turrilepas cf. wrightiana
Lepidocoleus cf. britannicus
Machaeridia n. gen. a, n. sp. a
INC. SEDIS
Hercolepas signata

Fig. 65.

Cornulitidae gen. *a,* sp. *a* may include more than one species but because of poor preservation safe conclusions are difficult. The specimens are characterized by having a small attachment surface and fairly distinct rings which occasionally carry short spines.

Cornulitidae gen. *b,* sp *a* is conspecific with *Cornulites serpularius sensu* Sowerby (in Murchison 1839, Pl. 26:6–9). The largest specimen is 4–5 cm long and clearly exhibits a cellular wall structure. In previous literature on Gotland the species has been referred to as *Cornulites serpularius.*

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Machaeridians

STEFAN BENGTSON

The Machaeridia are a poorly known group of Palaeozoic (Ordovician to Carboniferous) problematical fossils. Their triangular to rhomboidal calcitic plates, with characteristic ornament of raised growth lines, were disposed in pairs of imbricating rows to cover an elongated body or (less likely) organ. For details of the morphology and systematics of the group, see Withers 1926. Long considered to be echinoderms because of the alleged holocrystalline structure of the plates of some species (Withers 1926), the machaeridians have recently been shown to have a fine structure fundamentally different from that of echinoderm stereom (Bengtson 1977, 1978). At present the affinities of the group remain uncertain.

Although a few Gotland specimens have been described and figured (Aurivillius 1892:20; Moberg 1914:19, Pl. 2:23; Hede 1917:23, Pl. 2:9), the machaeridians of Gotland are basically undescribed. For this reason open nomenclature is used here, in the anticipation that current studies of Gotland machaeridians will soon produce a key to these preliminary designations. The material from Vattenfallet comprises about 400 separate plates and a specimen of *Lepidocoleus* cf. *britannicus* with 13 pairs of articulated plates. For the ranges in the section, see Fig. 65.

Faunal list

Machaeridia

Turrilepas cf. *wrightiana* (de Koninck, 1857); *T.* n.sp. *a*; *Lepidocoleus* cf. *britannicus* Withers, 1926; *L.* n.sp. *a*; Machaeridia n. gen. *a*, n.sp. *a*.

Lepidocoleus sp. indet. has also been recorded at 9.95–10.0 m, and unidentified machaeridian plates at 8.5, 9.3 and 18.75 m.

Remarks

Since 95 per cent of all machaeridian specimens found at Vattenfallet have been obtained through elutriation of marl, their distribution in the log to a very large extent reflects the availability of marl samples. Thus their absence in uppermost Högklint *b* and in Högklint *c* is most certainly artificial, since this now inaccessible interval lacks marly intercalations. Their relative scarcity in the Upper Visby Marl may be more real, judging from similar conditions in corresponding sections along the north-western coast of Gotland.

Because of lack of understanding of the zoological nature of machaeridians, their mode of life cannot be confidently reconstructed. It is likely that the plates formed a dorsal protective skeleton of a worm-shaped animal (Bengtson 1970:385–390), comparable to a scale-bearing annelid or a polyplacophoran, and so the machaeridians probably belonged to the vagrant epifauna. Their armour seems to have prevented efficient rapid movement. There is currently no evidence on the mode of feeding, although suspension-feeding can probably be ruled out.

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Hercolepas

STEFAN BENGTSON

A unique specimen of a peculiar problematical fossil, *Hercolepas signata* (Aurivillius), has been described from Högklint *d* at Vattenfallet (Aurivillius 1892:4–12, Figs. 1–8; see also Withers 1915:117–118, Fig. 3). Plates belonging to *Hercolepas* have now also been found in bituminous inter-reef deposits of the Halla Beds (upper Wenlock) of Hörsne 6. Originally described as a lepadomorph cirriped, *Hercolepas* must be considered to be of uncertain affinity. The homology suggested by Aurivillius of *Hercolepas* plates with the capitular plates of lepadomorphs, is not well founded (cf. Withers 1915:117), and the specimen is most certainly much less complete than Aurivillius supposed.

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Graptolites

ROLAND SKOGLUND

In the carbonate sequence of the outcrop area of Gotland graptolites are relatively rare. They were first described by Linnarsson (1879) and Holm (1890) and the knowledge was summarised by Hede (1918, 1942). The emphasis in these studies has been on graptoloids whereas dendroids have received very little attention.

The first record of graptoloids from Vattenfallet was published by Holm (1890). He mentioned the occurrence of *Monograptus priodon* from beds now classified as the Högklint Limestone, and figured (Holm 1890, Pl. 1:27–30) a large *Monograptus* sp. which according to him was from grey limestone of the "*Pterygotus*" Beds but from the nature of the rock it is probably from Högklint *c*. The specimen, 85 mm long, is the distal part of a *Pristiograptus* preserved in relief. Perner (1899) compared it with *Pristiograptus gotlandicus*, a species described from the Lower Ludlovian of Bohemia. Hede (1942) doubted Perner's identification and stated that the specimen did not agree with any species known to him. I find that it belongs to the *dubius* group. The width of the rhabdosome and the thecal spacing agree with those of *Pristiograptus dubius latus* Bouček.

Hedström (1910:1472) listed *Monograptus* sp. from Högklint *b–c* but the specimen cannot be traced. On a later occasion he recorded *Monograptus spiralis* var. *subconicus* Törnquist from the lowermost beds of the Upper Visby Marl at Vattenfallet (Hedström 1923:195, Fig. 2). Recently the specimen was re-examined by R.B. Rickards (Bassett & Cocks 1974:5) and found to be a part of a robust cyrtograptid. The specimen is entered in the log as *Cyrtograptus* sp.

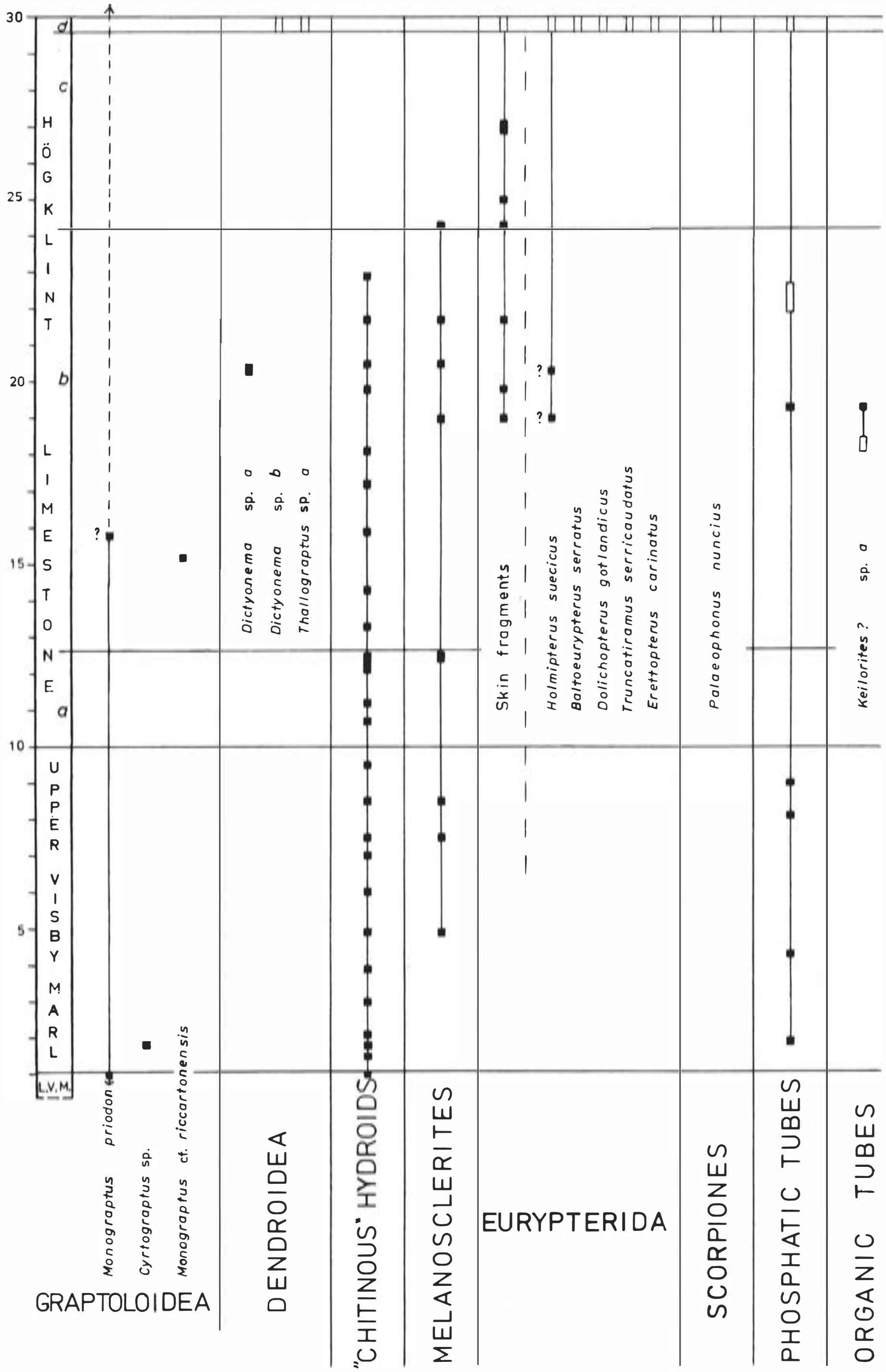
Bulman (1932, Pl. 6:1) figured a specimen of *Monograptus priodon* from Vattenfallet, isolated by Holm. The specimen is lost and no information exists as to its level.

A few additional specimens were found during the present study. It should be noted that systematic acid digestion of rock samples for graptolites would almost certainly have produced additional material. For various reasons no such work was carried out at Vattenfallet.

Annotated faunal list

Dendroidea (see Fig. 66)

Dictyonema sp. *a*, *D.* sp. *b*. An unusual dendroid, referred to by Lindström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5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
Monograptus priodon
Cyrtograptus sp.
Monograptus cf. riccartonensis
GRAPTOLOIDEA
Dictyonema sp. a
Dictyonema sp. b
Thallograptus sp. a
DENDROIDEA
"CHITINOUS" HYDROIDS
MELANOSCLERITES
Skin fragments
Holmipterus suecicus
Baltoeurypterus serratus
Dolichopterus gotlandicus
Truncatiramus serricaudatus
Erettopterus carinatus
EURYPTERIDA
Palaeophonus nuncius
SCORPIONES
PHOSPHATIC TUBES
Keilorites? sp. a
ORGANIC TUBES

Fig. 66.

(1888) as *Inocaulis* (*bellae* Hall & Whitf. aff.) and mentioned by Holm (1890:4), is common in Högklint *d*. Selected specimens were examined by Dr. R.B. Rickards who found that it belongs to *Thallograptus*. The species is entered in the log as *T*. sp. *a*. Unidentifiable fragments of dendroids occur also at 0.75, 10.90, 15.20, 17.30, 18.70, 19.10, and 20.25 m.

Graptoloidea
Monograptus priodon Bronn, *M*. cf. *riccartonensis* Lapworth (a proximal end with two thecae and a distal fragment with three thecae), *Pristiograptus dubius latus* Bouček (Högklint *c*), *Cyrtograptus* sp.

Remarks on correlation

The record of *Monograptus spiralis* from the base of the Vattenfallet section (Hedström 1923) for a long time confused the correlation of the Upper Visby Marl (Martinsson 1967:358–359). The specimen, found at 1.7–1.9 m, turned out to belong to *Cyrtograptus* and is indicative of an early Wenlock age for this level (Bassett & Cocks 1974:5), only 0.6–0.7 m above the boundary between the Lower and Upper Visby Marls. *Pristiograptus dubius latus* from Högklint *c* or *d* indicates a level not older than the *riccartonensis* Zone. Bassett & Cocks (1974:5) recorded *Monograptus* aff. *riccartonensis* from the Högklint Limestone, found in an exposure not far from Vattenfallet. The horizon possibly is lower Högklint *b* (Jeppsson, this volume). The occurrence of *M*. cf. *riccartonensis* in the lowermost Högklint *b* at Vattenfallet indicates that the base of the *riccartonensis* Zone extends downwards at least to the base of Högklint *b*. The correlation of other graptolite zones with the Vattenfallet sequence is uncertain because no distinctive species have been found.

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Echinoderms

CHRISTINA FRANZÉN

With a few exceptions, relatively little has been written on Gotland echinoderms. In 1878 Angelin's monumental work on Gotland crinoids, the *Iconographia Crinoideorum in stratis Sueciae siluricis fossilium,* was published, containing descriptions of 173 species referred to 42 genera. Prior to this only 13 species from Gotland had been described or mentioned by various authors. Angelin did not live to issue his own work, which may explain some of its shortcomings; the diagnoses of the various species are very brief, and there are no descriptions; the illustrations are often misleading, the specimens either being heavily restored (not always correctly) or composed of several individuals, in some cases even belonging to different genera. Thus, despite the great importance of the *Iconographia* it soon became evident that the Gotland crinoids were greatly in need of thorough revision. Wachsmuth & Springer (1879, 1881, 1885, 1886, 1888) revised some of the species, but did not have access to Angelin's material. Bather (1893) published a review of the Crinoidea Inadunata and Springer (1920) described the Crinoidea Flexibilia. Liljevall drew the excellent illustrations of Gotland material for both Bather and Springer.

In the past 50 years research on Gotland crinoids has been mainly on specialized groups or species (e.g. Ubaghs 1956a, b, 1958), and many groups are still in need of a thorough revision, particularly the Crinoidea Camerata.

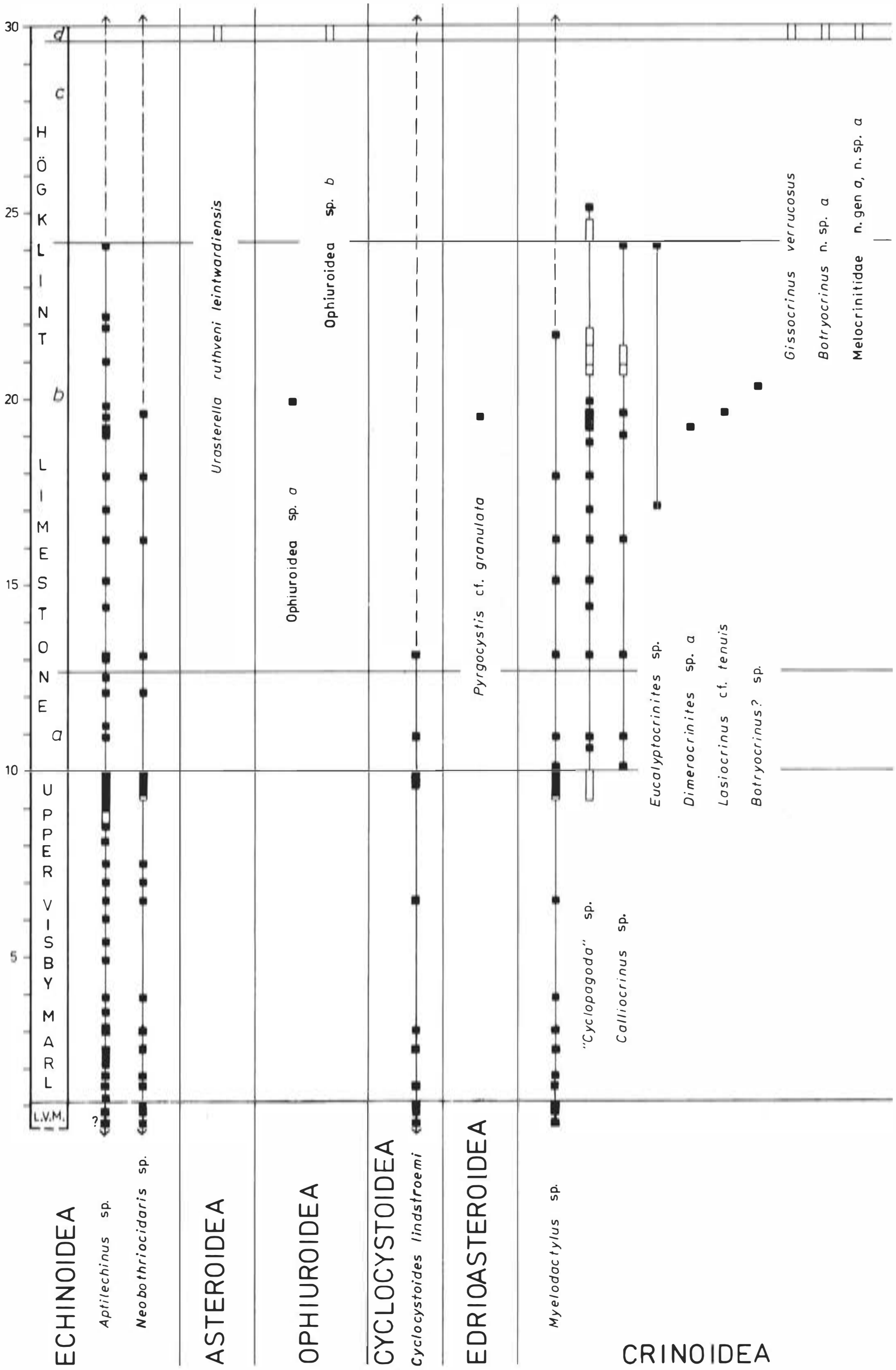
Literature relating to other echinoderm classes is even more sparse. Reference should be made on the following publications. Cystoidea: Angelin 1878; Regnéll 1945. Asteroidea: Spencer 1918 (a short note on *Urasterella* without illustration); Wienberg Rasmussen 1952. Echinoidea: Regnéll 1956. Cyclocystoidea: Regnéll 1945. Edrioasteroidea: Aurivillius 1892; Regnéll 1945.

