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

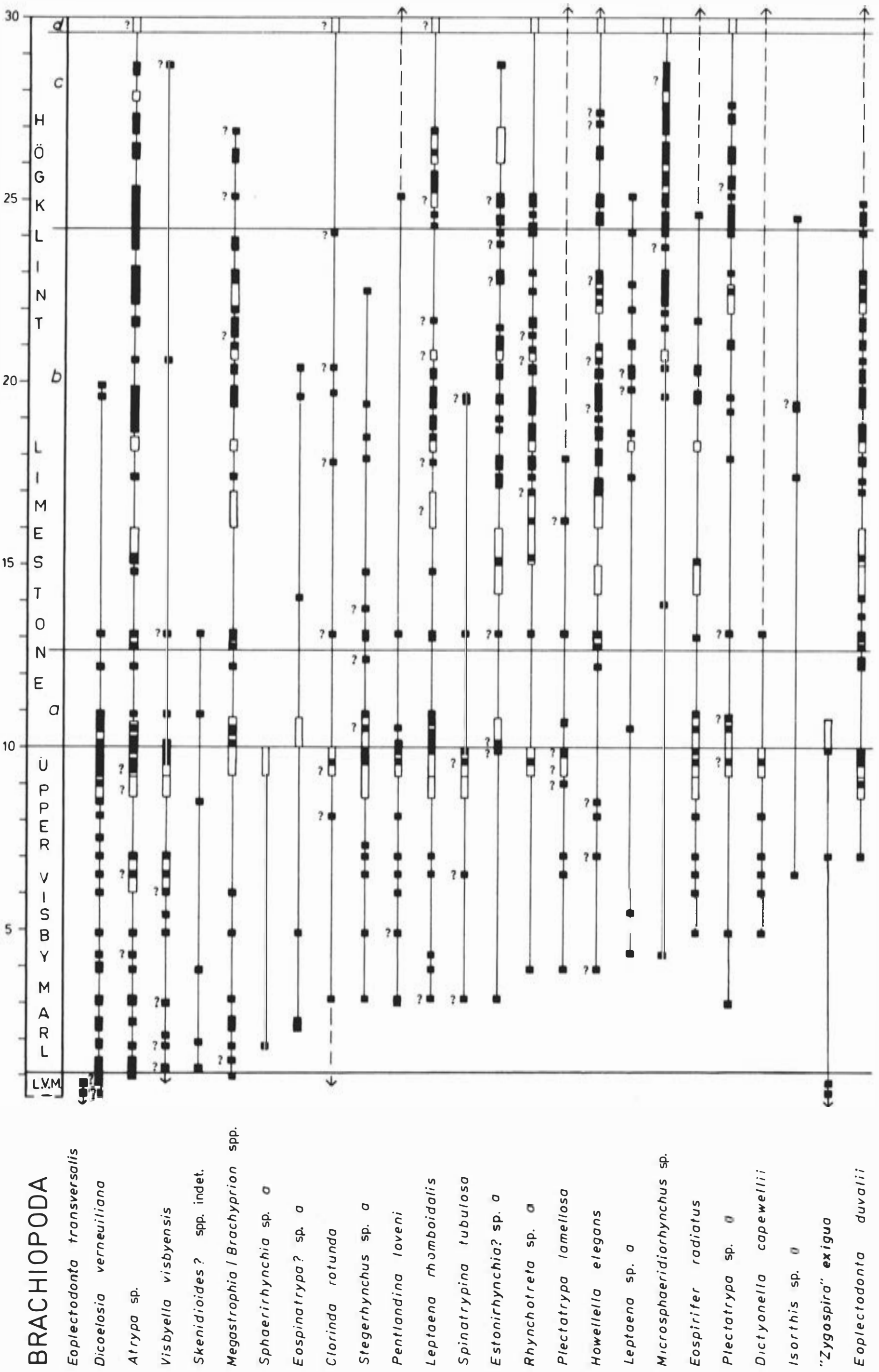
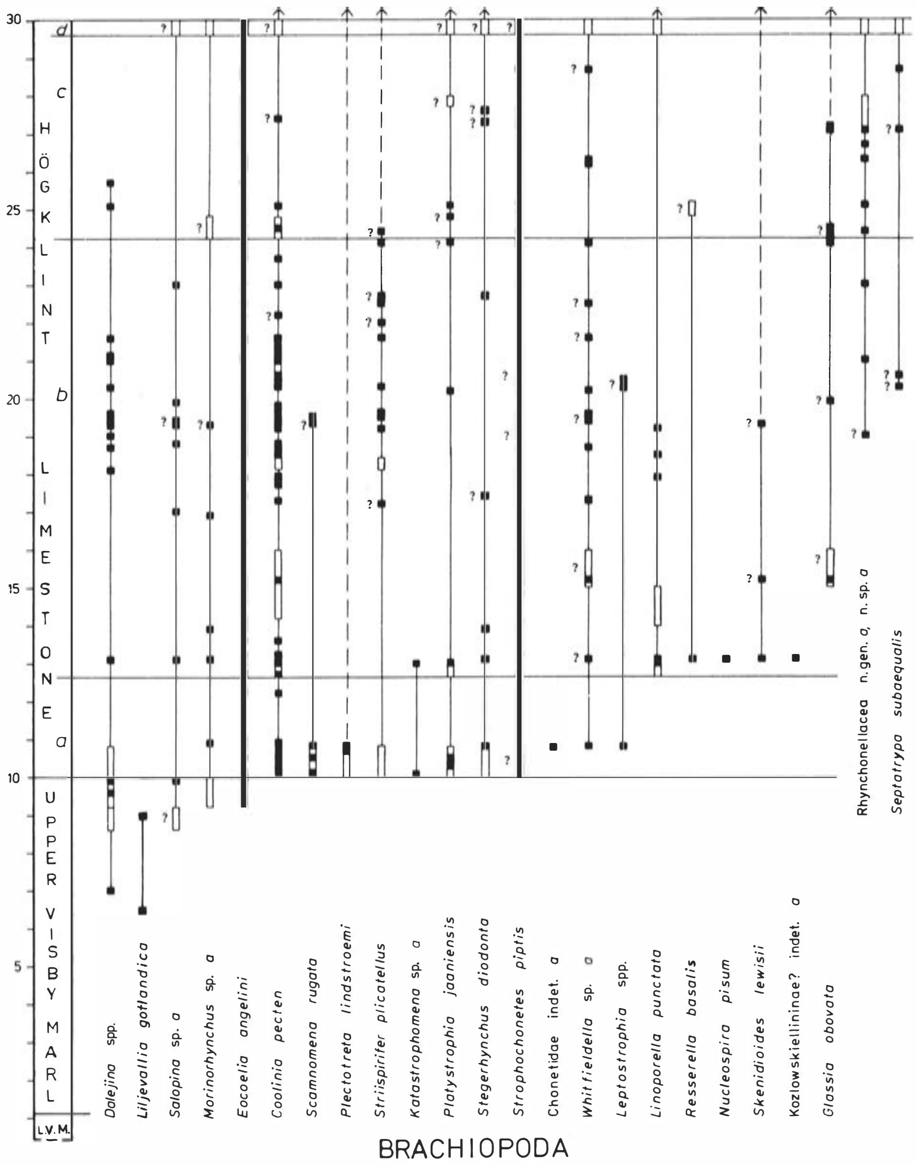

