ECOLOGICAL ASSOCIATIONS IN A REGRESSIVE SEQUENCE: THE LATEST ORDOVICIAN OF THE OSLO-ASKER DISTRICT, NORWAY

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ABSTRACT. Ten faunal associations are defined and documented from numerous collections made in the late Ashgill rocks of the Oslo-Asker district, Norway. The distribution of the associations is integrated with previous work on the sedimentology which demonstrated a regressive sequence caused by the eustatic fall in sea level due to the end-Ordovician glacial event. The associations in late Rawtheyan times were a *Tretaspis* Association in the deeper shelf, with an *Onniella* Association midshelf, which was also colonized in places by *Palaeoporella* thickets and by cystoids. The *Onniella* Association persisted into Hirnantian times, with the *Hirnantia* Association *sensu stricto* situated up-slope from it. Shallower still were the *Dalmanella*, *Hindella-Cliftonia*, and *Holorhynchus* Associations, with other associations dominated by bivalves and *Monocraterion* inhabiting the lower shoreface. More specialized *Thebesia* and *Brevilamnulella* Associations are also recognized, which colonized tidal channels and ooidal shoals at the top of the Ashgill sequence. The area was subsequently blanketed by the early Silurian transgressive deposits containing at their base specialized shelly faunas and then shales with graptolites, some of which can be attributed to the early Llandovery *acuminatus* Zone.

LATE Ordovician faunas in the Oslo-Asker district of Norway are found within a well-marked regressive sequence (Brenchley and Newall 1975) which provides an excellent framework in which to study the nature of the faunal associations and their environmental distribution. In spite of the fact that our locality collections tend to contain a small number of individuals, they are rich in species and it is possible to recognize recurrent associations which occur in consistent sequence in many laterally equivalent successions and apparently reflect a spectrum of environmentally controlled animal communities.

The vertical sequence of fossil associations can be related to a sequence of sedimentary facies, starting with mudstones of an open-shelf environment passing through various facies of the shoreface, and ending with oolite shoal and tidal channel facies. However, as well as the vertical arrangement of fossil associations there are also lateral changes in the fauna which are probably related to an Ordovician palaeoslope which declined eastwards from the Asker district towards the Oslo district. These lateral changes in fauna can be inferred because there are some distinctive lithological horizons, believed to be synchronous, which can be traced throughout most of the area, and thus enable us to establish some lines of correlation which are independent of the fauna.

Towards the end of the Ordovician there was an episode of extinction affecting several fossil groups (Newell 1967; Paul 1976; Rickards 1978) which caused a discontinuity between Ordovician and Silurian faunas, particularly in North America. This discontinuity has been related to lowered sea level associated with the end-Ordovician glaciation of 'Gondwanaland' (Sheehan 1973; Berry and Boucot 1973). Many late Ordovician faunas have a low diversity and are commonly represented by a single *Hirnantia* fauna which might possibly be associated with widespread cold surface waters (Sheehan 1979). However, some, possibly lower latitude, Hirnantian faunas can be relatively diverse (Bergström 1968; Williams and Wright 1981). The Hirnantian rocks of the Oslo-Asker district are believed to have formed in sub-tropical latitudes and contain faunas which are not only diverse but occur in several distinct associations.

This paper describes the late Ordovician associations, relates them to vertical and lateral environmental changes, and discusses the extent to which late Ordovician warmer water associations are modified by contemporaneous glacio-eustatic sea level changes.

