Ordovician benthic macrofaunal associations

By VALDAR JAANUSSON

A major problem in the quantitative analysis of Ordovician macrofaunal assemblages is not only to take into account groups in which individuals are no longer recognisable (most echinoderms, small bryozoans etc.), but also to integrate the data from large and small macrofaunas. In Baltoscandian carbonate rocks the quantitatively important constituents in the small macrofauna (adult dimensions c. 2–5 mm) are mostly gastropods and acrotretid brachiopods. The numerically dominant macrofaunal species belong to this size category. This suggests that because of difficulties in sampling, the importance of small macrofaunas has been underestimated in many cases.

In graptolitic shales, benthic large macrofaunas are very poorly represented. The small macrofauna is commonly dominated by small inarticulate brachiopods. It is customary to regard both these and associated small plectambonitacean brachiopods as epifauna attached to floating weeds, but all are more probably benthic. The rarity of large macrofaunal organisms in such shales may be due to unsuitable substrate, an oxygen-dependent zonation with large forms disappearing at higher oxygen levels than much of the small macrofauna, or the competitive disadvantage of large macroorganisms in areas of very low food supply.

Along the environmental gradient reflected in the transition from graptolitic shales to progressively coarser grained rocks, the successive benthic macrofaunal associations appear to have been more substrate-related than depth-dependent.

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The purpose of this paper is to summarise the available information on the composition of Ordovician benthic macrofaunal associations. Only level bottom associations are considered, not those of organic reefs or carbonate mounds. Hirnantian faunas are also excluded because they are discussed elsewhere in this book.

Studies of faunal associations require a quantitative approach. In Ordovician rocks such study may be said to have barely started, and therefore quantitative data are few and concentrated to certain areas. The data are insufficient for a synthesis, but some trends are discernible, and the main emphasis in this paper is on tracing such trends. A complicating factor at present is that there is some confusion as to how to obtain and evaluate the quantitative data and what to include and exclude. Thus many published data are difficult to compare because of different approaches in methodology.

For individual-based quantitative estimates of the composition of faunal assemblages a number of different sampling methods are available. The commonest are (1) bulk sampling in friable rock, (2) surface sampling, and (3) bulk sampling in hard rock (for a recent summary see Jaanusson 1979 b: 256–259). Almost all data available from Ordovician rocks are given in terms of individual-based frequencies, that is, groups in which individuals can no longer be recognised (most echinoderms, sponges if represented only by spicules, many small articulate brachiopods, ramose and fenestrate bryozoans, "chitinous" hydrozoans etc.) are seldom included, or the estimates hardly reflect their real importance. For example, studies on the composition of skeletal sand in Ordovician limestones (Martna 1955; Jaanusson 1972; Põlma 1972a, b; Lauritzen 1975; Gnoli & Serpagli 1980; Hints & Põlma 1981) show that echinoderms were important producers of ske-

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letal material, although they are rare or absent in data based on counting individuals. Echinoderm skeletons disintegrate easily into consistuent plates, which in turn are easily fragmented because each plate is porous and composed of a single crystal. That the relative frequency of echinoderms in Ordovician macrofaunal assemblages is almost always strongly underestimated can be shown in cases where the importance of various species can be evaluated in terms of sample-frequency (Hints 1979). Cystoids (e.g., Jaanusson *in* Bruton & Williams 1982: 38, Fig. 6) and crinoids were normally the commonest Ordovician echinoderm groups, but in the Upper Ordovician echinoids were also fairly common in places (Põlma *et al.* 1977). Conversely, the importance of articulate brachiopods is mostly much higher in individual-based data than in skeletal sand. Because of the tough, finely fibrous structure of the shell, the brachiopod skeleton does not break easily, and this contributes to the over-representation of articulate brachiopods in individual-based estimates. The original composition of skeleton-bearing faunal associations therefore differs widely from data on the frequencies of individuals obtained from the rock. The sample-frequency approach (Jaanusson 1979 b: 258–259) yields an estimate of the original composition of the skeleton-bearing fauna that is more in accordance with the composition of the skeletal sand. Because of the lack of other data, the discussion in this paper has to be based on individual-based quantitative data, but the above considerations should be borne in mind.

A serious problem is that the data published by various workers are not always comparable because of different tabulation conventions. This is particularly notable with regard to trilobites. In many papers only the dominant exoskeletal element of a species is considered and, in addition, the number of the element is divided by an arbitrary figure (up to ten) to account for ecdysis. For example, what for one worker would be a trilobite-dominated assemblage, would be dominated by another group for those who use a different tabulation convention for trilobites. Because of limitation of space the problem cannot be analysed here in detail. It is sufficient to mention that the effect of ecdysis is commonly vastly exaggerated (see also Cisne 1973), and that several assumptions on which recalculations are based are doubtful (such as that all specimens of the rarer exoskeletal element belong to individuals represented by the dominant element). The fact is that the primary quantitative data of many groups are distorted to varying degrees relative to the original number of individuals, but, on the other hand, recalculations of the data tend to increase the distortion of the original relative frequencies rather than vice versa. The original data presented in this paper, have not been recalculated.

The importance of various groups in macrofaunal assemblages can also be estimated in terms of volume (Walker 1972; Walker & Alberstadt 1975; Copper & Grawbarger 1978). This is a useful approach when large skeletons are involved (stromatoporoids and corals in organic reefs etc.) but it is difficult to apply where small fossils are involved. The quantitative information based on volume and number of individuals is not comparable.