Annotated faunal list

Crinoidea

Camerata (see Fig. 67).
Calliocrinus sp., *Eucalyptocrinites* n. sp. *a* (17.1 m), *E.* sp. (tegminal plate, 24.1 m), *Dimerocrinites* sp. *a* (complete crown), Melocrinitidae n. gen. *a*, n. sp. *a* (probably 39 specimens including complete crowns).

Inadunata
Myelodactylus convolutus Hall (13.1 m), *Myelodactylus* sp. (dissociated col-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d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
ECHINOIDEA
Aptilechinus sp.
Neobothriocidaris sp.
ASTEROIDEA
Urasterella ruthveni leintwardiensis
OPHIUROIDEA
Ophiuroidea sp. a
Ophiuroidea sp. b
CYCLOCYSTOIDEA
Cyclocystoides lindstroemi
EDRIOASTEROIDEA
Pyrgocystis cf. granulata
CRINOIDEA
Myelodactylus sp.
"Cyclopagoda" sp.
Calliocrinus sp.
Eucalyptocrinites sp.
Dimerocrinites sp. a
Lasiocrinus cf. tenuis
Botryocrinus? sp.
Gissocrinus verrucosus
Botryocrinus n. sp. a
Melocrinitidae n. gen a, n. sp. a

Fig. 67.

umnals), *Lasiocrinus* cf. *tenuis* (Bather) (4 calices), *Botryocrinus* n. sp. *a*, *B*.? sp., *Gissocrinus verrucosus* Bather (11 specimens), *Euspirocrinus spiralis* Angelin (Högklint *b*, exact level unknown), Crinoidea Inadunata sp. *a* (20.2–20.25 m).

Order indet.
Cyclopagoda sp. (columnals).

Edrioasteroidea

Pyrgocystis cf. *granulata* Aurivillius.

Cyclocystoidea

Cyclocystoides lindstroemi Regnéll.

Ophiuroidea

Ophiuroidea sp. *a* (one small disc), Ophiuroidea sp. *b* (Regnéll 1973, Fig. 4).

Asteroidea

Urasterella ruthveni leintwardinensis (Spencer) (Fig. 68A).

Echinoidea

Aptilechinus sp. (Fig. 68D–H), *Neobothriocidaris* sp. (Fig. 68B–C).

Holothuroidea

Sieve-plates (6 specimens) and hexaradiate wheels (2 specimens), all in the "*Pterygotus*" Beds.

An attempt was made to estimate the probable total number of crinoid species in various lithostratigraphical units, based on all available material from the section including dissociated columnals. According to these rough estimates the number of crinoid species is 9 in the Upper Visby Marl, 7 in Högklint *a*, 21 in Högklint *b*, 3 in Högklint *c*, and 6 in Högklint *d*. These figures are certainly not representative of the taxonomic diversity of the crinoid fauna in the section. In the Upper Visby Marl and in Högklint *a* the sampling is clearly inadequate in respect of columnals. Högklint *c* lacks marly intercalations and richly fossiliferous bedding planes which in other divisions have yielded the bulk of crinoid specimens.

Remarks

Although echinoderm remains occur everywhere through the Silurian sequence of Gotland, the difficulties in determining what genera or species or how many individuals they represent are almost insurmountable. Completely preserved echinoderms are extremely rare. On death their skeletons generally disintegrate rapidly through tissue decay. Although crinoid columnals are the echinoderm ossicles most frequently found, virtually nothing is known of their taxonomy. Attempts have been made in the Soviet Union and U.S.A. (e.g. Moore, Jeffords & Miller 1968; Moore & Jeffords 1968) to devise a classification and nomenclature based on isolated crinoid ossicles, but they have not yet gained widespread use outside the Soviet Union.

Crinoid taxonomy is based almost exclusively on morphology of the cup, the stem being known in only a few cases. Therefore, even though individual ossicles show distinct characters in size, articulation pattern, ornamentation or relative size and shape of the axial canal, it is not possible at present to assign them to species. Since columnal size and morphology frequently vary with position in the stem, figures in the annotated faunal list given for number of crinoid species are at best uncertain.

Dissociated crinoid columnals occur frequently in marl samples and on slabs from the Vattenfallet section, but it is quite obvious that the sampling has been inadequate. Intentions to erect a log and crinoid succession based on isolated columnals were abandoned as being unrealistic. There is no doubt, however, that crinoids formed a very important component of the benthic communities. One type of stem fragment (resembling the *Cyclopagoda* of Moore & Jeffords 1968, Pl. 10:1–2, 5–6) is so characteristic, that it has been included in the log. Generic affinity is not known.

Very few crinoid genera can be identified from dissociated ossicles alone. *Myelodactylus* is the only genus in the Vattenfallet section that can be identified with confidence on the basis of disarticulated columnals. *Calliocrinus* is recognized by its characteristic spines, normally attached to the calyx, while *Eucalyptocrinites* may be identified by the peculiar, elongated plates attached to the tegmen. The identification of the additional crinoid species mentioned in the faunal list is based primarily on morphology of calyx plates or brachials, and secondarily on characteristic columnals.

In Cyclocystoidea the stout submarginal plates are frequently preserved and easily identified (Regnéll 1945:216–219, Pl. 15:7–8, Textfigs. 28–29; Kesling 1966, Figs. 150:4–6, 151:3–4).

Echinoidea are represented only by dissociated plates and spines. However, the plates are so characteristic that there can be no doubt as to their generic affinity. *Aptilechinus* Kier (1973) is represented by ambulacral (Fig. 68D–F; cf. Kier 1973, Pl. 82:3, 5, Textfig. 1) and interambulacral plates (Fig. 68G–H; cf.

Kier 1973, Pls. 81, 83:1–2), the latter being found most frequently. *Neobothriocidaris* Paul (1967) is an Upper Ordovician echinoid not previously found in Silurian deposits. In the Vattenfallet material it is represented by poriferous plates (Fig. 68B–C; cf. Paul 1967, Textfigs. 2, 6). *Neobothriocidaris* plates are less common than those of *Aptilechinus*.

The Vattenfallet plates differ in surface ornament and details of morphology from the type species of *Aptilechinus* (= *A. caledonensis* Kier, 1973) and from *Neobothriocidaris* (=*N. peculiaris* and *N. minor* Paul, 1967) to such an extent, that they should probably be regarded as new species. This problem will be considered in a separate paper. In the log they are referred to as *Aptilechinus* sp. and *Neobothriocidaris* sp., respectively. Both were small species, at most 2.5 cm in diameter.

Echinoid spines are fairly common. They are small, longitudinally striated and slightly tapering towards the apex (Regnéll 1956, Pl. III:2). Both *Aptilechinus* (Kier 1973, Pl. 81–83) and *Neobothriocidaris* have spines of this type, making it impossible to refer the isolated specimens to a genus.

The *"Pterygotus"* Beds (Högklint *d*) are remarkable because of the fine preservation of the fossils; in some cases almost complete specimens are found, such as the starfish *Urasterella ruthveni leintwardinensis* (Fig. 68A; Spencer 1918:147), the ophiuroid figured by Regnéll (1973, Fig. 4; this specimen is unique among ophiuroids in having a small anal tube), and the crinoid *Gissocrinus verrucosus* (Bather 1893:172, Pl. 10:377–378; Franzén 1977, Fig. 6A). Several crowns of Melocrinitidae display arms and pinnules down to the finest detail.

The holothurian-type sclerites from the *"Pterygotus"* Beds are silicified, fairly poorly preserved and have been obtained from etched residues. Sieve-plates and wheels may also be present in ophiocistioids (Haude & Langenstrassen 1976). Although ophiocistioid teeth occur in younger strata on Gotland, they have not been found at Vattenfallet.

Ecological notes

Crinoids are mucociliary suspension feeders, adjusting their arms with the aboral side towards the current to form a filtration fan (Magnus 1963; Breimer 1969; Macurda & Meyer 1974; Breimer & Webster 1975). The tube feet bordering the ambulacral grooves produce mucus to entangle food particles which are then sent down the food-grooves towards the mouth by ciliary movements.

Palaeozoic crinoids were, with few exceptions, sessile, attached to the substrate by various types of holdfasts (Bather 1900: 106–107, 133–136; Ubaghs 1953: 720–722; Franzén 1977). In the Vattenfallet section, crinoid holdfasts have been obtained only from the *"Pterygotus"* Beds. In these beds wide-

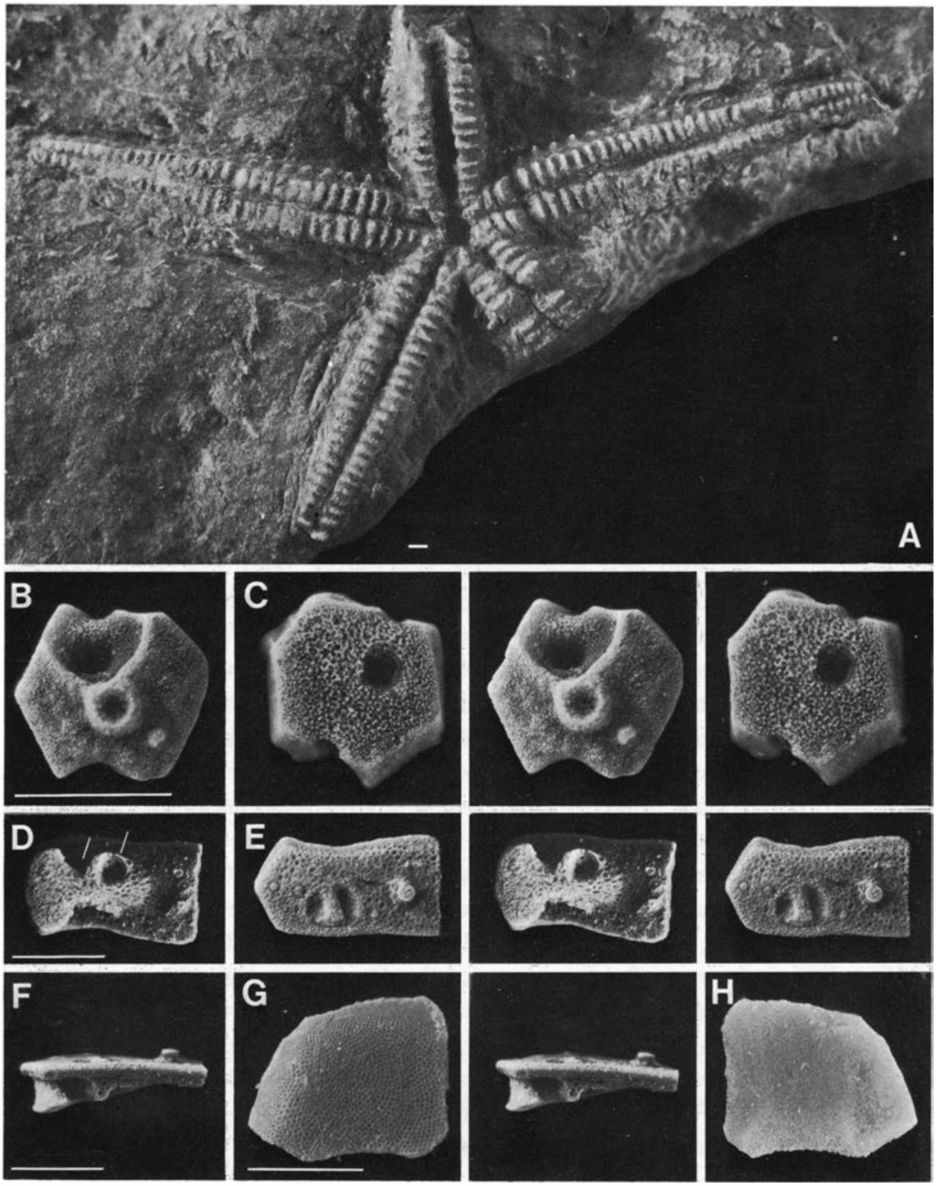

Fig. 68. A. *Urasterella ruthveni leintwardinensis*. Geological Museum, Dept. Invertebrate Palaeontology, University of Copenhagen. No. 231; ×2.5. B. Stereo pair of external side of poriferous plate of *Neobothriocidaris* sp. (cf. Paul 1967, textfig. 2); Vattenfallet, 9.5–9.6 m. Swedish Museum of Natural History (SMNH) Ec. 27616. C. Same specimen, internal view. D. Stereo pair of ambulacral plate of *Aptilechinus* sp., internal view. Thin white lines indicate position of pore openings (cf. Kier 1973, Pl. 82:4–5, textfig. 1); Vattenfallet, 9.2–10.0 m. SMNH Ec. 27615. E. Same specimen, external view (cf. Kier 1973, Pl. 82:3). F. Same specimen from oral side. G. Interambulacral plate of *Aptilechinus* sp. viewed from the coarse-meshed side of plate (cf. Kier 1973, Pl. 80:1–2); Vattenfallet, 6.5 m. SMNH Ec. 27613. H. Same specimen, viewed from fine-meshed side. Length of scale bars: 1 mm.

spread “roots” of branching radicular cirri occur, characteristic of soft substrates (Franzén 1977, Figs. 2E, 6A). At least some of them belong to *Gissocrinus verrucosus* Bather (Franzén 1977, Fig. 6A). Crinoids of the families Melocrinitidae and Botryocrinidae also occur in the *“Pterygotus”* Beds and were probably equipped with the same type of holdfasts. Fragments of cirri and dissociated cirrals have also been found at lower levels, but cannot be referred to individual genera or species because of their generalized appearance and lack of diagnostic features.

Some crinoids attach to hard objects, e.g., various shells, tabulate colonies or stromatoporoids, by cemented calcite discs (Franzén 1977, Fig. 2A). Attachment discs and other holdfasts occur in various Upper Visby and Högklint localities but, surprisingly, have not been found at Vattenfallet. There may be several reasons for this. One is simply that they have been missed due to inadequate sampling. The other is that the crinoids may have lived mainly in adjacent areas, particularly in association with reefs, where their holdfasts remained while their dissociated skeletons were deposited some distance away.

The physiological properties of the echinoderm skeleton, e.g., its porosity and lightness, permit transportation to some extent without particular abrasion of the individual ossicles. This makes it difficult to assess with certainty an allochtonous or autochtonous origin of the crinoid remains. Several genera, among them *Gissocrinus,* have been found only in fine-grained deposits while, e.g., *Calliocrinus* and *Eucalyptocrinites* on Gotland are known mainly from reefs and reef flank deposits. Remains of the latter two genera at Vattenfallet might indicate transport from the vicinity of nearby reefs.

Myelodactylus was probably eleutherozoic (Bather 1900: 146–147; Ehrenberg 1923). Columnals are not uncommon in the Vattenfallet material and have been obtained from fine-grained as well as coarse-grained deposits.

Very little is known of the ecology of the Cyclocystoidea. They were flat, disc-shaped animals, apparently without columns. They are generally classed as Pelmatozoa, which suggests an attached mode of life similar to that of edrioasteroids. However, some authors advocate a free-living mode of life (Nicols 1969: 109, Fig. 18C; Kesling 1966: U203).