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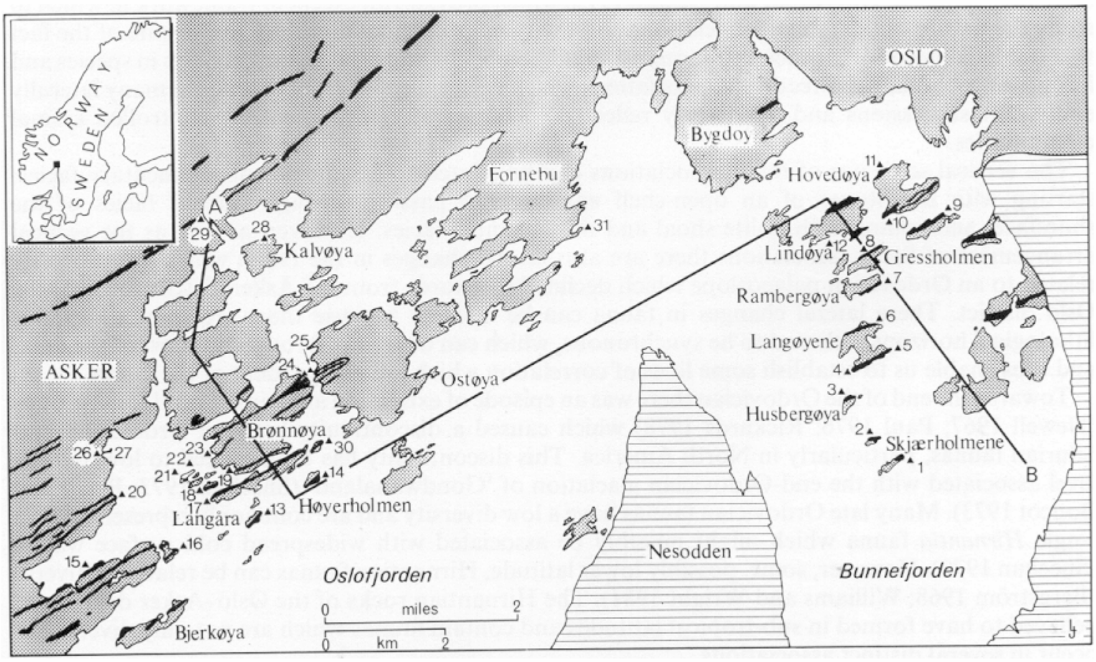
STRATIGRAPHICAL FRAMEWORK

Upper Ordovician rocks are repeatedly seen on the flanks of tight north-east- to south-west-trending folds in the Oslo–Asker district. The complete upper Ordovician sequence, described by Brenchley and Newall (1975), is seen at nearly thirty localities on the shores of the islands in the Oslofjord and the Bunnefjord and there are other less complete sequences exposed inland (text-fig. 1, localities 1–31). Faunas have been collected from nineteen of these sections (text-fig. 3) and the distribution of the fauna has been noted in all the others.