Serious methodological problems also arise when widely different size groups are combined in the same quantitative analyses. Marine zoologists (see Mare 1942) distinguish between meiofaunas (c. 0.5–2 mm), small macrofaunas (c. 2–5 mm) and large macrofaunas (larger than about 5 mm). Because of the effect of the frequency dominance of the smallest forms (Jaanusson 1979 b: 260–262) and differences in effective sampling methods, it is very difficult to integrate the meiofauna and macrofauna in the same analysis. For example, in my opinion, attempts to consider ostracodes together with the macrofauna (Bretsky *et al.* 1977; Pickerill & Brenchley 1979; Lockley 1980 etc.) have not led to reliable results. In most rocks it is also difficult to integrate small and large macrofaunas in the same analysis. In many Lower and Middle Ordovician limestones of Sweden various authigenic minerals (mostly glauconite and chamosite) fill cavities within small shells. Insoluble residues from such limestones abound in small gastropods of the size range of the meiofauna and small macrofauna (Jaanusson & Mutvei 1953, Pl. 4; Jaanusson 1955, Pl. 10, 1960, Pl. 1, 5:1; Dzik 1978, Fig. 5). The existence of this gastropod fauna would hardly have been recognised with normal sampling. Studies of thin sections show that it is also

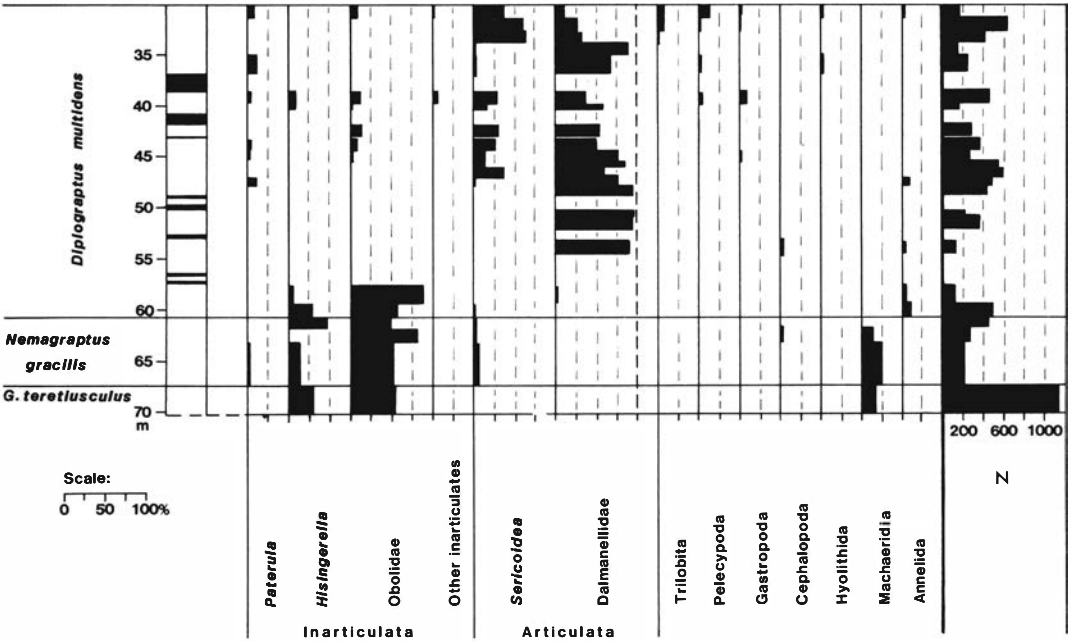

Fig. 1. Composition of the benthic microfauna in the lower part of the Koängen core, Scania, southern Sweden (S. Bergström & Nilsson 1974; Nilsson 1977), based on counts by Ragnar Nilsson (personal communication). In order to obtain an adequate sample size, data are pooled within various intervals of the core; note that this procedure causes a certain loss of resolution. Occurrences of less than 2% are not indicated. Black portions in the rock column refer to relatively thick bentonitic beds. Inarticulate brachiopods belong almost exclusively to the small macrofauna, while other groups represent the large macrofauna. Sericoidea *forms a borderline case with large adult valves somewhat exceeding a width of 5 mm (J. Bergström 1968, Fig. 6).*

present in many rocks without authigenic mineralisation. The gastropods include probable protoconchs (Dzik 1978) but possibly also small species which may have occupied a niche comparable to that of modern hydrobiids or small rissoids. Insoluble residues also invariably include numerous acrotretacean brachiopods in the size range of meiofauna and small macrofauna. The number of specimens of small inarticulate brachiopods vastly exceeds that of the total large macrofauna in many samples (for an example see Fig. 7). Finally, experience has shown that it is very difficult to obtain reliable quantitative data on the small macrofauna from a hard rock which can be compared with data on the large macrofauna in the same beds.

Thus, for several reasons meio- and macrofaunas should not normally be integrated in quantitative analyses of faunal assemblages, and in many cases it is also advisable to analyse small and large macrofaunas separately. In the following discussion small and large macrofaunas are integrated in the few cases where sampling has been adequate in this respect (e.g., Figs. 1–2,5), but because of the lack of reliable information mostly only the large macrofauna is considered.