Edrioasteroids were sessile suspension feeders using their tube feet for trapping plankton or organic particles from the surrounding sea water in a manner similar to that of the Crinoidea. Only one specimen has been found at Vattenfallet. Individuals of this genus probably lived anchored in soft mud or ooze (Regnéll 1966: U158).

Echinoids, ophiocistioids (?), holothurians (?), asteroids, and ophiuroids were all eleutherozoic epifaunal components of the Vattenfallet benthic communities. Echinoids were by far the most common (judged from the remains found). They were probably epifaunal browsers, scraping vegetable matter and attached organisms off vegetation and substrate with their jaws, or ingesting the topmost layer of the substrate for organic matter (Moore 1966: 77–78). In the Vattenfallet section they are common in the fine-grained sediments but fairly rare in coarse-grained material.

Ophiocistioids were free-living echinoderms probably feeding on detritus (Fell & Pawson 1966:10). It is doubtful, however, if this group is truly represented in the Vattenfallet material.

Recent holothurians have three food resources: plankton, detritus and the organic contents of mud and ooze which are collected with the tentacles or ingested while the animal is burrowing through the substrate (Pawson 1966: 65). These methods of feeding were probably also typical of fossil species. Very few holothurian remains have been found in the Vattenfallet material, and it has not been possible to assess how the animals lived.

Recent asteroids can be ciliary feeders, scavengers or facultative predators, but the majority studied are active predators (Feder & Møller Christensen 1966:96). Palaeozoic asteroids had developed all these types of feeding (Spencer & Wright 1966: U24–U25). *Urasterella* was probably a carnivore, preying on benthic organisms.

Some recent ophiuroids are plankton feeders which either lie buried in the mud with the tips of their arms extended into the water or attach to corals, sponges, etc. by two or three arms while waving the others through the water to trap plankton with their sticky tube feet. Some prey on organisms in or on the substrate while others climb corals and browse on the polyps. Most ophiuroids, however, appear to be scavengers, feeding on whatever organic matter they can find (Fell 1966: 132–134). Which of these modes of life is applicable to the Vattenfallet ophiuroids is not possible to decide.

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Conodonts

LENNART JEPPSSON

The history of conodont research on Gotland in the Hemse and younger beds has been outlined elsewhere (Jeppsson 1974). Very little has been done on faunas in the older beds. Fåhraeus (1969) described a small fauna from each of the Halla and Mulde Beds and two from the Klinteberg Beds. He also mentioned the presence of *Hindeodella sagitta* in the upper part of the Högklint Beds but gave no information on the locality. Bassett & Cocks (1974) reported conodonts from a block from the Högklint Beds about 450 m SW of Vattenfallet. I have previously (1969, 1974) published a few data on the distribution of conodonts in the Högklint, Tofta, Slite, Halla, and Mulde Beds.

Study of the conodont faunas in the beds below 20 m is based largely on a series of samples collected from the exposed part of the Vattenfallet section in 1970 and 1976. The levels of my samples were measured relative to index levels identifiable in the field. As the levels in the Liljevall collection are given in metres above sea-level, the levels of my samples were recalculated based on (1) the peg at 2.93 m above sea-level (samples below 7 m), (2) the contact between the Upper Visby and Högklint Beds at 10.02 m (samples G 70–20 to G 70–22), (3) the bentonite bed at 17.00 m (samples G 70–4 to G 70–9), (4) the reference level 21.97 m (samples G 70–1 to G 70–3). The error in the location of most of my samples relative to Liljevall's scale is probably less than ± 0.1 m. Two of my samples were collected at levels calculated to be slightly below 1.1 m which is the base of Liljevall's section. According to recently obtained data (see Introduction by Jaanusson, this volume) these samples are from the Lower Visby Marl.

For the interval between 20.0 and 29.6 m Liljevall's samples were used. Those from the *"Pterygotus"* Beds are from other old collections at the Riksmuseum and their exact level within Högklint *d* is not known. An attempt has been made here (Table 4) to relate these samples to the individual beds in Hedström's section (1904, see Jaanusson, this volume) but the result may not be correct in all details. One sample from the Riksmuseum (designated here as "Ptery 4") is most probably from some level within Högklint *c*. The sample lacks *Hindeodella sagitta*, and also the relative frequency of the other species does not conform with that of the conodonts in the *"Pterygotus"* Beds. In Table 4 the sample is tentatively placed adjacent to that at 25.6–25.8 m, but it is possible that it originates from another level.

The samples were processed as described by Jeppsson (1974). All fractions larger than 90 um were picked. All fragments with the basal cavity tip preserved were counted, but no others, irrespective of whether or not these were

sample numbers etc.	levels in metres a.s.l.	amount dissol-ved grams	number of ele-ments per kilogram	Ps. b.b	Pan. sp.	*H. excavata*						*L. excavata*						*H.* n.sp. aff. *confluens*					
						sp	oz	ne	hi	pl	tr	ne	hi	tr	grey.	wall.	cris.	sp	oz	ne	hi	pl	tr
l s.	? 29.83-29.98	500	48	•	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-
Dark ms.	? 29.75-29.83	500	10	•	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Herm.	? 29.69-29.75	930	23	•	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V. testudo	? 29.62-29.64	ca 2kg		•	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soft	? 29.60-29.62	385	5	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	28.0-28.4	475	208	1	5	1	2	1	3	4	2	-	X	-	1	-	-	-	-	2	1	2	1
	27.65-28.0	400	85	-	1	5	1	1	1	1	-	1	2	-	-	-	-	-	-	1	1	-	1
	26.28-26.37	500	10	-	1	-	-	-	1	1	-	-	1	-	-	-	X	-	-	-	-	-	-
"Ptery 4"	?	1200	163	-	46	7	9	14	13	15	2	2	11	3	4	4	4	2	2	1	6	1	2
	25.6-25.8	270	37	-	1	-	1	-	X	1	-	X	1	-	-	-	-	-	1	-	-	-	-
	24.60-24.70	145	83	-	1	-	-	-	1	X	-	1	2	-	-	1	-	-	-	-	-	1	-
	23.70	285	193	-	19	2	4	X	2	1	-	2	2	-	4	-	2	2	-	3	1	-	1
	22.90	195	190	-	14	1	-	X	3	2	1	-	3	-	1	1	-	1	2	1	2	-	-
	22.40-22.50	245	363	-	32	5	2	5	4	3	3	1	7	1	2	1	1	3	-	-	4	3	3
	20.40-21.40	180	278	-	19	2	-	-	1	-	-	1	2	X	4	-	-	2	1	X	4	3	1
	20.40	185	351	-	31	3	2	1	2	3	1	1	1	-	-	-	-	-	1	-	3	1	2
G70-1	19.87	500	256	-	70	2	2	1	5	4	2	1	3	1	-	2	2	1	2	1	1	2	1
	19.25			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G70-2	19.24-19.29	2500	574	-	864	47	44	39	51	32	19	5	20	4	14	4	5	10	7	9	18	10	7
G70-3	18.52-18.57	500	260	1	59	6	8	6	8	3	3	1	2	-	-	-	-	4	1	2	7	1	3
G70-4	17.45	500	266	-	87	5	3	-	6	3	1	1	1	-	1	1	1	2	-	-	-	2	-
G70-5	16.00-16.10	500	428	-	169	11	5	4	4	6	3	-	1	1	-	-	-	-	-	-	1	-	-
G70-6	15.33-15.41	2500	1007	-	1600	136	91	129	180	140	55	12	23	2	12	2	3	5	7	2	14	7	2
G70-7	14.38-14.48	500	476	1	136	25	9	13	11	11	2	1	4	-	5	-	2	-	1	-	1	-	-
G70-8	13.33	2500	508	-	812	70	43	45	68	58	17	6	15	3	11	1	4	5	4	3	5	5	-
G70-9	12.38-12.43	500	1166	1	453	7	13	9	21	19	6	5	8	2	6	2	2	2	2	-	3	1	-
G70-21	11.20-11.23	2500	133	3	105	40	34	21	47	28	17	3	9	2	3	2	2	3	-	1	-	-	-
G70-20	10.02-10.04	3670	82	20	155	7	5	5	13	1	3	11	24	6	8	10	5	1	-	-	-	-	-
G70-22	8.94	500	108	-	44	-	1	-	2	1	1	-	2	1	1	-	-	-	-	-	-	-	-
G70-19	6.49-6.54	500	70	-	29	-	1	-	1	-	1	-	-	1	1	1	-	-	-	-	-	-	-
G70-18	5.59	500	98	-	33	1	1	1	1	2	1	-	5	-	-	2	-	-	-	-	-	-	-
G70-17	4.26-4.33	500	90	-	38	-	1	-	-	1	1	1	-	-	1	-	1	-	-	-	-	-	-
G70-16	3.06-3.16	500	72	-	30	-	-	-	-	1	-	-	1	-	-	2	-	-	-	-	-	-	-
G76-8	2.58-2.62	2000	62	2	110	-	1	-	2	-	-	-	1	1	-	-	-	-	-	-	-	-	-
G70-15	1.86-1.96	1300	353	-	425	-	-	-	-	2	-	1	5	1	1	2	-	-	-	-	-	-	-
G76-7	1.73-1.78	2000	8	-	12	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
G70-14	0.99-1.06	840	201	-	139	4	2	1	1	2	-	-	-	1	1	1	-	-	-	-	-	-	-
G76-6	0.94-0.99	2000	25	-	31	1	2	X	1	1	X	-	1	1	-	2	-	-	-	-	-	-	-
				29	5576	389	287	296	452	346	141	57	158	31	81	42	34	44	32	26	72	41	24

TABLE 4. Number of specimens of each element in each sample. In the full reference to the sample numbers, they are to be followed by the initials LJ to separate them from other samples collected by others in 1970 from Gotland. Samples from the "*Pterygotus*" Beds were received with a short identifying description. The abbreviations used in the table are based on these and I have tentatively correlated them with Hedström's (1904) layers as follows.

Ligonodina sp. a				H. gulletensis						H. confluens						L. c.	H. sagitta rhenana						Ligonodina sp. b				ε	in-det.	total
ne	hi	tr	pl	sp	oz	ne	hi	pl	tr	sp	oz	ne	hi	pl	tr		sp	oz	ne	hi	pl	tr	hi	tr	pl	oz			
-	-	-	-	1	-	1	2	1	-	-	-	-	-	-	-	•	5	3	1	4	2	1	•	•	•	•	•	-	24
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1	-	1	-	1	1	•	•	•	•	•	-	5
-	X	-	1	-	-	-	-	-	-	-	2	-	X	1	-	•	6	3	-	1	2	-	•	•	•	•	•	1	21
2	4	2	2	-	-	-	-	-	-	-	2	-	2	1	4	•	13	5	1	8	5	2	2	1	2	1	3	-	63
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1	-	-	-	-	-	•	•	•	•	•	-	2
-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	•	13	13	11	17	17	1	•	•	•	•	•	-	99
-	-	-	-	1	-	-	-	-	-	1	-	-	1	-	-	•	6	1	1	3	4	-	•	•	S. c.	H. ramulif. sp	oz	-	34
-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	•	•	•	•	•	•	•	•	-	5
2	1	-	-	10	4	2	4	6	4	3	1	2	4	-	-	2	•	•	•	•	•	•	•	•	•	2	1	-	196
1	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	1	•	•	•	•	•	•	•	•	•	-	-	-	10
-	-	-	-	3	-	-	-	-	-	1	1	-	-	-	-	•	•	•	•	•	•	•	•	•	•	-	-	-	12
1	-	-	-	-	3	3	1	1	-														•	•	1	-	-	-	55
										6	6	2	9	2	4	3	45	25	15	33	31	5							
-	-	-	-	2	-	1	-	1	-														•	•	-	-	-	1	37
1	-	-	1	2	3	X	2	-	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	89
-	-	-	-	2	2	1	2	2	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	-	-	-	50
-	-	-	-	-	1	2	5	3	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	1	65
-	-	-	-	7	3	4	5	1	2	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	1	-	2	128
-	-	-	-	-	-	-	-	-	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	1	-	-	1
1	3	3	3	37	19	13	41	20	8	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	4	-	-	8	1369
-	-	-	-	3	1	3	2	3	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	-	-	1	130
-	-	-	-	6	3	3	2	3	2	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	133
-	-	1	-	1	2	1	1	2	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	214
2	8	3	1	11	12	5	16	17	3	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	16	1	1	-	2518
-	-	-	-	3	4	-	2	3	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	1	-	1	238
5	6	3	5	12	9	9	25	7	2	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	11	-	-	-	1269
1	-	2	-	4	-	1	2	3	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5	-	-	2	583
-	-	-	-	2	-	-	2	-	-	•	•	•	•	•											1	5	2	-	332
2	5	1	-	•	•	•	•	•	•	•	•	•	•	•	P. p. procerus sp	oz	ne	hi	pl	Gen. et sp. in-det.	D. kentuckyensis ne	hi	tr	oz/pl	2	9	2	7	302
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	1	-	-	54
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	35
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	1	-	-	-	-	1	49
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	-	-	-	-	-	-	-	-	45
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	1	1	-	-	-	36
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	2	3	2	-	-	-	-	124
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	11	4	-	-	-	-	-	2	1	-	2	1	1	-	459
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	-	-	-	-	-	-	1	1	-	-	15
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2	-	1	1	1	1	2	-	-	-	7	1	-	1	169
•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	-	-	-	-	-	-	-	1	-	6	-	-	2	50
18	27	15	13	108	66	49	114	74	25						14	4	1	1	1	2	2	4	6	3	60	24	7	28	9020

Soft=light-coloured soft shaly limestone=layer 2; *V. testudo=Valdaria testudo* bed=layer3; *Herm.=Herrmannina* bed=layer 5; Dark ms=dark grey mudstone=layer 6; ls=light-coloured limestone=layer 7. *Ps. b. b.=P. b. bicornis;* S. c.=other simple cones; *Pan* sp.=*Panderodus* spp.; *L. c.=L. confluens;* ε=“*H. confluens*” morphotype ε.

identified. In a few cases the presence of identifiable but uncounted specimens is marked with an x in Table 4. The sample from the *V. testudo* beds was originally processed at the Riksmuseum for the purpose of searching for agnathan scales.

Conodont zonation

Early Wenlockian conodonts were first described by Walliser (1962, 1964). His zonation has been used in most subsequent publications, but correlation with the standard chronostratigraphy has remained a matter of different opinions. Recent research on British conodont faunas (Aldridge 1972, 1975a, b) has clarified the earliest Wenlockian sequence, but the steady extension of the known ranges of various species makes it uncertain whether the zonal boundaries in use are everywhere synchronous. The publication by Barrick & Klapper (1976) was recieved too late to be used here.

In terms of conventional conodont zones, the beds at Vattenfallet below 2.0 m belong to the *Pterospathodus amorphognathoides* Zone, those above 27.6 m to the *Hindeodella sagitta* Zone, and most of the intervening beds to the *Kockelella patula* Zone. The evidence for the presence of the *P. amorphognathoides* Zone is the presence of *Pterospathodus pennatus procerus* and of several other named units, all of which are known only from this zone or older strata. *Kockella patula* itself has not been found in the Vattenfallet section, but the *K. patula* Zone is known to occur elsewhere between the *P. amorphognathoides* and *H. sagitta* Zones. The presence of the *H. sagitta* Zone is evident from the occurrence of *Hindeodella sagitta* in the section. However, *H. sagitta* has a narrow ecological range and it often occurs only where other conodonts are rare or absent (compare Table 4 and Walliser 1964, Table 2).