30
25
20
15
10
5
d
c
b
a
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
BRACHIOPODA
Eoplectodonta transversalis
Dicoelosia verneuiliana
Atrypa sp.
Visbyella visbyensis
Skenidioides? spp. indet.
Megastrophia / Brachyprion spp.
Sphaerirhynchia sp. a
Eospinatrypa? sp. a
Clorinda rotunda
Stegerhynchus sp. a
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. ß
Dictyonella capewellii
Isorthis sp. ß
"Zygospira" exigua
Eoplectodonta duvalii

Fig. 58.


30
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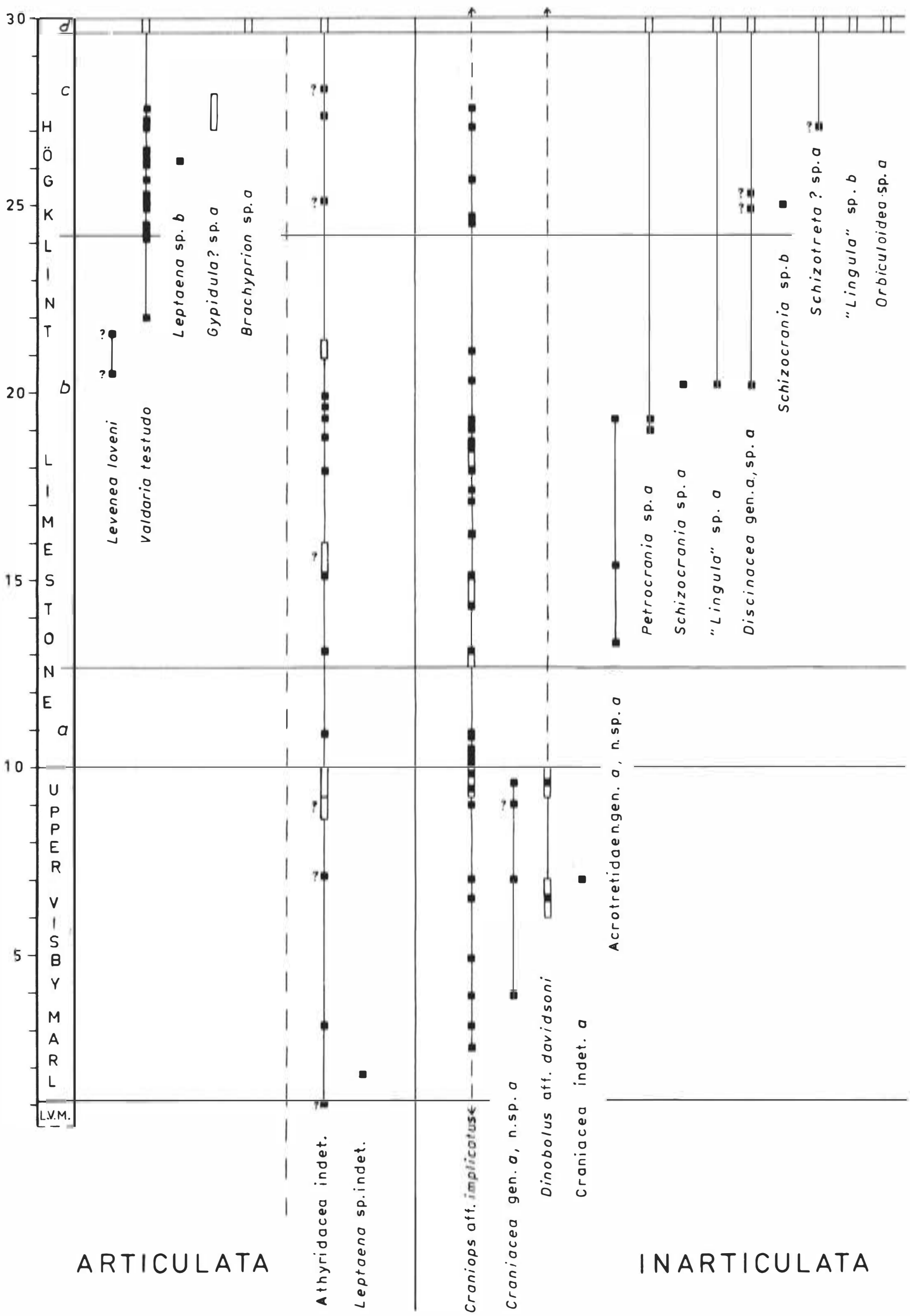
HÖGKLINT LIMESTONE
UPPER VISBY MARL
L.V.M.
?
Dalejina spp.
Liljevallia gotlandica
Salopina sp. a
Morinorhynchus sp. a
Eocoelia angelini
Coolinia pecten
Scamnomena rugata
Plectotreta lindstroemi
Striispirifer plicatellus
Katastrophomena sp. a
Platystrophia jaaniensis
Stegerhynchus diodonta
Strophochonetes 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
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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 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).