The term *assemblage* is used here for faunal remains in a sample and *association* for a consistent co-occurrence of taxa. The existence on the sea floor of communities that form discrete ecological entities in which various species are dependent on each other because of strong biological interaction is doubtful. Most species are distributed individually in an overlapping manner and form continua along environmental gradients (Gray 1974).

A great number of various major taxonomic groups provide dominant species in Ordovician macrofaunal assemblages in terms of relative

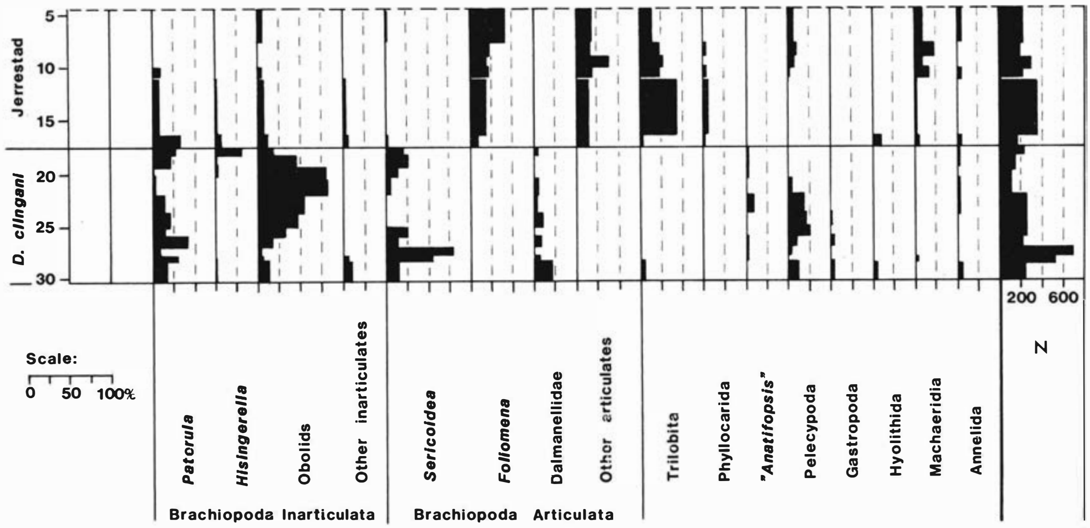

Fig. 2. Composition of the benthic macrofauna in the upper part of the Koängen core, Scania, southern Sweden (Nilsson 1977), based on counts by Ragnar Nilsson (personal communication). In this core there is a break between the Dicranograptus clingani *Zone and the Upper Ordovician Jerrestad Mudstone (*Dicellograptus complanatus *and* D. anceps *zones), comprising the* Pleurograptus linearis *Zone. None of the trilobite species in the Jerrestad Mudstone reaches as high as 10% of the total fauna. See also explanation of Fig. 1.*

frequency of individuals. Such groups are articulate and inarticulate brachiopods, trilobites, leperditiid ostracodes, bryozoans, pelecypods, gastropods, cephalopods, tentaculitoids (see Hurst 1979), hyoliths (see Jaanusson & Mutvei 1982, Fig. 5), cystoids, and in places probably also some other benthic group. In addition, there are assemblages without any obvious dominant species (equitaxial associations; see Appendix, samples 4–5; from personal observations, the large macrofauna in the Ashgill rocks (5a) in Ringerike, Norway, also appears to have a similar equitaxial composition). A benthic macrofauna without numerically dominant species is unusual (for recent discussion see Jaanusson 1979 b: 259–261), and in such cases the question arises as to whether the dominant species might have been soft-bodied organisms.

Examples are given below of various Ordovician associations, separately for each major taxonomic group that provides dominant species and with emphasis on successions of associations that were controlled by environmental gradients. The majority of the available quantitative data on the composition of the fauna is from the Middle Ordovician, and this is considered first in the following discussion.

Brachiopod associations

A common environmental gradient reflected in the lithological transition from graptolitic shale to coarser grained, shelly deposits, can be illustrated by data (Figs 1, 2) provided by Ragnar Nilsson from the Koängen boring in Scania, southern Sweden (Nilsson 1977). In graptolitic shales from *Glyptograptus teretiusculus, Nemagraptus gracilis* and basal *Diplograptus multidens* zones, large macrofaunas are very rare and machaeridians form the dominant component. The non-graptoloid fauna consists mainly of inarticulate brachiopods, mostly obolids, in the size class of small macrofauna. Such an abundance of small inarticulates is a fairly common phenomenon in graptolitic shales (Ruedemann 1934; Bulman 1964). It is customary to interpret the inarticulates as epifauna attached by their pedicles to floating weeds. However, this is hardly probable (see also Cisne 1973) for several reasons which cannot be fully discussed here. Lingulelline obolids, which form an important constituent of the small macrofauna in several portions of the core (particularly in the *G. teretiusculus* Zone), were obviously endobionts; large lingulellines have frequently been found in vertical life position, and they had a mode of life and function of the fleshy pedicle comparable with those of modern lingulids. Obolellines and paterulids most probably also belonged to the endofauna. In my view, the problem in this context is not the relative abundance of small inarticulates but the rarity of associated large benthic macrofaunal organisms. Several explanations are possible. (1) The very fine grained terrigenous mud was an unsuitable substrate for large skeleton-bearing organisms. (2) There may have been an oxygen-dependent zonation of the fauna, with the large skeleton-bearing macrofauna disappearing at higher oxygen levels than much of the small macrofauna. (3) The large macrofauna may have had a competitive disadvantage over the small macrofauna in areas of very low food supply.