Aldridge (1975b:613) noted that at its type locality the Llandovery/Wenlock boundary is straddled by the *P. amorphognathoides* Zone. Conodonts indicating this zone "however, are absent from strata more than one metre above the boundary . . . This faunal change concurs with a lithological change from fine blue-grey mudstone to buff calcareous silstone. The disappearance of *P. amorphognathoides* and associated forms is thus directly or indirectly related to a change in facies, and the upper limits of these species in the Wenlock type area cannot be used as a guide in correlation". In Vattenfallet too, the presumed upper boundary of the zone is somewhat below a lithological change, namely from fine-grained calcilutites to a mixed calcarenitic-calcilutitic sequence, reflecting an increase in water energy (Jaanusson, this volume). In terms of depositional environment this change may be comparable to that in the type Wenlock area (Bassett *et al.* 1975). As discussed in the faunal list below the sp elements of *P. pennatus procerus* from Vattenfallet are of the kind which occur

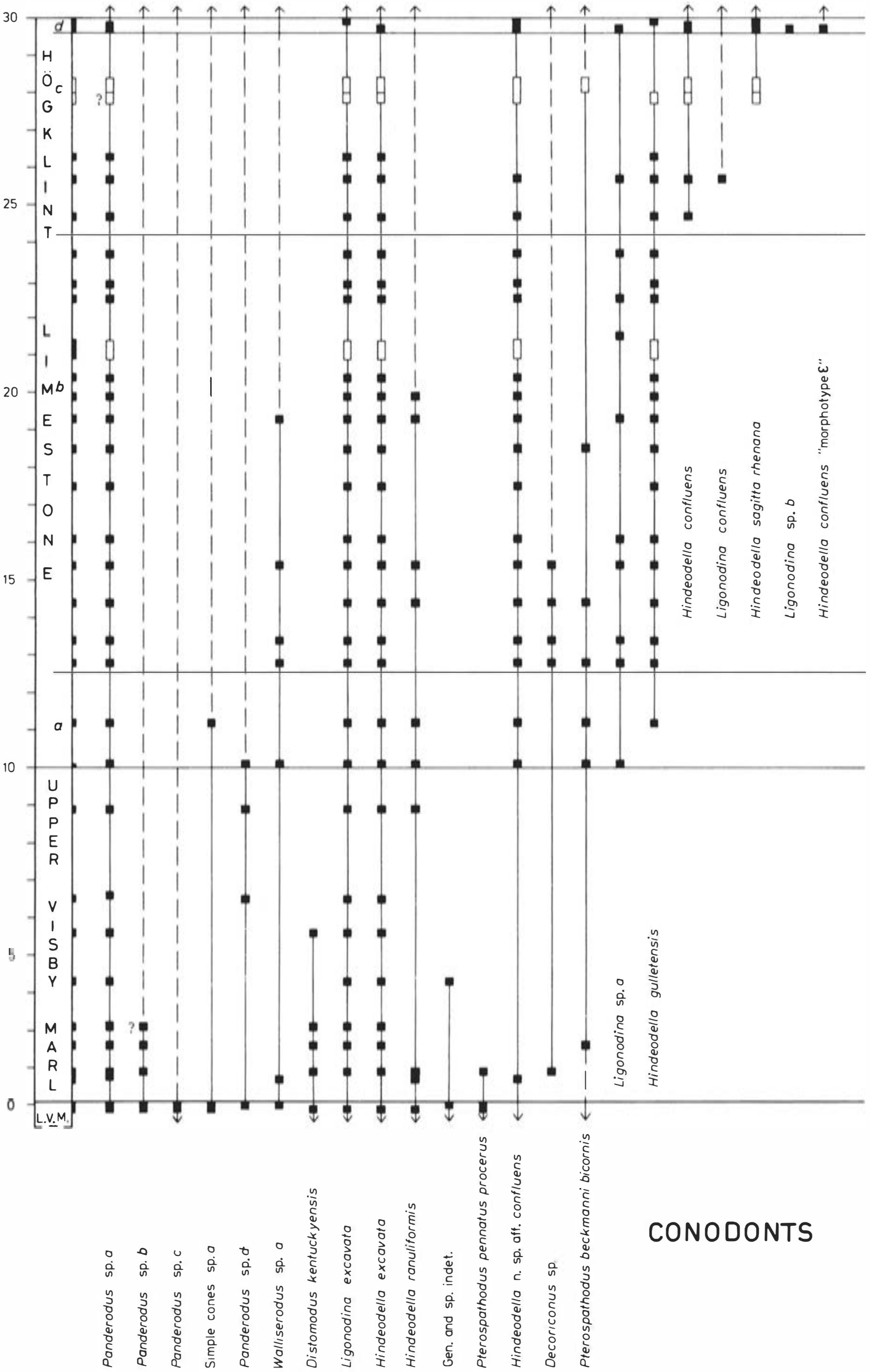
30
25
20
15
10
5
0
d
c
b
a
HÖGKLINT
LIMESTONE
UPPER VISBY MARL
L.V.M.
?
Panderodus sp. a
Panderodus sp. b
Panderodus sp. c
Simple cones sp. a
Panderodus sp. d
Walliserodus sp. a
Distomodus kentuckyensis
Ligonodina excavata
Hindeodella excavata
Hindeodella ranuliformis
Gen. and sp. indet.
Pterospathodus pennatus procerus
Hindeodella n. sp. aff. confluens
Decoriconus sp.
Pterospathodus beckmanni bicornis
Ligonodina sp. a
Hindeodella gulletensis
Hindeodella confluens
Ligonodina confluens
Hindeodella sagitta rhenana
Ligonodina sp. b
Hindeodella confluens "morphotype ε"
CONODONTS

Fig. 69.

close to the Llandovery-Wenlock boundary. Recently there has been general agreement that the Upper Visby Marl is earliest Wenlockian in age (Martinsson 1967:359: Bassett & Cocks 1974, Fig 1; Laufeld & Jeppsson 1976, Fig. 4). The conodont evidence thus supports this dating.

The sample identified by Aldridge from the Högklint Beds south of Vattenfallet also contained *M. riccartonensis* Zone graptolites (Bassett & Cocks 1974). No information was originally given as to the possible level of the block within the Högklint Beds, but it is from the railroad section that Hede (1940:24) listed as exposing Högklint *b* (M.G. Bassett, personal communication). The sample evidently lacks *Hindeodella sagitta* (only *"Hindeodella priscilla"* could possibly refer to that taxon), contains *Panderodus,* a rather high frequency of *Hindeolla excavata* (four of the six elements were identified), and *Decoriconus (Drepanodus aduncus).* The sample may also contain *Hindeodella* n. sp. aff. *confluens* and *H. gulletensis* (judging from some of the names listed) whereas *Ligonodina excavata* seems to be missing. The fauna is closest to that from the lower part of Högklint *b* (cf. Laufeld & Jeppsson 1976, Fig. 4).

Aldridge (1975b) reported Walliser's (1964, Pl. 22:8) *Spathognathodus* n. sp. from the Barr Limestone, which correlates approximately with the graptolite zone of *Monograptus riccartonensis.* This species was named *Spathognathodus walliseri* by Helfrich (1975; compare also with *S. corpulentus* Viira, 1975) who described it as a descendent of *S. ranuliformis. Spathognathodus* is a junior subjective synonym of *Hindeodella.* If this taxon is part of a lineage in which *Hindeodella ranuliformis* is an older segment (that is, the taxon is not an offshoot of *H. ranuliformis* which occurs contemporaneously with younger representatives of this species), then the occurrence of *H. ranuliformis* as high as 19.87 m in the Vattenfallet section may indicate that the top of the *M. riccartonensis* Zone is above that level (cf. Laufeld & Jeppsson 1976, Fig. 4).

Frequency-distribution of conodonts

Fig. 70 illustrates variations in both the absolute and relative frequencies of conodonts in the Vattenfallet samples. The relative frequency curves are expressed for each species as percentages of the total number of extracted elements, while the absolute frequencies are plots of the numbers of conodont elements per kilogram of rock (see also Table 4). Both curves are based on numbers of discrete elements rather than estimated numbers of individuals, since there is still some uncertainty in the number of elements per individual, and I consider that diagrams based on such estimates would give a less reliable picture. For some samples in which the number of elements extracted is too small to give even a broad picture of frequencies, data have been combined and plotted at a level in the middle of the combined interval; in Fig. 70 the horizontal lines indicate the centrally plotted line for each sample or combined samples. Some curves showing minimal variations have been exaggerated for clarity (amount of exaggeration shown as 5×, 25×, etc.), but in each of these cases the standard curve is also drawn to facilitate easy comparison with all other samples. Because of lack of space the discussion of these curves and their ecologic significance has had to be cut out.

Annotated faunal list and descriptions of species

Pseudoneotodus beckmanni bicornis Drygant, 1974

Drygant (1974) described this taxon from the Kitaigorod Formation of Podolia, most of which is of early Wenlockian age (Laufeld 1971). I have earlier (1974) noted that a population from the Slite Marl differs from Ludlovian specimens of the genus. The collections from Vattenfallet are older than those from the Slite, and the differences are still more pronounced. In these collections there are specimens with two well developed tips but there is a gradation between them and forms with only one tip. Drygant's collections also contained both one- and two-tipped specimens, which he described as belonging to two separate species but in the discussion he indicated that they might be conspecific. Thus, either there are two separate lineages, one with two-tipped elements which died out early and another with one-tipped elements, which continued into the Emsian (for the distribution in time of the latter taxon, see Link & Druce 1972), or there is one single lineage in which evolution led to a decrease in variation in the elements. The gradual change between the collection from Vattenfallet, the Slite Marl and the late Ludlovian indicate that there is one lineage only and that both one- and two-tipped elements occurred within the same population. The differences between early Silurian and younger populations are, however, so great that these should be described as different subspecies. The name *P. bicornis* was based on a specimen of the older subspecies. This subspecies is regarded here as consisting of those populations which include individuals with two-tipped elements. At present, it is unclear whether each individual had a series of elements ranging from one-tipped to typical two-tipped forms, or if this variation indicates variation between individuals. Four specimens in Drygant's collections have three tips, and these were described as *P. tricornis*. Such specimens are probably only the end members of the variation series in the elements of *P. b. bicornis*.

P. beckmanni had a fairly narrow ecological range as is evident from its scattered distribution. At Vattenfallet it was found in only seven samples but this is probably due, at least in part, to its low frequency. It is most common in sample G 70–20 (10.02–10.04 m). *Hindeodella ranuliformis* is similarly distributed in the section.

Panderodus spp.

Panderodus sp. *a* dominates throughout the section. Three additional species are confined to the lower part of the section (entered in the log, Fig. 69, as *P.* sp. *b, P.* sp. *c* and *P.* sp. *d*). *P.* sp. indet. has been recorded from 27.65–28.0 and 29.75–29.83 m. There is considerable ontogenetic variation in *Panderodus* sp. *a* at Vattenfallet, with the

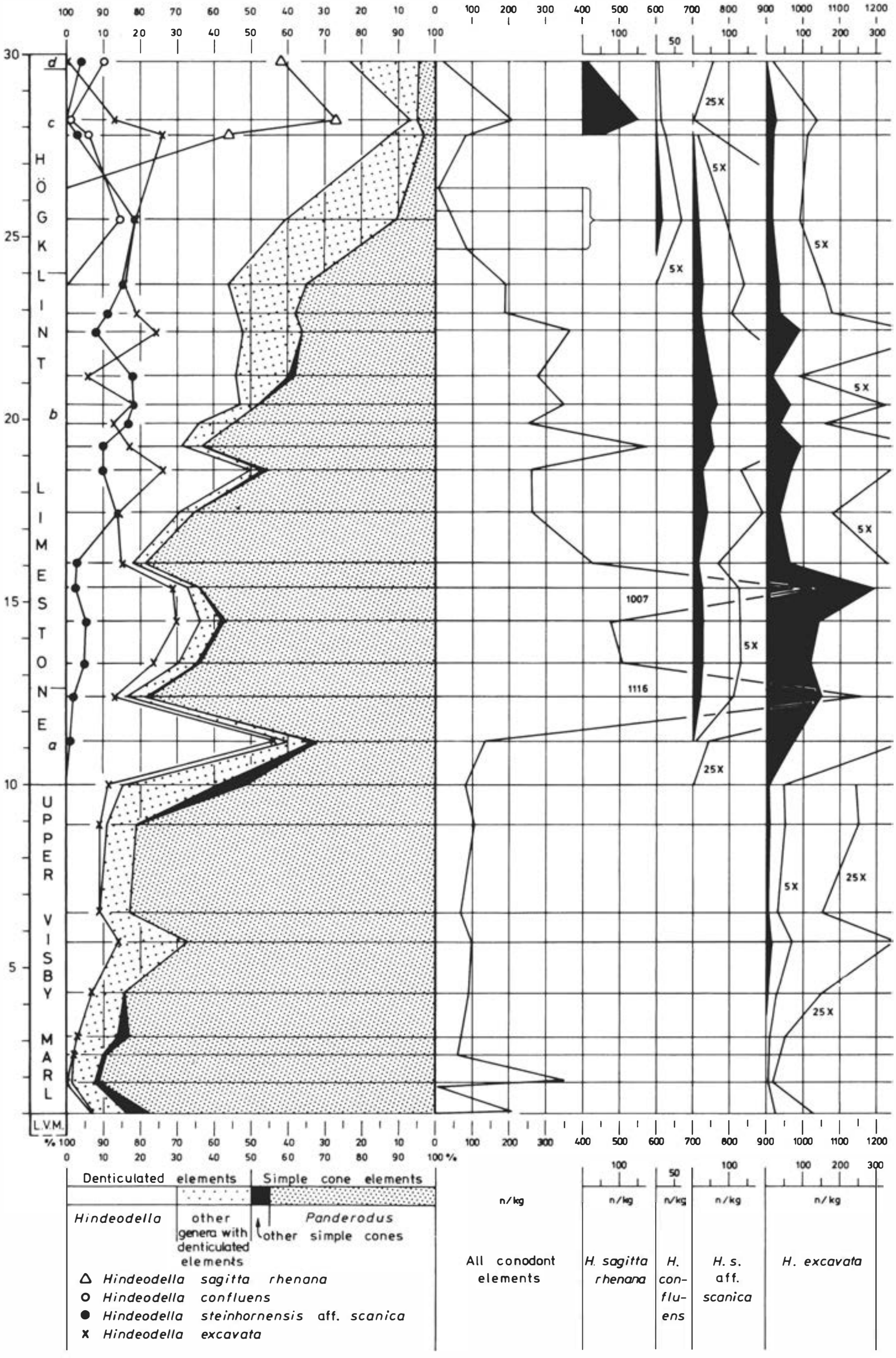

Fig. 70. Absolute and relative frequency curves for conodont species in the Vattenfallet section. See text for full explanation.

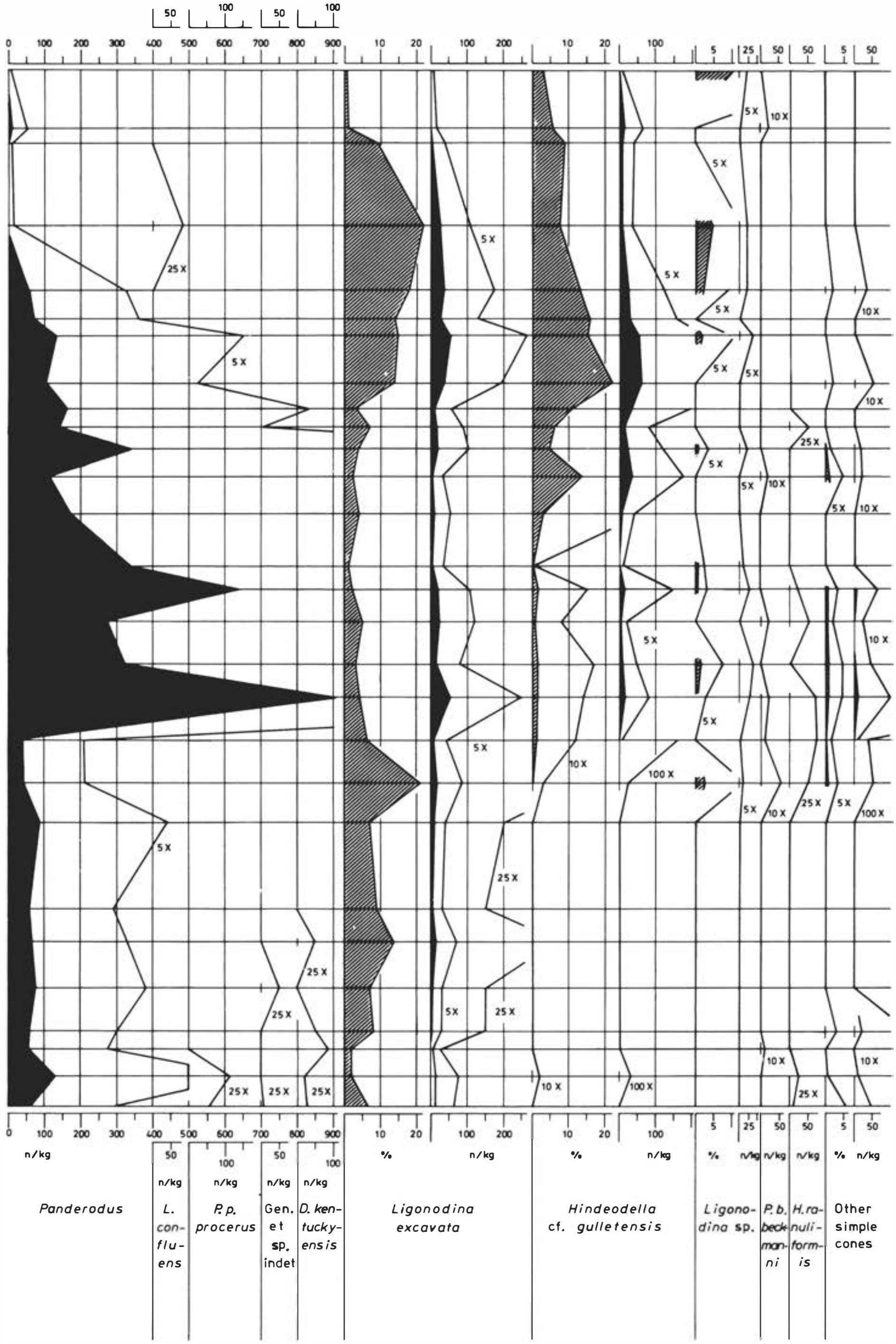

Fig. 70 continued.

largest specimens occurring in samples G 70–19 to G 70–21 inclusive (i.e. uppermost Visby Marl and Högklint *a*). These four samples also demonstrate the maximum range in size, but in most other samples large specimens are not present.