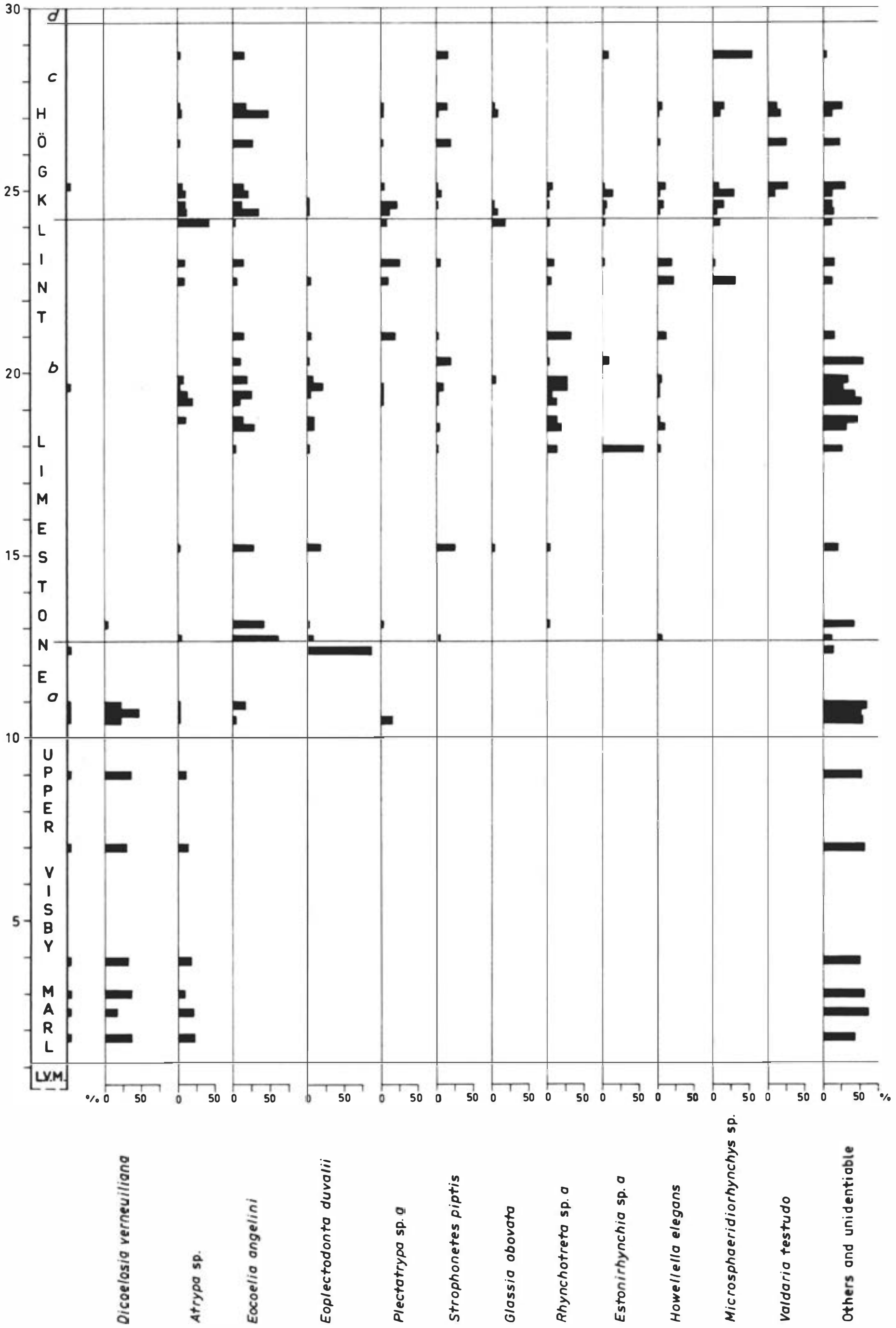


Fig. 61. Percentage frequencies of those articulate brachiopod species which form at least 15 per cent of the total articulate brachiopod fauna in at least one sample. See text for full explanation.

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.