The articulate brachiopods normally found in Middle Ordovician graptolitic shales are small aegiromenines, such as *Sericoidea* and *Chonetoidea,* in the size class of small macrofauna but with large adults of several species somewhat exceeding 5 mm in width. It has been claimed that these forms also lived as epiplanktic epifaunas (Havliček & Vaněk 1966: 39–40; Havliček 1967; J. Bergström 1968) or were attached to algal fronds which sank to the bottom (Sheehan 1976). However, aegiromenines obviously lacked a pedicle, and it is difficult to understand how their shells were attached (see also Hurst 1979: 225). It is probable that these forms, like many other plectambonitaceans, had a recumbent mode of life, lying free on the sediment surface.

With increasing coarseness of the substrate dalmanellids become a common or even dominant component of the large macrofauna (Figs. 1–2). A pair of species, consisting of a recumbent aegiromenine and a pedunculate dalmanellid, forms an important macrofaunal consistuent in many Middle Ordovician shales and mudstones (see also Hurst 1979 and Lockley 1980).

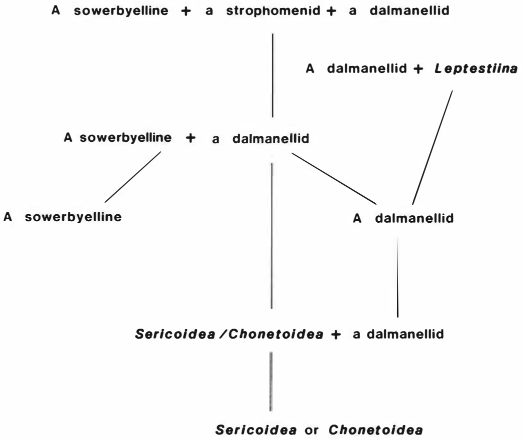

Fig. 3. Diagrammatic presentation of a common Middle Ordovician succession of articulate brachiopod associations along the gradient from graptolitic shales to coarser grained rocks.

In somewhat coarser sediments sowerbyellines (*Viruella, Sowerbyella* or *Thaeorodonta,* rarely *Eoplectodonta*) appear to replace aegiromenines as dominant recumbent macrofaunal forms. Williams *et al.* (1981: 685) suggested that sowerbyellines were mobile, but this appears to be very unlikely. The earliest known assemblages in which a sowerbyelline forms the dominant constituent of the large macrofauna occur in the Fairfach Group (upper *Didymograptus murchisoni* Zone) of Wales (Williams *et al.* 1981). In these beds *Viruella antiqua* (Jones) occurs in association with a common dalmanellid, and such an association of a recumbent sowerbyelline and a pedunculate enteletacean species as dominant elements in skeleton-bearing large macrofaunas is widely distributed in the Middle and Upper Ordovician. It has been described from the British Isles (Hurst 1979; Pickerill & Brenchley 1979; Lockley 1980; Williams *et al.* 1981) and the U.S.A. (Fox 1962; 1968; Bayer 1967; Bretsky 1970a; Titus & Cameron 1976; Cisne & Rabe 1978; Rabe & Cisne 1980). A similar association characterises parts of the upper Middle Ordovician Saue beds of the Keila Stage in north-western Estonia (Appendix, sample 2). The sowerbyelline and dalmanellacean species also occur separately in almost unitaxial assemblages, crowding bedding planes or thin beds (see Appendix, sample 3). At a further stage, a relatively large, common or even dominant strophomenacean species, normally with a recumbent mode of life and thus belonging to