Other simple cones

In addition to the elements of *Panderodus*, a few juvenile specimens of other simple cones have been found, 30 of which belong to a single species of *Walliserodus*. Associated with these occur 15 elements of the kind which Cooper (1975) referred to *Decoriconus*. Aldridge (1975:613) reported an apparatus which may well belong to the same species from the earliest Wenlockian Buildwas Formation. However, the nomenclature of the species is currently unclear, and my specimens are too few to contribute to a better understanding. A few other simple cone elements which may belong to one or more other genera also occur at Vattenfallet.

Distomodus kentuckyensis Branson & Branson, 1947 *sensu* Klapper & Murphy, 1974 (1975)

Fig. 71:15–17

One reconstruction of the apparatus of this species was published by Klapper & Murphy (1974) and another by Cooper (1975). There is little agreement between their synonomy lists, although there is better agreement on the overall appearance of the apparatus. The most important difference is that elements of the kind that Klapper & Murphy included in their reconstruction, according to Cooper occur in several different species together with different platform elements, while no platform was included by Klapper & Murphy. Cooper's reconstructions lead to the closely similar platforms identified previously as *Icriodina* and *Icriodella* being included in apparatuses which differ markedly in their composition and in the appearance of the other elements, while the "non platform elements" of *Distomodus* are indistinguishable from those of other apparatuses that contain very different platforms. *D. dubius,* which is closely related to *D. kentuckyensis,* lacks a platform (for numerical data see Jeppsson 1974, Table 1; about the same number of specimens are now available from Gotland, and none of the platform elements found is associated with them). I therefore regard the reconstruction by Klapper & Murphy as the most probable one, since it is comparable with that of the apparatus of the younger species.

The basal part of the white matter in those elements which undoubtedly belong to *D. kentuckyensis* (as the name is used here) is identical to that described for *D. dubius* (see Jeppsson 1972:56, 1974, Pl. 1:4 A) and this is probably a detail common for all species of the genus.

The most obvious difference between *D. kentuckyensis* and *D. dubius* is that at least some elements of the former have much better developed processes and denticles. In the Vattenfallet collection this is true of the tr and oz-pl elements (symbols for elements are those used for *D. dubius* by Jeppsson 1974) and the denticles are generally coarser than those of *D. dubius*. My collections are not yet large enough to determine whether *D. kentuckyensis* evolved into *D. dubius,* or whether the two species overlap for any length of time.

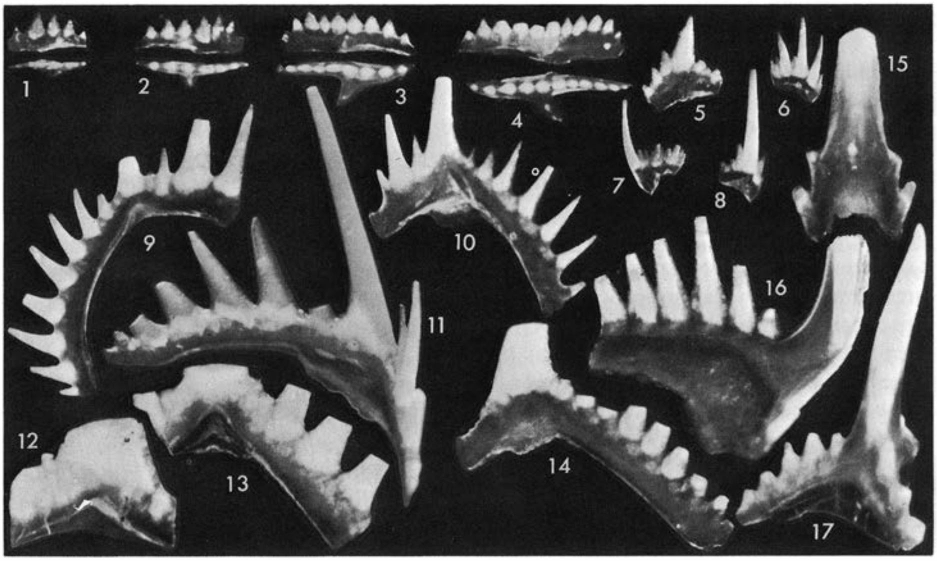

Fig. 71. All specimens are ×40. Photograph Sven Stridsberg.

1–8. *Pterospathodus pennatus procerus.* 1–5 sample G 70–15 (1.86–1.96 m, Upper Visby Marl) and 6–8 from sample G 70–14 (0.99–1.06 m, Lower Visby Marl). 1. An about 0.26 mm long sp element in lateral and oral view. LO 5102t. 2. An about 0.36 mm long sp element in lateral and oral view. LO 5103t. 3. An about 0.44 mm long sp element in lateral and oral view. LO 5104t. 4. An about 0.55 mm long sp element in lateral and oral view. LO 5105t. 5. A small oz element in inner lateral view. LO 5106t. 6. A small ne element in inner lateral view. LO 5107t. 7. A small hi element in inner lateral view. LO 5108t. Note the two extra basal cavity tips beneath the two largest denticles. 8. A small pl element in lateral view. LO 5109t. Note the extra basal cavity tip beneath the large denticle on the anterior process.

9–14. *Ligonodina* sp. *a*. 9. A pl element in inner lateral view. LO 5110t. Sample G 70–6 (15.33–15.41 m, Högklint *b*). 10. Inner lateral view. LO 5111t. Sample G 70–6 (15.33–15.41 m, Högklint *b*). The specimen is probably an ne element. 11. A large hi element in inner lateral view. LO 5112t. Sample G 70–8 (13.33 m, Högklint *b*). 12. Ne element in inner lateral view. L0 5113t. Sample G 70–20 (10.02–10.04 m, basal Högklint *a*). 13. A tr element in posterior view. L0 5114t. Sample G 70–20 (10.02–10.04 m, basal Högklint *a*). 14. Medium-sized ne element in inner lateral view. RM Co 11. Sample "Ptery" 4.

15–17. *Distomodus kentuckyensis.* 15. A large tr element in posterior view. LO 5115t. Sample G 70–15 (1.86–1.96 m, Upper Visby Marl). 16. A large hi element in inner lateral view. LO 5116t. Sample G 70–15 (1.86–1.96 m, Upper Visby Marl). 17. A Large oz-pl element in oblique antero-oral view. LO 5117t. Sample G 70–16 (3.06–3.16 m, Upper Visby Marl).

Pterospathodus pennatus procerus (Walliser, 1964)
Fig. 71:1–8

Pterospathodus pennatus procerus was originally described as a species of *Spathognathodus*. Nicoll & Rexroad (1968) transferred it to *Neospathognathodus* and it was placed in *Llandoverygnathus* by Aldridge (1975b). Several authors have agreed on the close relationship between this species and *Pterospathodus amorphognathoides* described by Walliser (1964), and Klapper & Murphy (1974) regarded *Llandoverygnathus* as a junior synonym of *Pterospathodus*.

According to Klapper & Murphy *Pterospathodus* includes three species with the same morphological limits that Walliser (1964) proposed for the three species which he typified with sp elements from this genus, viz. *P. celloni* (Walliser, 1964), *P. pennatus* (Walliser, 1964) and *P. amorphognathoides* Walliser, 1964. At that time only sp elements were included, while the other elements were treated as several distinct species of other genera: *Ozarkodina adiutricis, O. gaertneri, Carniodus carnus, C. carnulus, C. carnicus, C. eocarnicus, ?C. carinthiacus, Neoprioniodus subcarnus,* and *Roundya latialata*. It is also probable that *R. brevialata* and *N. costatus* include elements of *Pterospathodus*.

Current limits of the species of *Pterospathodus* are based mainly on the number and arrangement of the lateral processes on the sp element. *P. amorphognathoides* includes specimens with sp elements in which the lateral process branches into two at its first (or second) denticle. The posterolateral branch is much shorter than the other one. *P. pennatus procerus* includes specimens with sp elements lacking this short branch. However, the variation described in the number and arrangement of the lateral processes (Walliser 1964; Nicoll & Rexroad 1968) shows that this character varies within a population, and there is still a need for revision within this group.

The sp elements from Vattenfallet are closest to those figured by Walliser 1964, Pl. 15:4, 7, 8 from the uppermost part of the *P. amorphognathoides* Zone. Jaeger & Schönlaub (1970) showed that graptolites from the lowermost strata of this Zone indicate that it cannot be older than latest Llandoverian. Another specimen of this kind was figured by Aldridge (1972, Pl. 3:16) from latest Llandoverian (C_6) beds, and the Vattenfallet material now indicates that this type of sp elements has been found very close to the Llandoverian/Wenlockian boundary in all three areas (cf. Laufeld & Jeppsson 1976, Fig. 4).

Description. – Only those specimens found at Vattenfallet are described here and other collections supporting the present reconstruction will be described separately elsewhere.

The sp element. Apart from the specimen in Fig. 71:4 my specimens are smaller than those figured by Walliser (1964, Pl. 15:2–8), and the largest is only slightly larger than Walliser's smallest figured specimen. The difference in denticulation probably depends on the size difference. The ontogeny of the lateral process can be followed in the figured specimens. The smallest has an asymmetrical basal cavity but no lateral process, and the second smallest has a thin ridge from the basal cavity lip up to a ledge on the side of the element, where the ledge is drawn out into a tip. In the second largest figured specimen there is also a thin ledge on the inner side. Both ledges are poorly developed anteriorly of the basal cavity-centre and one is drawn out into a triangular tip, the anterior margin of which is directed slightly anteriorly and the posterior margin is directed obliquely anteriorly. The basal cavity has a similar shape and is connected with the ledge, but there is a constriction between them, so that their edges are distinct except at the tip of the triangular part. Orally there is a thin ridge running out to the tip of this triangular area, where there is a low denticle lacking white matter. The largest figured specimen is similar but the lateral process carries two denticles, the inner one of which has white matter. This stage is critical in the development of the lateral process. The aboral surface shows that it remained unbranched throughout growth.

The oz element. In agreement with the sp elements the studied specimens are small. The anterior process is curved inwards. The denticles are compressed, with sharp edges. There is a thin ledge on the inner side of the posterior process at the level of the denticle "roots" in the largest specimens. There is also a ledge on the outer side of both processes. The basal cavity is expanded below the cusp and the central part of the posterior process, but not below the anterior one. As in the sp elements no extra basal cavity tips have been seen. The cross section of the cusp of the largest specimens is triangular, the anterior and posterior edges forming two sharp corners. The third corner is at the outer surface, and is very blunt. Basally this forms an extra, antero-laterally directed and very short branch of the basal cavity. In most characters these specimens agree with those included in "*Neoprioniodus costatus*". Most elements included under this name lack the character expected of ne elements, but they can easily be compared with the three-branched oz elements found in many genera of Prioniodontacea. In these genera the outer antero-lateral process is very short and the weakly developed process found in the oz element of *P. p. procerus* may be a rudiment of it.

The ne element. One specimen has been found which may belong here. It is an evenly arched and slightly bowed structure with the denticles curved slightly inwards. The cusp cannot be distinguished from the large denticles as these have their own basal cavity tips. For further discussion see below.

The hi element. Only one specimen has been found. Originally, elements of this kind belonging to *Pterospathodus* were identified as *Neoprioniodus subcarnus,* but they lack the characters of ne elements. A comparison with *Amorphognathus* shows that they are actually hi elements. In my specimen the posterior process is formed by two larger denticles with their own basal cavity tips, interspaced with slightly smaller denticles. The inner lateral edge is very prominent on the cusp as is usual in hi elements. Basally it is slightly serrated, but no true denticles are formed.

The pl element. One specimen probably belongs here. The following definitions are used in its description: anterior-posterior is defined as the direction between the edges of the cusp; and the figured side is outer. The posterolateral process is directed slightly outwards with the posterior edge of the cusp continuing inside it below its denticles, which are curved slightly inwards. The innermost denticle of the anterior process has its own basal cavity tip and is directed slightly outwards. The basal cavity is conical and expanded both inwards and outwards below the whole unit.

The tr element. No specimen was found. Its general appearance should be that of those included in *Roundya latialata*.

Origin and comparison. – Many details as described above relate *Pterospathodus* to *Prioniodus* and its relatives, many of which were included in the superfamily Prioniodontacea by Lindström (1970).

A comparison with *Amorphognathus* shows that the sp elements have a simpler but basically similar construction. Lindström (1964:91) discussed this constructional pattern, and the sp element of *Pterospathodus* can easily be compared with his Fig. 33E. Characteristically for this pattern the outer lateral process begins at the cusp, in contrast to the inner process which is connected to a denticle on the posterior process. This offset of the inner and outer lateral processes has also been found in *Pterospathodus* (see, e.g., the description of *P. amorphognathoides* in Nicoll & Rexroad 1968:56 and their Pl. 40:5). In the sp element of *Amorphognathus* (see Lindström 1964, Fig. 33E) the inner antero-lateral branch is longer than the postero-lateral one. This is true also of *Pterospathodus,* in which genus the latter branch is sometimes absent, as mentioned earlier. The curvature of the posterior process is also similar, as are many other details. The sp elements of *Amorphognathus* are not mirror-images of each other. Consistent differences in relative size and directions of the processes and in the denticulation are not known, but should be looked for in the sp elements of *Pterospathodus*.

Similarities in the oz element are discussed above.

The ne element in *Amorphognathus* is very different from that of those other Prioniodontacea in which it has been identified (see Bergström 1971). The element of *Pterospathodus*, for which the name ?*C. carinthiacus* has been used, has long remained enigmatic. Many other elements of *Pterospathodus* have fewer "extra" processes than the corresponding elements in *Amorphognathus*, and it is reasonable to expect that this is also true of the ne element. With this in mind, it can be compared with, e.g., the ne element of *Amorphognathus tvaerensis* Bergström, 1962 *sensu* Bergström 1971 (figured in Bergström 1962, Pl. 1:1–5).

The hi element is closely similar to those of several genera of the *Prioniodus* group. The directions of the processes, the alternating denticulation of the posterior process, the separate basal cavity tips in the large denticles, and many other details are all alike.

The pl element is usually tetraprioniodiform in Prioniodontacea. The element tentatively identified as the pl element of *Pterospathodus* cannot yet be compared with these but the strange "symmetry" of it could indicate that it may be derived from an element with more processes.

The tr elements of *Pterospathodus* were previously identified as *Roundya*, and like the hi element they are closely similar to those of other Prioniodontacea.

The identification of the complete apparatus of *Pterospathodus* thus indicates the relationships with other genera, and like the "*Icrio* group" and *Distomodus* it turns out to be a post-Ordovician representative of the Prioniodontacea. Of the many genera included in that taxon, *Amorphognathus* is the only one known to have an ne element which can be compared with that tentatively identified in *Pterospathodus*. This character and the others discussed above indicate that *Pterospathodus* is probably a Silurian representative of the family Balognathidae.