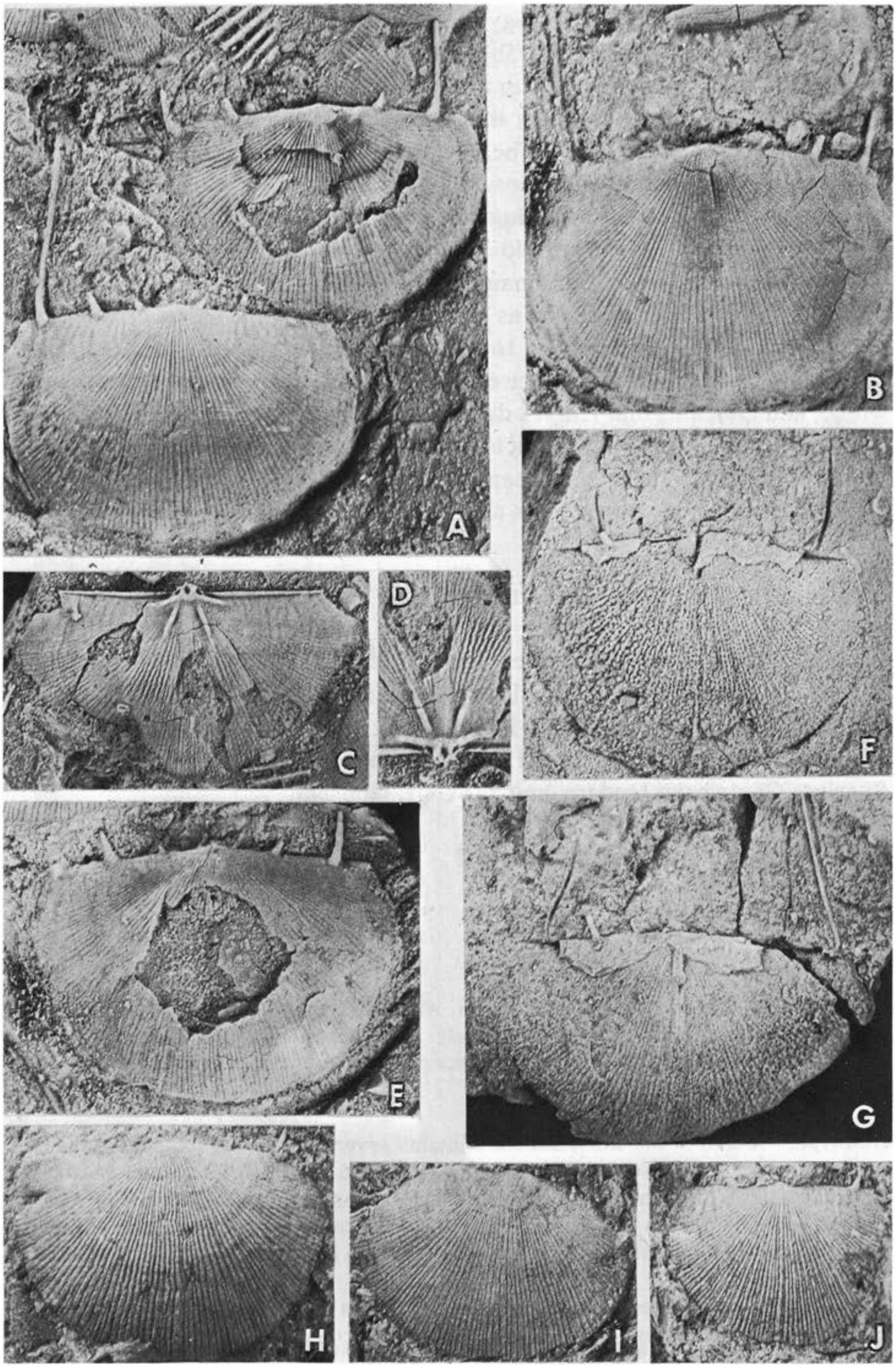
Superfamily: Chonetacea Bronn, 1892

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	3'2'1'13
RM Br106495b	9.5	14.0	13.0	3'2'23
RM Br106494a	11.5	16.0	14.6	2'3
RM Br106494b	11.7	16.5	14.6	3'2'1'123
RM Br106495c	9.3	15.6	–	–
SGU Type 78	11.8	16.5	15.0	2'3
SGU Type 79	10.3	18.9	16.1	3'2'1'23
SGU Type 81	9.6	–	–	–
SGU Type 82	7.4	–	9.8	1'12
SGU Type 80	9.9	–	–	2'1'123

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.

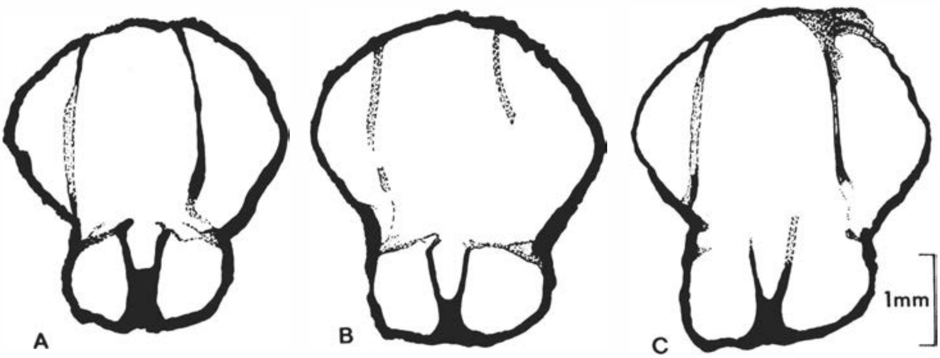


Fig. 63. Serial sections (peels) of *Septatrypa subaequalis* n. sp. RM Br62773. See Fig. 64 P–Q for illustration of complete shell. A=3.0 mm from posterior tip of pedicle valve, B=3.5 mm, C=4.0 mm. Note the slender dental plates, deep lateral cavities, stout dorsal septum, and slender-walled, deep septalium.