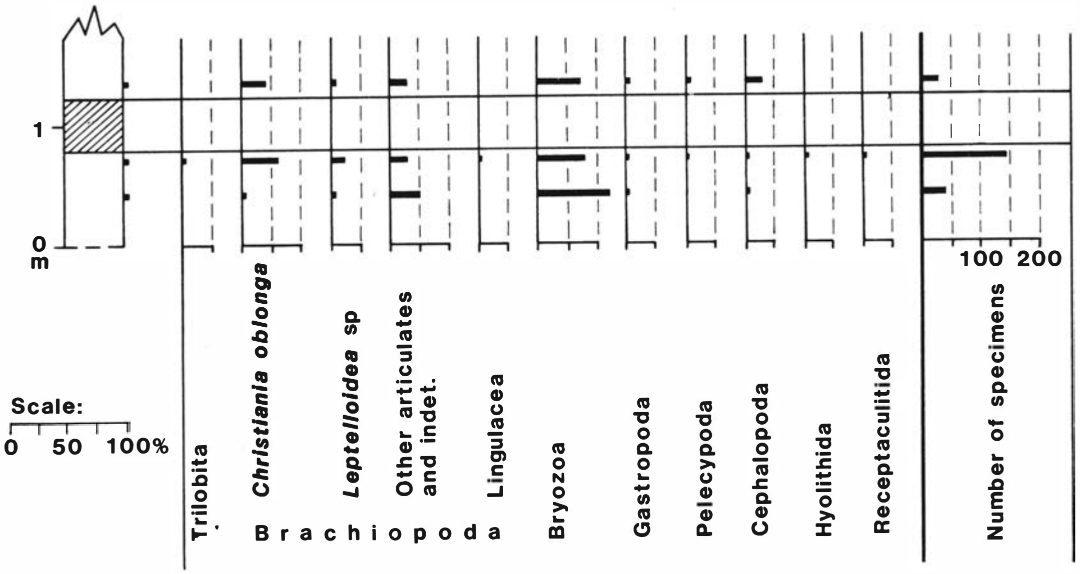

Fig. 4. Composition of the large macrofauna in the Kallaste Beds of the Lasnamägi Stage (upper Didymograptus murchisoni *Zone), Kadaka quarry (Rõõmusoks 1970:52), north Estonia; surface sampling by V. Jaanusson in 1940. The portion in the rock column with diagonal shading refers to the index dolomite bed. The composition of the large macrofauna in contemporaneous limestones (lower Folkeslunda Limestone) of the central Baltoscandian confacies belt is shown in Fig. 7 (see also Jaanusson & Mutvei 1982:7).*

the soft bottom epifauna, accompanies a sowerbyelline and an enteletacean species (e.g., Cisne & Rabe 1978; Pickerill & Brenchley 1979; Hurst 1979; Rabe & Cisne 1980). In another, fairly distinctive association the sowerbyelline species is replaced by a species of *Leptestiina,* a recumbent form of about the same size, which occurs in association with a common to dominant dalmanellid species (Hurst 1979; a similar association characterises the Moldå Topoformation of Sweden).

The succession of Middle Ordovician brachiopod associations along the environmental gradient beginning with graptolitic shales is summarised diagrammatically in Fig. 3. There are associations with other dominant brachiopods, but their relationship to the environmental gradient under consideration is not clear. The small strophomenacean *Foliomena,* of about the same shape and size as small sowerbyellines, is the dominant brachiopod in certain Upper Ordovician mudstones (Fig. 2; Sheehan & Lesperance 1978, Table 1; Harper 1979, 1980), in a habitat which appears to be roughly comparable to that of *Sericoidea* or *Chonetoidea.*

In some Middle Ordovician environments the fairly small and globose strophomenacean *Christiania,* a probable ambitopic form, provides the dominant macrofaunal species (Fig. 4; *C. subquadrata* at the base of the Arline Formation in Tennessee etc.).

Several Middle and Upper Ordovician associations in which an articulate brachiopod species is dominant have a biogeographically restricted occurrence. This is particularly evident in some very shallow water assemblages of the North American Midcontinent Province, where rhynchonellaceans such as *Rostricellula* (Walker & Alberstadt 1975; Shaw 1980; the genus is known to be dominant in several other areas), *Ancistrorhyncha* (e.g., Corbin Ranch Formation of the Arbuckle Mountains, Oklahoma) and *Orthorhynchula* (Bretsky 1969, 1970a), and the atrypid *Zygospira* (Bretsky 1969, 1970a; Copper & Grawberger 1978) are very common in places.

The Lower Ordovician brachiopod associations along the gradient beginning with graptolitic shales are poorly known. Fjelldal's (1966)

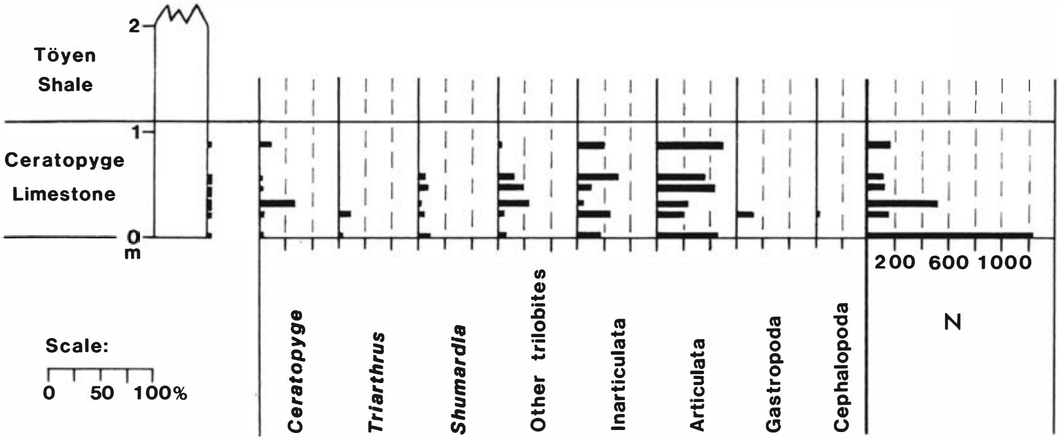

Fig. 5. Composition of the macrofauna in the uppermost Tremadoc Ceratopyge Limestone at Bjerkåsholmen, Oslo Region (after Fjelldal 1966). Bulk sampling. The relative frequencies are shown only for those trilobite genera that form 10% or more of the total fauna in at least one sample.

data from the uppermost Tremadoc Ceratopyge Limestone of the Oslo region, Norway (Fig. 5) show a dominance of small orthid brachiopods among which *Nanorthis? christianiae* (Kjerulf) is the dominant species. Such small species, belonging to the small macrofauna or somewhat larger, are mostly homoeomorphs of later dalmanellids and provide dominant species in many Lower Ordovician assemblages. Examples are *Nanorthis? suecica* Tjernvik in the *Armata* Limestone (*Tetragraptus phyllograptoides* Zone) of Sweden and *Ranorthis parvula* Rubel in the Mäeküla beds (*Phyllograptus densus* Zone) of northern Estonia. The earliest known assemblage in which enteletaceans provide the dominant species is in the Vääna Limestone (Volkhov Stage, middle *D. hirundo* Zone) of northern Estonia (Appendix, sample 1), and from then on enteletaceans form an important constituent in many assemblages.