Ligonodina excavata (Branson & Mehl, 1933) *sensu* Jeppsson, 1972

The apparatus of this species has been described previously (Jeppsson 1972). Large collections are now available, and it is clear that the overall appearance of the elements varies greatly. Parts of this variation are ontogenetic as, for example, in the basal cavity which is especially large in large walliseriform and cristagalliform elements, but is less conspicuous in small specimens. With age, the processes grew considerably in thickness (producing the large basal cavity), so that the original direction, curvature and twisting of the processes and denticles were obliterated.

Another fairly variable character is the direction of the processes. For example, the short anterior process of the hi element can be directed or curved inwards, or inwards and more or less downwards. And finally there is another, as yet uninterpreted variation, which also occurs in *L. elegans* (see Walliser 1964, Pls. 30:34, 36; Jeppsson 1974:22, Pl. 3:13–15). In both species the process of one of the oz-pl elements can originate differently at the cusp. In *L. elegans* the two processes of the detortiform element originate close to one another on the anterior side of the compressed cusp, and the base of the cusp is expanded strongly posteriorly in some specimens in the same way as in the tr element (Walliser 1964, Pl. 30:36; Jeppsson 1974, Pl. 3:12). In other specimens the processes originate on opposite sides of the cusp and are strongly arched and bowed (Walliser 1964, Pl. 30:34; Jeppsson 1974, Pl. 3:13). The third type of specimen differs from the second in that the processes are much less arched and bowed (Jeppsson 1974, Pl. 3:15). No intermediate specimens have been found. In *L. excavata* this variation is found in the walliseriform element. Typical walliseriform elements correspond to the first variety of the detortiform element in *L. elegans* (the processes in all the elements of *L. excavata* are less strongly curved than the corresponding ones in

L. elegans), while other specimens are greilingiform (derived from *Lonchodina greilingi;* this name had been used on different elements from different species). The alternative explanation that two species are present, the other element of which are indistinguishable, does not seem probable, particularly since the same phenomenon is found in *L. elegans* where it lacks taxonomic significance.

The apparatus of *L. excavata* resembles that of *Oulodus oregonia* (Branson, Mehl & Branson) as reconstructed by Sweet & Schönlaub (1975) to such an extent that they may well be congeneric. The oldest generic name is *Ligonodina*.

Ligonodina confluens Jeppsson, 1972

A single specimen occurs in the sample at 25.6–25.8 m. Had this been the only one in beds of early Wenlockian age, the presence of the species there would have remained doubtful as it might have originated in contamination, but there are also two more specimens in the "Ptery 4" sample. The two samples compare further in the presence of *Hindeodella gulletensis* and *H.* n. sp. aff. *confluens,* and the absence of *H. sagitta,* and the two are therefore probably of about the same age. The three specimens (and a few fragments) are poorly preserved, and it is not possible to determine whether the early Wenlockian population varies from those in the late Ludlovian.

Ligonodina sp. *a*

Fig. 71:9–14

The following details, among others, are common for two or more elements. The cusp and the relatively few, robust denticles are not fused even in mature elements. Basally the denticles are strongly compressed, and even at the tip some of them lack the circular cross section usually found in elements of *Ligonodina.* Even the cusps are strongly compressed. The ontogeny of the elements is still poorly known, and some juvenile specimens included may not belong here. However, the construction of the denticles, cusps and other details is so closely similar in the different elements, when mature, that an apparatus with the appearance described below and illustrated in Fig. 71:9–14, fairly certainly exists. This apparatus probably also included an oz element.

Description and comparison.—The elements are similar to those of *Hindeodella confluens* and *H.* n. sp. aff. *confluens* in their general construction. The preliminary description below emphasizes the differences from *H.* n. sp. aff. *confluens* in order to facilitate their separation. The descriptions are based on mediumsized and large, characteristic specimens. The denticles have a very broad base and rapidly taper distally, so that in lateral view especially the anterior side is basally concave.

The ne element. The cusp is very broad and strongly compressed (cf. the ne element of *Distomodus*). The short process is longer than in *H.* n. sp. aff. *confluens* and has a couple of denticles on some specimens. The long process carries denticles that are about twice as broad as those of *H.* n. sp. aff. *confluens.* They are also directed more perpendicular to the process and not fused to one another.

The hi element. In many specimens the cusp is very broad, like that in *H.* n. sp. aff. *confluens,* but in one specimen from the *V. testudo* bed it has a rounded cross section a short distance above the processes. The posterior process is arched and bowed similar to that of *H. gulletensis.* It is also twisted, so that the denticles are directed obliquely outwards in relation to the plane of the cusp. The angle between the processes is rather variable, but is larger than in the hi element of *H.* n. sp. aff. *confluens.* The anterior lateral process is longer than in the latter species. The best identifying characters are the unfused denticles and the relation between the cusp and posterior process.

The pl element. The cusp is broad, sharply edged basally, and twisted in such a way that distally the anterior edge is directed obliquely inwards. The posterior process is short and perpendicular to the cusp as in *H. confluens*. It often has only two or three denticles, the second of which is usually the largest. The anterior process is long, slightly bowed, and arched. Its denticulation is similar to that of the long process of the ne element. Some specimens included here may actually be the unidentified oz element. The best preserved of them are more evenly bowed, and both processes are short.

The tr element. The cusp is not compressed but has a more triangular cross section with a posterior corner. The inner basal cavity lip forms a very high and narrow fold which is elongated in a posterior direction. The processes are nearly straight.

Hindeodella excavata (Branson & Mehl, 1933) *sensu* Jeppsson 1969

Recent discussions of this species are given by Jeppsson (1974:14–15, 25–31) and Klapper & Murphy (1974:33–37).

The pre-Wenlockian part of this lineage remained poorly known for some time. The species does not appear in the Carnic Alps until the Wenlockian *K. patula* Zone (Walliser 1964) but Aldridge (1975b) extended its known distribution down to the base of the Fronian (Upper Llandovery) and questionably into the Idwian. Thus the presence of *H. excavata* throughout the Vattenfallet section is not unexpected. Like *H. confluens, H. steinhornensis* and *L. excavata* it is a late immigrant into the Cellon area of the Carnic Alps.

The specimens from Vattenfallet are slightly different from younger forms, particularly the hi element which differs in having a large variation in curvature and direction of the anterior process (cf. Barrick & Klapper 1976).

Hindeodella confluens Branson & Mehl, 1933, *sensu* Jeppsson 1969.

Considerable information has been published on this species (e.g. Jeppsson 1969, 1972, 1974, 1975, 1976; Klapper & Murphy 1974; Helfrich 1975) and *H. confluens* is now one of the most studied Silurian conodont species.

The reconstruction of the apparatus of *H.* n. sp. aff. *confluens* shows that there are currently also some problems in separating the elements of early specimens of *H. confluens* from those of its close relatives.

As the oldest specimens of *H. confluens* at Vattenfallet have been found below *H. sagitta rhenana*, they are probably the oldest yet recorded. The three specimens of the sp element from the bed with *Valdaria testudo* are very different from typical specimens but resemble those described by Klapper & Murphy (1974) as morphotype ε. The other elements of *H. confluens* in this sample are quite typical, but the sample also contains several well preserved specimens, which at present cannot be identified. It is possible that the anomalous sp elements belong instead with these elements in a different species.

Hindeodella n. sp. aff. *confluens* (Branson & Mehl, 1933)

Fig. 72:5–13.

A distinctive form related to *H. confluens* occurs at Vattenfallet. The oz, pl and tr elements in particular are related in having very short and broadbased denticles and cusps. These elements, and the hi element, are also grouped together in having stronger curvature of the processes with more acute angles between them as compared to *H. confluens*. All elements have the same colour as those of *H. confluens*. The species described here has been found previously in Britain by Aldridge (1972, e.g. Pls. 5:6, 27, 7:19, 8:14) but as I have not yet been able to study all relevant types it is described here under open nomenclature.

Description. – The sp element. The denticulation is more regular than in *H. confluens*. In contrast to most but not all sp elements of *H. confluens*, a high anterior end is not developed in larger specimens. The internal construction of the anterior end is, however, similar, with white matter lacking or restricted to the denticle tips. The cusp and denticles are slightly broader than those of *H. confluens* and this character may be used to identify small specimens. As in *H. confluens*, the "roots" of the cusp and the denticles radiate from a point anterior the basal cavity tip and of the tip of the cusp "root". This, and the fact that the cusp and denticles are much broader, distinguish the sp elements of this species from those of *H. gulletensis*.

The oz element. The processes are considerably shorter and the cusp dominates much more than in the oz element of *H. confluens*. The posterior process is curved smoothly inwards and twisted in such a way that the aboral side is directed obliquely inwards in mature specimens. The "roots" of the denticles of this process are more or less fused with each other and the "root" of the cusp. The anterior process is only slightly twisted, but is obliquely connected to the cusp, in such a way that the aboral edge is directed obliquely inwards, and the denticles obliquely outwards. These and several other characters distinguish this element from the corresponding one of *H. confluens*.

The ne element is closely similar to that of *H. confluens*, and is generally difficult to separate from that species.

The hi element. In many specimens, the anterolateral process is in a plane nearly perpendicular to the posterior process, which distinguishes this element from that of *H. confluens*. It is also directed downward more than in *H. confluens*. No specimens with a complete posterior process occur in my collection, but it seems probable that it is shorter and more twisted than in *H. confluens* (compare the well preserved specimen in Aldridge 1972, Pl. 8:14).

The pl element. The curvature of and the angles between the cusp and the processes, together with the denticulation and many other details are similar to those on the hi and tr elements. The posterior process is centrally bowed and has about four denticles, free from one another; the outermost or the second outermost is the largest, but not as large as the cusp. The anterior process is short and usually straight distally. The inside of the basal cavity is expanded, forming a marked corner closer to the anterior than to the posterior process.

The tr element. The arrangement of the processes in relation to the cusp is similar to that of the anterior process of the oz element. Thus they are directed strongly inwards (in the tr element this is the same as backwards), and obliquely connected to the cusp, in such a way that the aboral margin is directed obliquely inwards and the denticles obliquely outwards. The processes are short and the denticles few and very broad.

Hindeodella ranuliformis Walliser, 1964

Fig. 72:1–4

The apparatus of this taxon has been unknown apart from the sp element. The species is generally rare (e.g. Walliser 1964 found only four specimens of the sp element in four samples from Cellon) and it is also rare at Vattenfallet where only one sp element per 500 grams was found in most of the samples with the species. The colour and denticulation of the sp elements indicate that *H. ranuliformis* belongs to the *H. confluens* group, and it could possibly be suspected that the other elements were mixed with those of other species in this group. However, such species were absent in sample G 70–20 which produced a total of nine sp elements of *H. ranuliformis* and two oz elements.

Fig. 72. Magnification ×40. Photograph Sven Stridsberg.

1–4. *Hindeodella ranuliformis*. 1. An about 1.30 mm long sp element. LO 5118t. Sample G 70–20 (10.02–10.04 m, basal Högklint *a*). 2. An about 1.1 mm long sp element. LO 5119t. Sample G 70–20 (10.02–10.04 m, basal Högklint *a*). 3. An about 0.41 mm long sp element. LO 5120t. Sample G 70–14 (0.99–1.06 m, Lower Visby Marl). 4. A large oz element. LO 5121t. Sample G 70–20 (10.02–10.04 m, basal Högklint *a*).

5–13. *H*. n. sp. aff. *confluens*. 5. An about 1.5 mm long sp element. LO 5122t. Sample G 70–21 (11.20–11.23 m, Högklint *a*). The specimen is intermediate in size between the two sp elements of *H. confluens* figured in Jeppsson 1974, Pl. 5:8–9. Parts of the basal filling are preserved. 6. An about 1.1 mm long sp element. LO 5123t. Sample G 70–8 (13.33 m, lower part of Högklint *b*). The specimen is intermediate in size between the two sp elements of *H. confluens* figured in Jeppsson 1974, Pl. 5:7–8. 7. An about 0.8 mm long sp element. LO 5124t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). The specimen corresponds in size to that of *H. confluens* figured in Jeppsson 1974, Pl. 5:5. 8. An about 0.3 mm long sp element. LO 5125t. Sample G 70–6 (15.33–15.41 m, lower part of Högklint *b*). The specimen is only slightly smaller than the sp element of *H. confluens* figured in Jeppsson 1974, Pl. 5: 1. 9. A large oz element. L0 5126t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). The large white spot on the posterior part of the cusp is probably a foraminifer. If so, it indicates that the specimen has been lying exposed on the bottom some time before being embedded in the sediment. 10. A medium-sized ne element. LO 5127t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). 11. A medium-sized hi element. LO 5128t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). 12. A large pl element. LO 5129t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). 13. A large tr element in oblique view. L0 5130t. Sample G 70–6 (15.33–15.41 m, Högklint *b*).

14–22. *H. gulletensis*. 14. An about 1.3 mm long sp element. LO 5131t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). The specimen is intermediate in size between the sp elements of *H. s. scanica* pictured in Jeppsson 1974, Pl. 9:5–6. 15. An about 1.0 mm long sp element. LO 5132t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). The specimen is intermediate in size between the two sp elements of *H. s. scanica* pictured in Jeppsson 1974, Pl. 9:4–5. 16. An about 0.6 mm long sp element. LO 5133t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). The specimen is intermediate in size between the sp elements of *H. s. scanica* pictured in Jeppsson 1974, Pl. 9:2–3. 17. An oz element with the anterior process about 0.3 mm long in inner lateral view. LO 5134t. Sample G 70–6 (15.33–15.41 m, Högklint *b*). The specimen is intermediate in size between the oz elements of *H. s. scanica* pictured in Jeppsson 1974, Pl. 9:9–10. 18. An ne element in inner lateral view. LO 5135t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). Among the ne elements of *H. s. scanica* pictured in Jeppsson 1974 it is closest in ontogenetic age to that in Pl. 10:2. 19. An hi element in inner lateral view. LO 5136t. Sample G 70–2 (19.24–19.29 m, Högklint *b*). 20. A large pl element in inner lateral view. LO 5137t. Sample G 70–2 (19.24 – 19.29 m, Högklint *b*). 21. A small pl element in inner lateral view. LO 5138t. Sample G 70–6 (15.33–15.41 m, Högklint *b*). 22 A large tr element in anterior view. LO 5139t. Sample G 70–8 (13.33 m, Högklint *b*).

23–33. *H. sagitta rhenana*. All the specimens are from sample 28–29 m (Högklint *c*) except the tr element in 33. All specimens belong to Riksmuseet. 23. An about 0.8 m long sp element in lateral and oral view. RM Co 12. 24. An about 0.6 mm long sp element in lateral and oral view. RM Co 13. 25. An about 0.4 mm long sp element in lateral and oral view. RM Co 14. 26. One of the largest found oz element in inner lateral view. RM Co 15. 27. An oz element in inner lateral view RM Co 16. 28. An ne element in inner lateral view. RM Co 17.29. An hi element in inner lateral view. RM Co 18. 30. A large pl element with short posterior process in inner lateral view. RM Co 19. 31. A small pl element with short posterior process in inner lateral view. RM Co 20. 32. A large pl element with long posterior process in inner lateral view. RM Co 21. 33. A large tr element in posterior view. RM Co 22. From the *Valdaria testudo* bed in the *"Pterygotus"* Beds (Högklint *d*). The picture gives the false impression that the processes are straight. They are directed obliquely backwards at the origin, and their oral edges are strongly curved, directed nearly backwards in the middle and directed outwards at the tips.


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They have the expected shape, and probably belong to *H. ranuliformis*. Altogether 24 sp elements have been found in the section, and it is to be expected that the other elements also occur. However, they are probably included among the corresponding elements of other species.

Description. – The sp elements from Vattenfallet agree closely with earlier descriptions. The shape of the denticle "roots" is seen in the partial growth series in Fig. 72:1–3 (the specimen in Fig. 72:2 has an extra denticle on the basal cavity lip).

The oz element. This element is similar to that of *H. confluens* but can be distinguished from contemporaneous specimens of the latter by its more robust shape and the very broad cusp. The processes are lower and the denticle "roots" originate slightly higher up in the process. All these characters should of course be compared in specimens which are of equal length.