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.

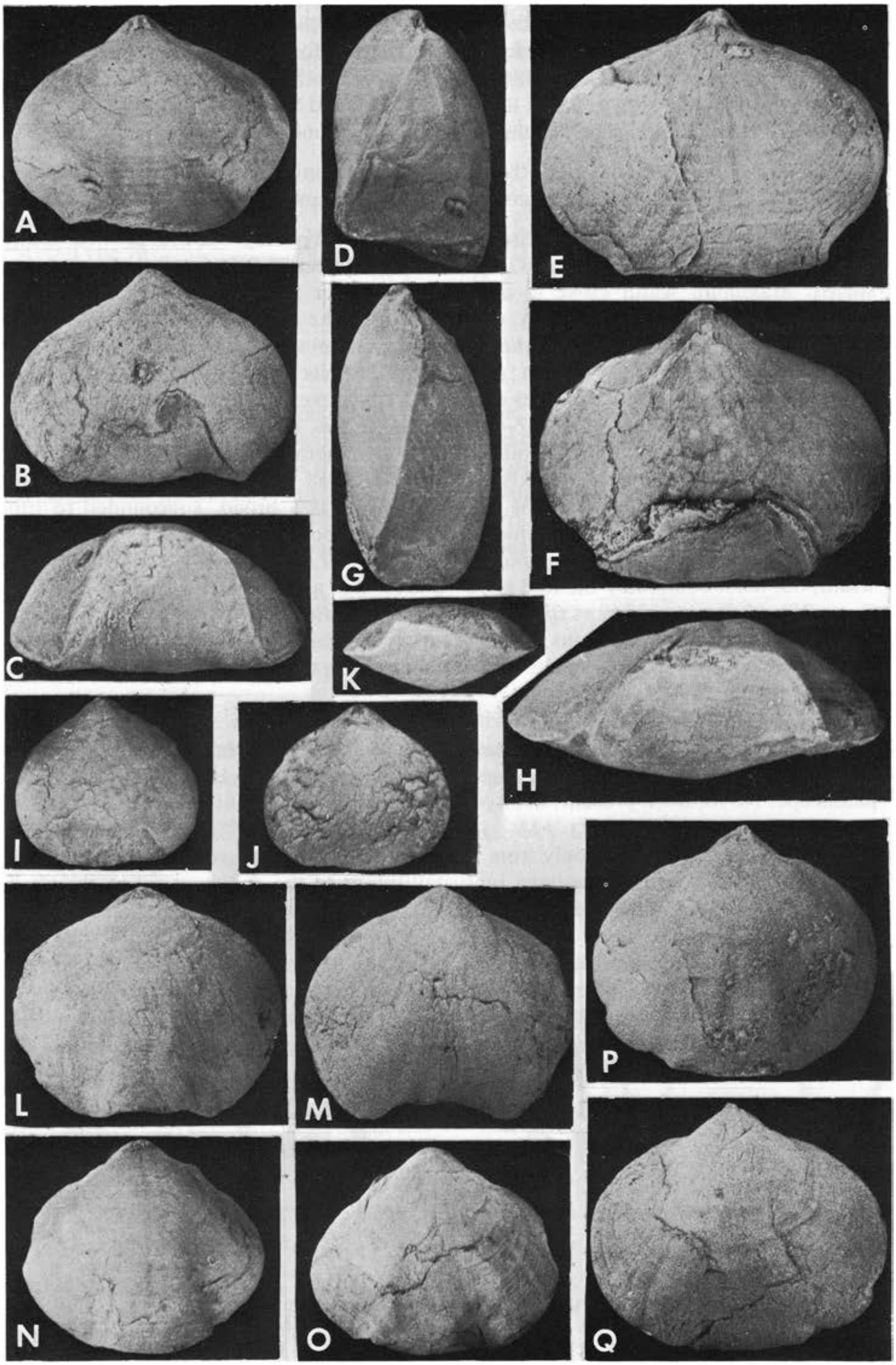
Description. – Outline initially subcircular, becoming subpentagonal with growth. Width commonly about 90 % of length (O.R. 78–101 %, mean 89.2 % in 19 well preserved shells). Maximum width close to or slightly anterior to mid-length. Posterolateral margins gently curved and widely divergent from the 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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