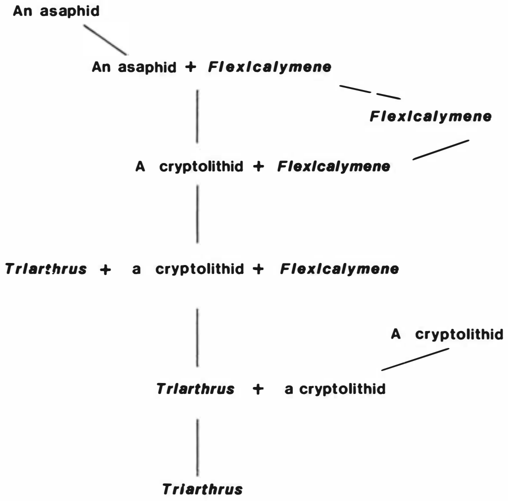

Fig. 6. Diagrammatic presentation of a common Middle Ordovician succession of trilobite associations along the gradient from graptolitic shales to coarser grained rocks.

Trilobite associations

A diagrammatic presentation of a Middle Ordovician succession of trilobite associations along the environmental gradient beginning with graptolitic shales, is given in Fig. 6. The olenid *Triarthrus* tends to be a common to dominant component at the transition from graptolitic shales to graptolitiferous mudstones (Cisne 1973; Fortey 1975: 347; Cisne & Rabe 1978; Rabe & Cisne 1980); similar *Triarthus*-dominated assemblages occur, for example, in the upper part of the Örå Shale, *Dicranograptus clingani* Zone, of Jämtland, northern Sweden). This is a low-diversity, Middle Ordovician equivalent of the Upper Cambrian-Arenig olenid-dominated associations which have a much higher taxonomic diversity of olenids in

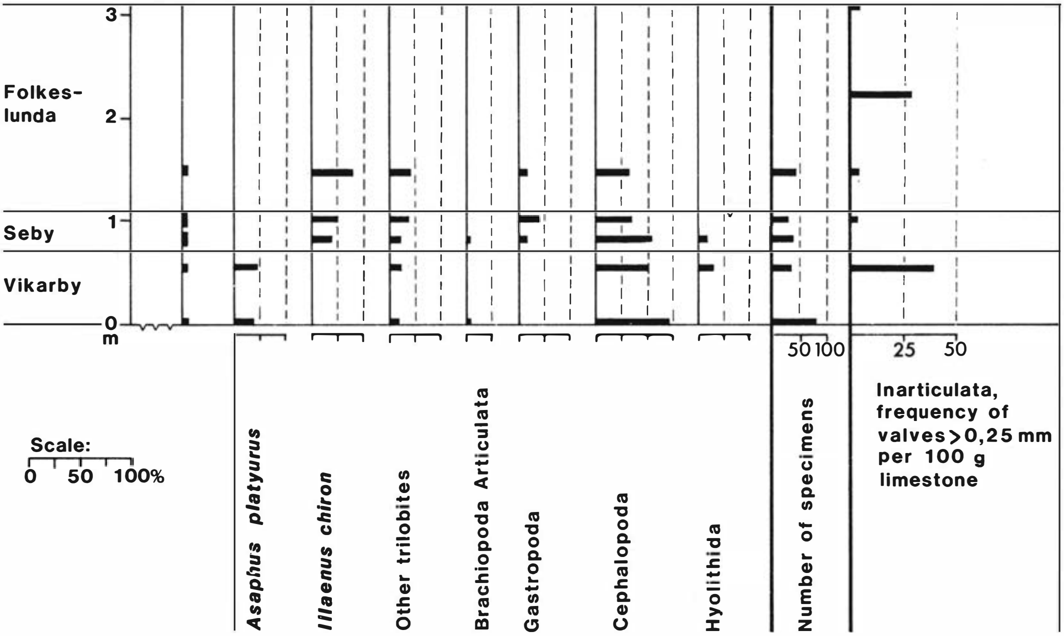

*Fig. 7. Composition of the large macrofauna in the Vikarby, Seby and Folkeslunda Limestones (*Didymograptus murchisoni *Zone) at Vikarbyn (Jaanusson & Mutvei 1953), Siljan district, central Sweden. Bulk sampling by V. Jaanusson and H. Mutvei in 1947. The column on the right shows the frequency of inarticulate brachiopods, mainly acrotretaceans, in the insoluble residue from five limestone samples treated with acetic acid.*

a roughly similar habitat. In sediment reflecting increased water energy, *Triarthrus* commonly occurs in association with a subdominant to dominant *Flexicalymene* or a trinucleid species (Cisne 1973). At a somewhat later stage *Flexicalymene* occurs either alone (Cisne & Rabe 1978; Williams *et al.* 1981) or together with either trinucleid or an asaphid species. At about this stage a trinucleid is also the dominant trilobite species, not only in the Middle Ordovician (Brestky & Brestky 1975; Hurst 1979; Lockley 1980) but also in the pre-Hirnantian Upper Ordovician (J. Bergström 1973; Sheehan & Lespérance 1978, Table 1). Further stages are difficult to analyse at present owing to the paucity of quantitative information, and because of differences in tabulation conventions between various published data.