Hindeodella gulletensis (Aldridge, 1972)

Fig. 72:14–22

This species was originally identified as a species of *Spathognathodus,* and only the sp element was described. The sp elements from Vattenfallet differ slightly from those of the British population and possibly belong to another subspecies. *Hindeodella gulletensis* differs from contemporaneous members of the *H. confluens* and *H. excavata* groups chiefly in having closely spaced denticles and thin cusps on the non sp elements, and by the fact that the posterior process of the hi element is usually bowed inwards in its central part. As a result, the cusp is not in line with the main part of the posterior process. Large specimens also differ in colour, those of *H. gulletensis* being more greyish. In all these and many other aspects *H. gulletensis* agrees closely with *H. steinhornensis*. The denticles do not alternate in size, i.e. *H. gulletensis* has the same kind of denticulation as *H. s. scanica*. The description below emphasizes differences from the latter taxon in order to facilitate their separation. For a comparison with *H. sagitta rhenana* see under that species.

Description. – Cusps and denticles are not so thin and needle-like as in the non sp elements of *H. s. scanica*.

The posterior process of the sp element is only slightly more than half as long as the anterior process. The cusp is less prominent than in most sp elements of *H. s. scanica,* the processes of which are also more equal in length. The denticles on the posterior process have the deepest "roots"; they are deeper than the "root" of the cusp and much deeper than any of the "roots" of the denticles on the anterior process. A difference in the depth of the denticle "roots" also occurs in the sp elements of *H. s. scanica,* but it is less pronounced. The basal cavity does not reach as high up in the processes beneath the cusp as in *H. s. scanica*.

The oz element has short and fairly high processes and is thus easily distinguished from that of *H. s. scanica*. In typical specimens the denticles are more closely spaced than in *H. confluens*. However, by overgrowth of some denticles the number of tips decreases. On the anterior process the denticle "roots" are pointed, while they are square in *H. confluens* in lateral view. This character is useful only in relatively large specimens, and is not often seen on the innermost denticles since these are too narrow to show it.

The ne element. The long process is more straight and directed more obliquely downwards than in *H. s. scanica,* and the short process is very short and has only two or three denticles. Thus the element lacks the arched u-shaped aboral margin so characteristic of *H. s. scanica.*

The hi element. The denticles are coarser than those of *H. s. scanica.* In similarity with the other non sp elements the compressed cross section of the cusp continues to quite a high level (in *H. s. scanica* it rapidly becomes nearly circular distally).

The pl element. The posterior process is short and usually its angle with the cusp is slightly more than 90°, whereas in *H. s. scanica* it is usually long and forms an acute angle with the cusp. When viewed laterally (Fig. 72:20) this element resembles a juvenile pl element of *H. confluens,* but in fact the anterior process is curved strongly inwards. Also, the posterior process, cusp and denticles are curved more or less inwards. The processes can be slightly twisted. All those parts of the pl element of *H. confluens* are straight, except for the anterior process which is more or less curved and arched.

The tr element differs from that of *H. s. scanica* only in minor details of the cusp and denticles, as noted above for other elements, but is otherwise similar.

Conclusions.—*H. gulletensis* can be distinguished from *H. s. scanica* in a number of small details as noted above, and from all other described subspecies of *H. steinhornensis* in having denticles which do not alternate in size. Lack of space excludes a discussion on the nomenclatorial subdivision of the *H. steinhornensis* lineage, but perhaps the acquisition of alternating denticulation should be used as the starting point of *H. steinhornensis,* and the subspecies with a regular denticulation regarded as *H. gulletensis.* If so, the subspecies *H. s. scanica* should be transferred to *H. gulletensis.*

Hindeodella sagitta rhenana (Walliser, 1964) *sensu* Aldridge 1975a

Fig. 72:23–33

The first (partial) reconstruction of the apparatus of *H. sagitta* was made by Walliser (1964) who noted that the sp and oz elements belong together. That this was only a partial reconstruction was evident (e.g. Walliser 1972) from a comparison with better known congeneric species. The reconstruction of the complete apparatus was made independently by Jeppsson (1974:36) and Aldridge (1975a). Aldridge's study was particularly thorough and included collections from the type locality.

Description.—The population from Vattenfallet differs slightly from the specimens figured by Aldridge (1975a, Pl. 47), who noted that the most apparent difference between *H. s. rhenana* and *H. s. sagitta* is the consistently more delicate nature of the *H. s. sagitta* elements. In this aspect the Vattenfallet population approaches *H. s. rhenana.*

The sp element. As expected the number of denticles varies slightly with size. The three figured specimens are 0.44, 0.55 and 0.82 mm long and have 11, 14 and 14 denticles, respectively; unfigured specimens have similar numbers. In this respect they agree with *H. s. rhenana.*

The oz element. The number of denticles is great, and in specimens of comparable size there are probably more denticles than in the *H. s. sagitta* oz element figured by Aldridge (1975a, Pl. 47:14).

The ne elements. The ne element of *H. s. rhenana* has up to four denticles on the anterior process, whereas *H. s. sagitta* has only one or two (Aldridge 1972). The Vattenfallet specimens have from one to three denticles (more commonly one or two).

The hi element. The denticles vary in size in the same way as those of the hi element of *H. s. sagitta* figured by Aldridge (1975a, Pl. 47:15). This size variation develops early in ontogeny.

The pl element. Aldridge (1975a:331) noted that the pl element of *H. s. rhenana* has a short posterior process, whereas in *H. s. sagitta* it is about as long as the anterior process. There is little doubt that the short posterior process is a primitive feature. It occurs in *H. excavata, H. confluens* and *H. gulletensis,* the oldest member of the *H. steinhornensis* lineage. However, the length varies considerably in most populations, except in those of *H. confluens.* The presence of both long and short processes in *H. steinhornensis* as well as in *H. sagitta* could indicate that the long process predated the separation of these two lineages and that the difference between different subspecies is only a difference in the frequency of the two kinds of pl element. In the Vattenfallet population of *H. sagitta* there are pl elements with a short posterior process as well as specimens with a long posterior process, the former being more common.

The tr element. Aldridge (1975a) described no obvious difference in the tr element of the subspecies apart from the denticulation.

Discussion. – Walliser (1964) described three subspecies of *H. sagitta.* The Vattenfallet population is clearly different from *H. s. bohemica* in the shape of the basal cavity of the sp element. This agrees with Aldridge's conclusion (1975a, b) that *H. s. bohemica* characterizes the late part of the Homerian (i. e. late Wenlockian). As described above the Vattenfallet collection is closest to *H. s. rhenana.* Some differences may be apparent only because small collections have been studied, but it is more probable that most or all of the differences are due to the fact that we have studied different populations. Further studies are needed to evaluate these differences.

Gen. et sp. indet.

There is one fragment of a platform element in each of the samples G 70–14 and G 70–17 consisting of the tip of a process with no indication of the branching of the element. A direct comparison with well preserved specimens would probably help to identify them.

Unidentified specimens

Those broken elements having preserved characters that can be completely matched with species definitely identified in the samples have been counted as belonging to that species. Similarly, poorly preserved hi elements which belong in either *H. excavata* or *L. excavata* have been included in the one of these species with which they have most in common, provided that both species occur in the sample. Other such problems have been tackled in a similar way. However, there are also some additional specimens which are too poorly preserved even to be identified in this way, and they are included in the unidentified group discussed here.

There are also, however, some better preserved elements which for other reasons have remained unidentified. Some may be malformed specimens but others probably represent one or more of the elements of otherwise unknown species. It is possible that this group includes between one and five species.

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Agnathan vertebrates

TOR ØRVIG

Vertebrates were first recorded from the Silurian of Gotland by Rohon (1893) and Lindström (1895), and subsequently by Spjeldnaes (1950), Martinsson (1966), Gross (1968a; 1968b), and Janvier (1971). The most comprehensive vertebrate faunas may be recognised in three stratigraphical subdivisions, viz. the Halla Beds (late Wenlockian), the Hemse Beds (Leintwardinian) and the Burgsvik Sandstone (early Whitcliffian), and at the Riksmuseum collections of vertebrate microfossils are currently being assembled from these and other horizons. Characteristic constituents of much of this material are detached scales of those ostracoderms (Palaeozoic agnathans) referred to collectively as thelodonts.

The thelodonts, whose relations to other ostracoderms are still somewhat obscure, possessed a dermal skeleton consisting exclusively of minute scales, not unlike some type of selachian placoid scales. In time they range from late Llandoverian to early Eifelian. There is very little evidence on which to discuss their mode of life, but they may have been benthic deposit-feeders. Detached thelodont scales have proved useful for correlation of certain Silurian and Lower Devonian strata (Mark-Kurik 1969; Ørvig 1969:236–237; Turner 1973; etc.).

At Vattenfallet, a single, complete thelodont scale was recovered by L. Jeppsson in a sample at 27.65–28.0 m (Högklint *c*), processed for conodonts. It was associated with some fragments of other scales, not commented on further here. This is the earliest known occurrence of agnathans from Gotland.

The complete scale (Fig. 73) which is 0.5 mm long, has a flat crown, oval in

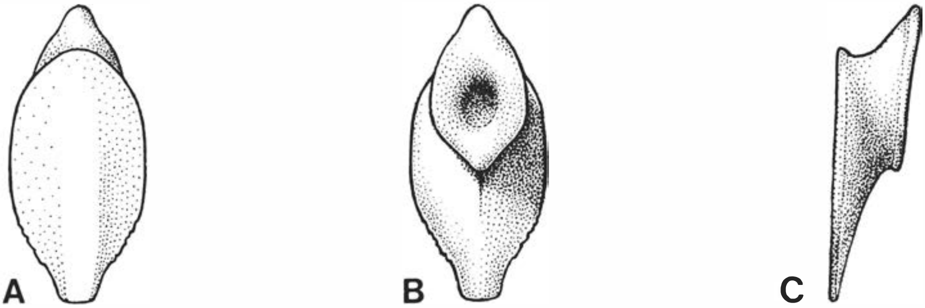

Fig. 73. Thelodontida gen. et sp. indet. Vattenfallet 27.65–28.0 m (Högklint *c*). Scale in superficial (A), basal (B) and lateral (C) view, orientated with the anterior end upwards. Approximately ×80. RM C2300.

superficial view, and a small, stalk-like basal plate in its anterior part. Nothing similar has previously been found in either the Silurian of Gotland or in Llandoverian or Wenlockian strata elsewhere. The only thelodont scales to which, in fact, it seems to bear a certain resemblance are some of those named *Nikolivia oervigi* from the Dittonian of Podolia (Karatajūtė–Talimaa 1968, Pls. 1:1–2, 2:1), and *Amaltheolepis* from the Emsian–early Eifelian of Spitsbergen (Ørvig 1957, Fig. 3F,K,L). Such resemblances, however, are hardly significant.

Since the single thelodont scale from Högklint *c* could not be used for histological investigation, no attempt is made here to give it a generic or specific name. Any new occurrence of vertebrates in the lower part of the Silurian of Gotland is naturally of great interest and search for such material should be encouraged.

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Phosphatic tubes

STEFAN BENGTSON

Narrow tubes composed of phosphate, most of them found in acid-resistant residues, have been recorded at Vattenfallet at several levels (Fig. 66). The walls of the tubes are laminated, and there may be fine annulations on the outer surface. The shape and cross section are usually somewhat irregular. Observed diameters vary from 0.1 to 1.0 mm, and the angle of divergence from just a few degrees to about 10°. Tubes of this kind are currently referred to the Order Hyolithelminthes Fisher, 1962. They can be assumed to have housed a sedentary worm-like animal. Some recent sedentary polychaetes contain phosphatic minerals in their tubes (Vinogradov 1953:235–237), and phoronids, by virtue of their close affinity with brachiopods and bryozoans (with regard to phosphate secretion in bryozoans, see, e.g. Martinsson 1965), may also be suspected of having once been capable of secreting phosphatic tubes. What kind of animal did in fact inhabit the tubes from Vattenfallet is at present open to speculation.

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Organic tubes

KRISTER BROOD

The Vattenfallet material includes two specimens of brown to black organic tubes, roughly 1 cm in diameter but somewhat deformed by compaction of the sediment. The tubes appear to belong to *Keilorites,* in the same group as *K. squamosus* (Phillips), but probably represent a new species which is here referred to as *K.* sp. *a* (for the range see Fig. 66).

Keilorites has previously been recorded from Gotland as *Trachyderma,* both from the Upper Visby Marl (Lindström 1888) and the Hemse Beds (Lindström 1895:11). The species from the Hemse Beds is different from that in Högklint *b* at Vattenfallet.

The current interpretation of such organic tubes (Howell 1962:W155) is that they were probably the mucous housing of annelid worms. However, there is as yet no indisputable evidence to confirm that they belonged to this group.

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Ecology and faunal dynamics

VALDAR JAANUSSON

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

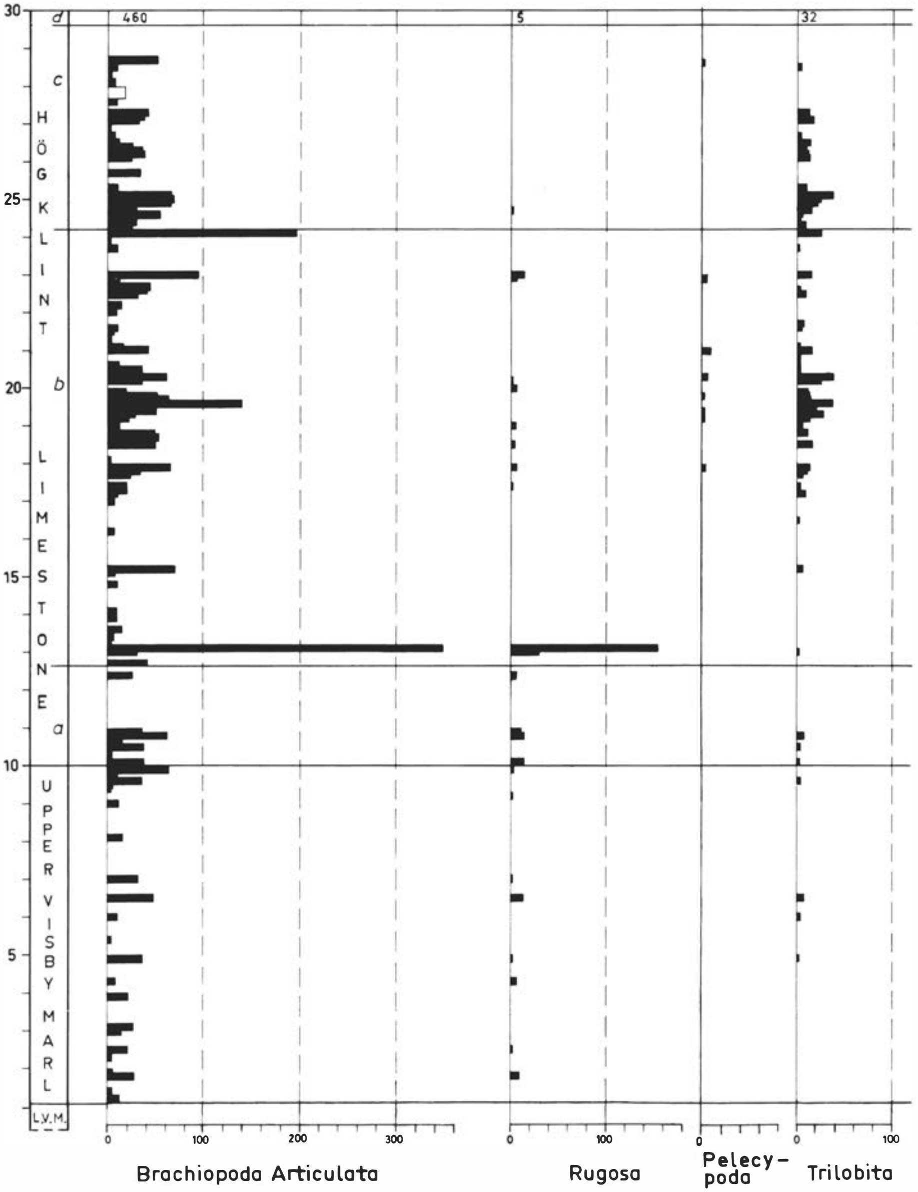


Fig. 74. Frequencies of articulate brachiopods, rugose corals, pelecypods, and trilobites in the Vattenfallet material (mainly Liljevall's collection). Only such data in which the precision of the level is within 20 cm are included, and levels with less than 3 specimens are not shown. The columns record 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"