The described succession of Middle Ordovician trilobite associations is developed parallel to, but largely independent of that of brachiopod associations along the same environmental gradient. Trilobites and articulate brachiopods frequently occur in association but the correlation along the gradient is not very close, implying that the environmental factors that controlled the distribution of these two groups were partly different. In the Koängen core (Figs. 1–2) the Middle Ordovician sequence is almost devoid of trilobites; conversely, the *Triarthus* association tends to be very poor in articulate brachiopods.

Fortey (1975) analysed the succession of upper Lower Ordovician trilobite associations along the same gradient from Ny Friesland, Spitsbergen. There the olenid-dominated association has a far higher taxonomic diversity than in the Middle Ordovician, and is followed by assemblages in which nileids form an important constituent. In the contemporaneous rocks of the central Baltoscandian belt *Nileus* is also common, and here it appears to be characteristic of mud bottoms, now represented by calcilutites and mudstones; on skeletal sand bottoms the genus is rare to absent, as are other nileids. In Ny Friesland the nileid-rich beds are succeeded by high energy, shallow water limestones in which *Illaenus* is the dominant component in a fauna of North American type. In the central Baltoscandian belt, the dominant forms in the roughly contemporaneous calcarenites are the endemic genera *Megistaspis* (lower part) and *Asaphus* (upper part; Jaanusson & Mutvei 1982, Fig. 6).

Middle Ordovician successions of trilobite associations have been described from Canada by Chatterton & Ludvigsen (1978 a) and Shaw (1980). Many taxa in the associations of the carbonate platform are restricted to the North American Midcontinent Province. Particularly characteristic is the association with *Bathyurus* and related bathyurids (see also Ludvigsen 1978 b) which is widely distributed in North America (Jaanusson 1979 a, Fig. 7). A succession of trilobite associations along an inferred environmental gradient in Kazakhstan was outlined by Apollonov (1975).

Pelecypod associations

Pelecypods form an important accessory component in many Ordovician assemblages, but they are particularly common in terrigenous siltstones and sandstones where a particular species is often dominant (e.g., Bretsky 1969, 1970a, b; Bretsky & Bretsky 1975; Spjeldnæs 1979). Many of these common Ordovician clams were byssaly attached epifaunal suspension feeders. In some Middle and Upper Ordovician limestones of the North American Midcontinent region pelecypods are also fairly common (Bayer 1967; Copper & Grawbarger 1978) or even dominant in places (Bretsky *et al.* 1977).

Along the environmental gradient from graptolitic shales pelecypods occasionally form an important constituent of the macrofauna, especially in the *Sericoidea/Chonetoidea*–dalmanellid association (Fig. 2; Hurst 1979). The dominant forms there, such as *Similodonta,* were infaunal deposit feeders.

Some other associations

Ordovician leperditiid ostracodes are confined almost exclusively to the North American Midcontinent Province. In many places they form the dominant macrofaunal component in assemblages from very shallow water carbonate deposits (Hatfield 1968; Walker 1972). The association commonly has a very low taxonomic diversity and it obviously inhabited a somewhat extreme environment.

Cephalopod-dominated assemblages appear to be mostly allochthonous, transported and sorted. Assemblages in which cephalopods are dominant characterise, for example, certain beds in the "Orthoceratite Limestone" of the central Baltoscandian belt, especially the Middle Ordovician portion of the limestone (Fig. 7). In these beds abundant orthocone cephalopod conchs are associated with large disarticulated asaphid or illaenid trilobites, the asaphids at several horizons being almost exclusively large pygidia. In places the accumulation of cephalopod conchs occurs in association with probable desiccation cracks and stromatolitic algal mats (Larsson 1973), suggesting supratidal conditions. The only modern analogue known to me in which cephalopod conchs are the dominant skeleton-bearing constituents, is on the sandy beaches just east of the southernmost point of Gran Canaria, north of Punta de Maspalomas. Here, above high-water level, two separate counts of skeleton-bearing organisms showed conchs of *Spirula* (71% and 76%) to be the dominant component of the assemblage, together with *Sepia* (4% and 7%), clams, the cirripede *Lepas,* crabs, and a few fronds of *Halimeda.*

Discussion

The environmental gradient reflected in the lithological succession from various bedded limestones through argillaceous, nodular limestones ("marls") and mudstones to graptolitic shales is mostly regarded as being related to increasing depth of the sea. The biofacies succession along this gradient is therefore fairly generally assumed to have been controlled by depth. However, the tendency for hydrodynamic water energy to decrease with increasing water depth has many exceptions, and for this reason this depositional model should not be applied indiscriminately. In particular, in a lithological succession which involves both carbonate and terrigenous sediments, the effect of competitive sedimentation should be considered. In such cases the sediment type, whether predominantly carbonate or terrigenous, is determined by a competition in the sediment supply from two different sources, i.e. from areas producing carbonate particles and those supplying terrigenous material. Thus if little or no terrigenous material were available for deposition in the mudstone belt, the resulting rock would very probably have been limestone. The effect of competitive sedimentation should be carefully considered particularly in basins or troughs such as the Scandinavian Caledonides or Appalachians, in which deposition was pronouncedly assymetrical with the deposition of carbonates on one side and predominantly terrigenous material on the other. In such areas much of the fine carbonate material was supplied from the cratonic side of the basin and the terrigenous material from the opposite side. In such conditions graptolitic clay could well have been deposited within the same basin at the same depth as carbonate mud or even in shallower waters.