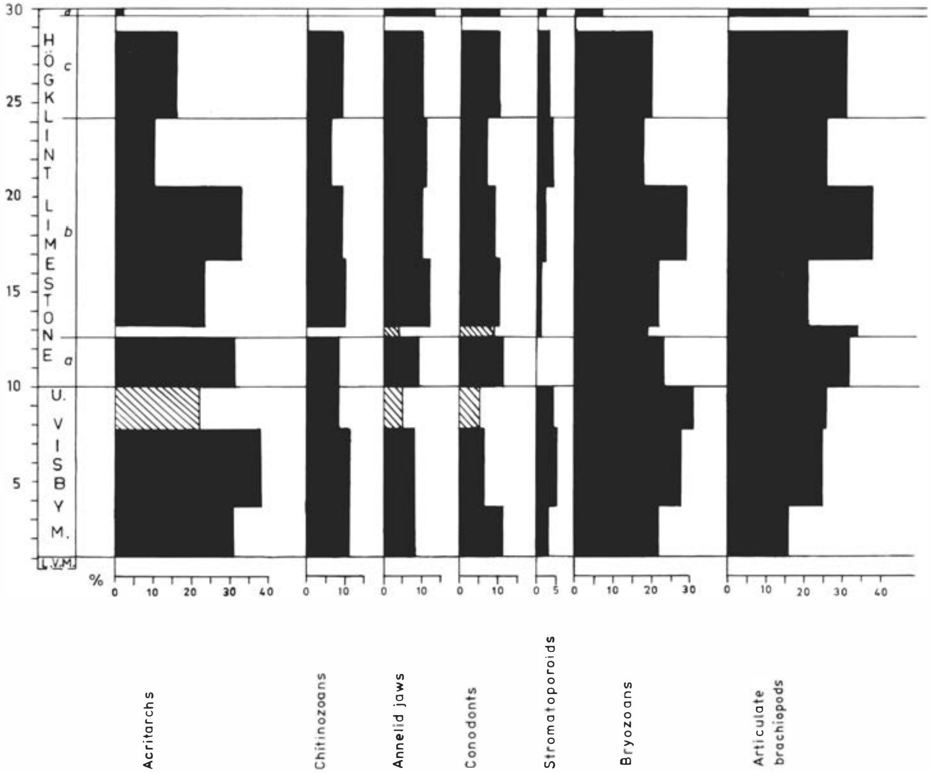


Fig. 75. Species frequencies in different parts of the Vattenfallet section. Continued on Fig. 76. From the lowermost beds of Högklint *b* (12.65–13.2 m) no samples have been analysed for acritarchs and chitinozoans. For a few groups some intervals have not been adequately sampled; such intervals are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

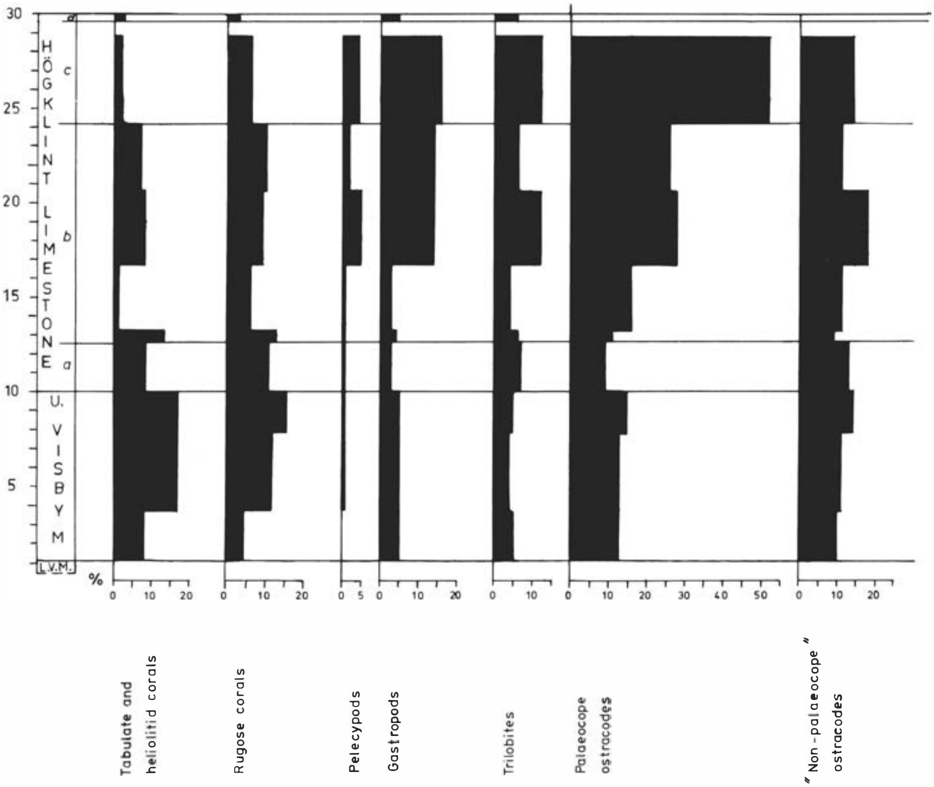


Fig. 76. Species frequencies in different parts of the Vattenfallet section. Continued from Fig. 75. Högklint *d* has not yet been searched exhaustively for ostracodes.

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

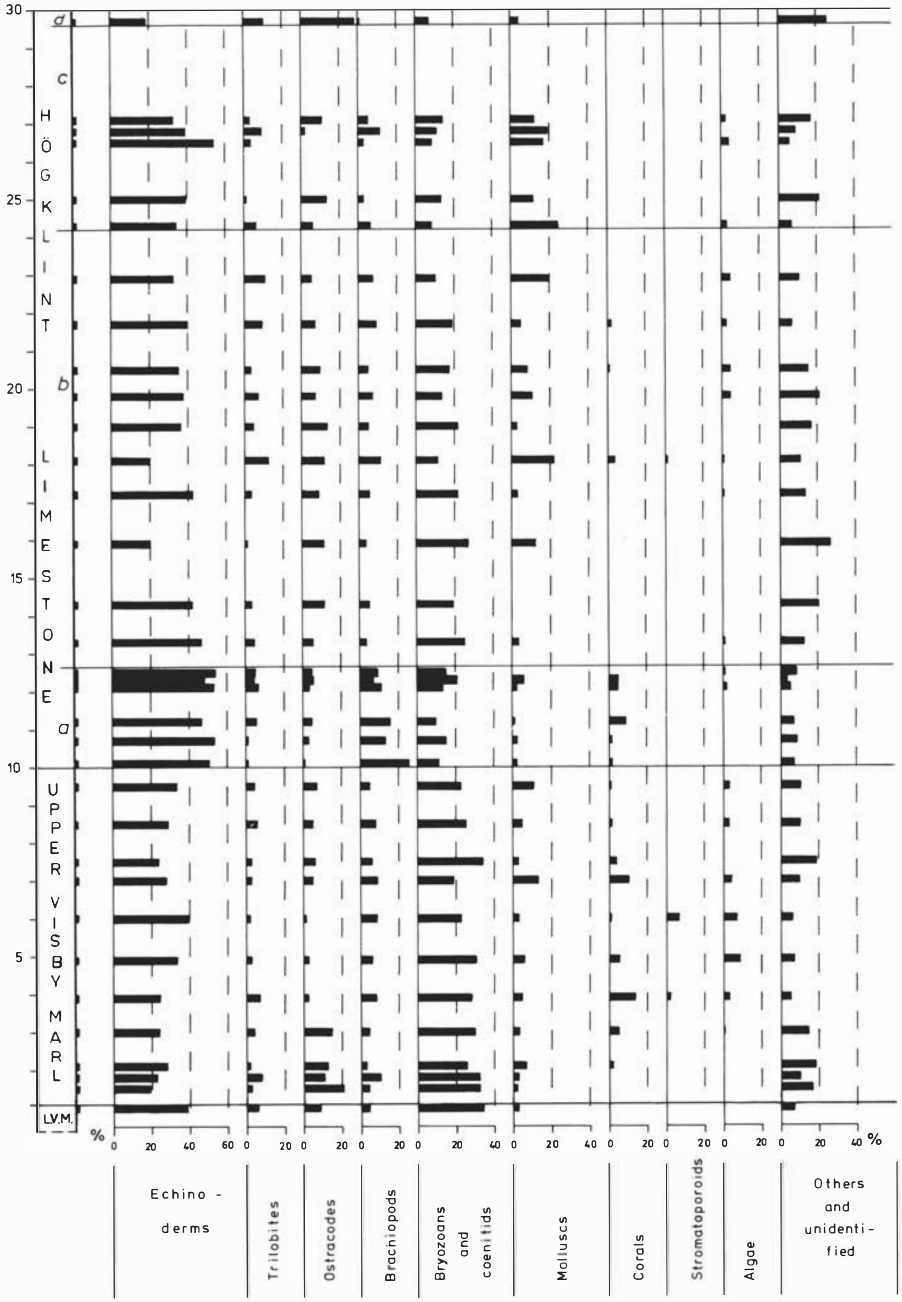


Fig. 77. Composition of skeletal sand in selected limestone beds. For full explanation see text. Compare also Fig. 5 for the content of skeletal sand in the rock.

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.

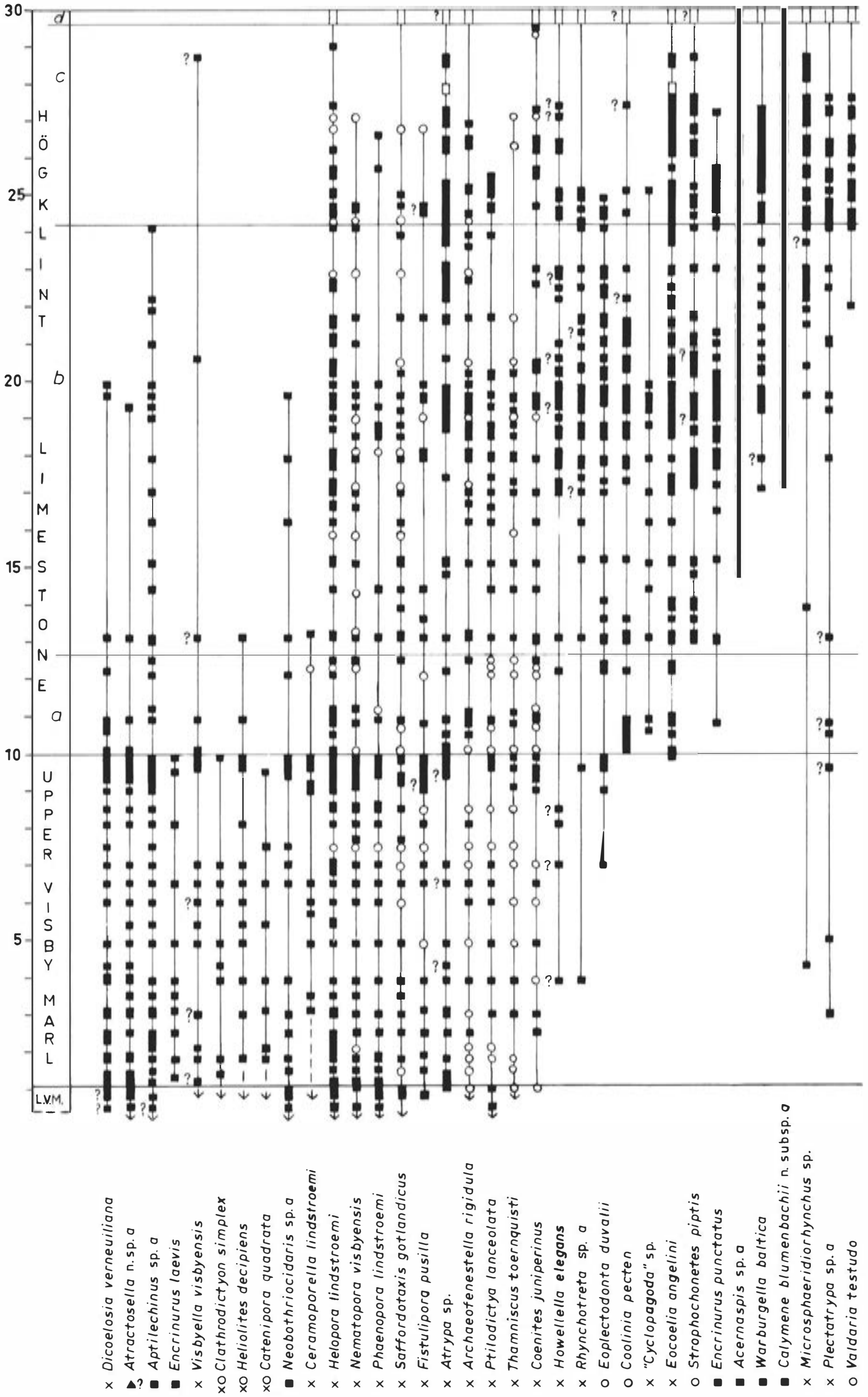
Hard-bottom epifauna, AMAN

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.

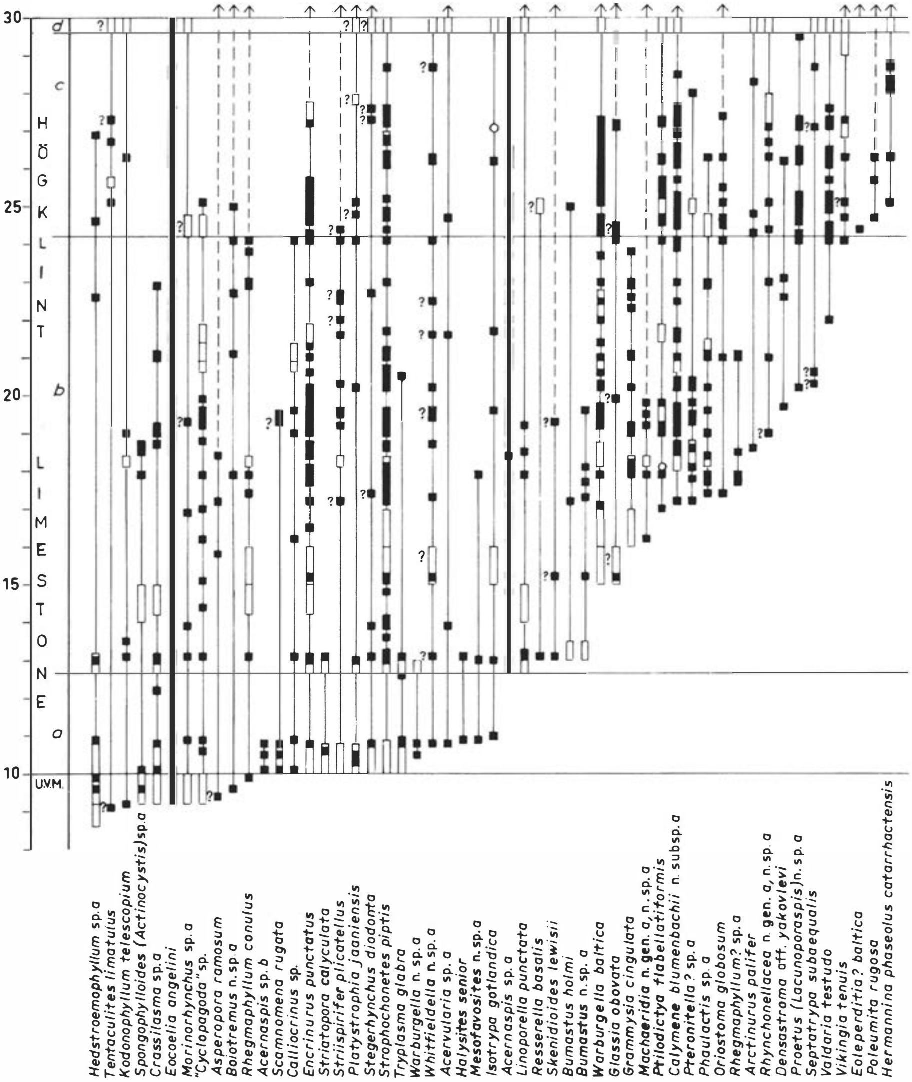


Fig. 79. Species appearing in the uppermost Upper Visby Marl or in the Högklint Limestone. For full explanation see text.

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.

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SGU = Sveriges Geologiska Undersökning

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