The important ecological point in this context is that below a particular, fairly inconsiderable depth, the depth-dependence of the benthic fauna is relatively slight and is normally overshadowed by the dependence on the substrate. In the general dependence of benthic animals on depth conditions within the archibenthal region, the effects of temperature frequently overshadow those of hydrostatic pressure. In northern Europe, for example, the deposition of modern fine terrigenous mud (of a type that might become lithified into a rock comparable to graptolitic shale) begins mainly at a depth of about 200–250 m, but in some fjords the same sediment is produced at depths as low as 30 m, and eurythermal elements of the fauna adapted to this type of substrate follow the sediment type. In other geographical settings a comparable mud could be deposited in even shallower water. For this reason, in the distribution of various benthic associations of fossils more attention should be focused on the physical properties of the substrate than on assumed depth conditions.

The associations of fossils outlined diagrammatically in Figs. 3 and 6 appear to be basically substrate-dependent, although the distribution of the constituent species was also controlled by temperature, hydrostatic pressure, oxygen content of the sea water, and quantity as well as type of nutrients. A problem in assessing the available data on Ordovician faunal associations is the frequent lack of basic information on the properties of the substrate, and particularly the sediment grain size, in carbonate rocks.

The taxonomic diversity of the skeleton-bearing fauna in fine grained subtidal rocks, either carbonate or terrigenous, tends to be much lower than in rocks that were deposited at higher water energies. However, account should be taken of the fact that such fine grained bottoms were inhabited mainly by soft bottom infaunas, and that in comparable modern environments the importance of skeleton-bearing animals in the total fauna is much lower than in many environments associated with a higher water energy, particularly in those that are inhabited also by hard-bottom organisms (see also Craig & Jones 1966). Thus the taxonomic diversity of skeleton-bearing animals does not necessarily reflect the overall diversity of the fauna, soft-bodied organisms included.

The distributional patterns outlined above indicate that shallow water associations on the platforms tend to be geographically restricted, whereas faunas along the margins of the cratons, mainly in fine grained, argillaceous or terrigenous rocks, have a wider spatial distribution (see also Fortey 1975 and Ludvigsen 1978 a). Because the fine grained bottoms extend into deep water there is a wider spatial continuity of the environment, and this decreases the biogeographical differentiation, even when the environment extends into shallow water where it can be inhabited by eurythermal representatives of the fauna adapted to such a substrate.

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Appendix

Quantitative estimates of the composition of large macrofaunas from the Ordovician of Estonia, referred to in the text. Surface sampling, 1–3 by V. Jaanusson in 1940, 4–5 by V. Jaanusson, R. Männil and H. Neuhaus in 1940.

1. Volkhov Stage, Vääna Beds ($B_{II}\beta$). Mäekula. N = 28. Brachiopods: Articulata, 86%, Inarticulata, 2%, Bryozoa: 12%, Trilobita: 1%. Commonest species: *Paurorthis parva* (Pander) 60%, *Productorthis obtusa* (Pander) 21%.
2. Keila Stage, Saue Beds. Jälgimägi quarry (Rõõmusoks 1970: 257). Surface A is about 0.2 m above surface B. N = 54. Brachiopoda Articulata: 41 specimens, Bryozoa: 9, Pelecypoda: 1, Cephalopoda: 2, Gastropoda: 1. Commonest species: *Sowerbyella forumi* Rõõmusoks 28%, *Horderleyella kegelensis* (Alichova) 26%, *Clinambon anomalus* (Schloth.) 9%, *Strophomena ? occidens* (Oraspõld) 8%. B (N = 33): Brach. Art. 26 specimens, Bryozoa 5, Hyolithida 1. Commonest species *Sowerbyella forumi* 58%, *Horderleyella ? kegelensis* 6%, *Clinambon anomalus* 6%.
3. Keila Stage, Saue Beds. Saue quarry (Rõõmusoks 1970: 256), uppermost exposed beds. N = 66. Brachiopoda: Articulata 56 specimens, Gastropoda: 4, Trilobita: 2. Commonest species: *Horderleyella ? kegelensis* 62%, *Clinambon anomalus* 18%.
4. Vormsi Stage, Vormsi, Saxby N. N = 51. Brachiopoda: Articulata 21 specimens (Orthacea 15, Enteletacea 2, *Eoplectodonta schmidti* 3, *Strophomenacea* 1), Inarticulata (*Pseudolingula quadrata*) 1, Bryozoa: 7, Rugosa: 2, Heliolithida 3, Stromatoporoidea 1, Gastropoda: 5, Trilobita: 5, Dendroidea: 6, Conulariida: 1. The only relatively common species: *Nicolella* n. sp. 16%.

6. Pirgu Stage, Cormsi, Hosholm. N = 37. Brachiopoda Articulata, 11 specimens (Orthacea 2, Enteletacea 1, Plectambonitacea 1, Strophomenacea 3, Porambonitacea 1, Atrypacea (*Eospirigerina*) 3, Bryozoa: 4, Rugosa: 3, *Palaeofavosites* 5, other Tabulata 4, Heliolithida: 2, Gastropoda: 2, Trilobita: 3, Dendroidea: 1, Cephalopoda: 2. No dominant species.

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