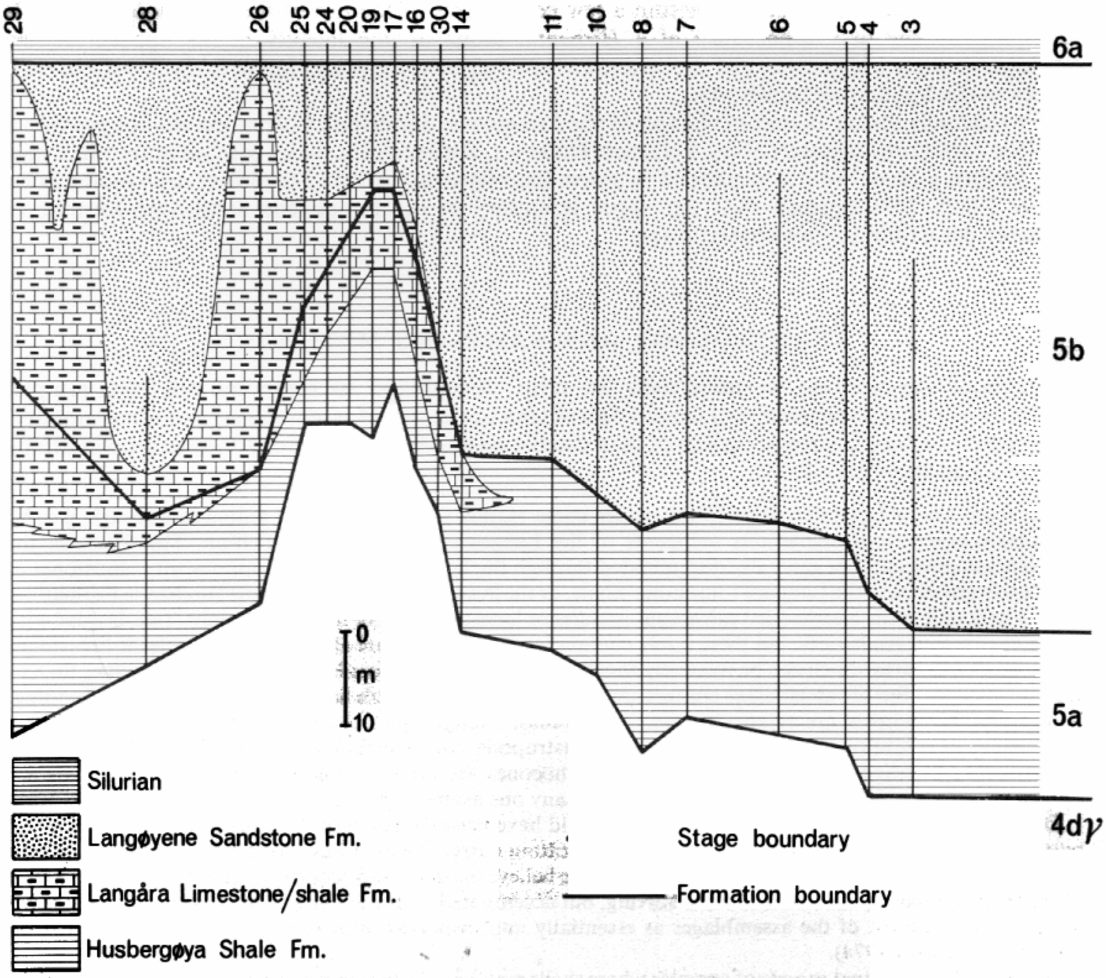
The upper Ordovician rocks of the area occur as three formations, with a lower Husbergøya Shale followed by two laterally equivalent formations, the Langøyene Sandstone in the east and the Langåra Limestone–Shale Formation in the west. There is, however, some intertonguing of the three formations in the middle part of the area (text-fig. 2). We have modified the stratigraphical profile shown in figure 3 of Brenchley and Newall (1975) to emphasize the deep erosion and channelling which is found in the north-west part of the area. The mainly coarse-grained sediments which fill the channels have been included within the Langøyene Sandstone Formation.

We have found it useful to continue using, in an informal way, the long-established Norwegian Etasjer, even though Owen (1978) and Bruton and Owen (1979) have recommended that their use be discontinued. Initially the Etasjer were based on lithostratigraphical criteria, though later they were given chronostratigraphical status (Code of Stratigraphical Nomenclature for Norway, 1969). The upper Ordovician Etasjer are shale/nodular limestone rhythms chiefly from 10 to 50 m thick. They are clearly developed within the Oslo–Asker district but cannot be correlated more widely, so there appears little justification for more than their local use. However, because the rhythm boundaries reflect changes in deposition from suspension of mainly argillaceous material in a shelf environment it is possible that the boundaries are synchronous throughout the local area (but see Bruton and



TEXT-FIG. 1. Locality map showing the position of the principal sections through Stage 5 in the Oslo–Asker district. The Precambrian is shown with horizontal shading, the Lower Palaeozoic with stipple, and Stage 5 is shown black. The line A–B shows the position of the stratigraphic profiles shown in text-figs. 3, 7, and 8.

Owen 1979 for an alternative view). This suggestion is supported, as far as the Stage *5a* boundaries are concerned, by the precise lithological similarity of the Stage *5a* sequences in the Oslo–Asker district from section 3 to section 25 in text-fig. 2. Each section shows a sharp change at its base from the nodular limestones of *4dγ* to the shales of *5a*, and contains a very distinctive development of large spreiten-bearing ichnofossils (Pl. 85, fig. 5) particularly cf. *Trichophycus* (Seilacher and Meischner 1965) about 3 m above the base. Interbedded with the succeeding shales are thin sandstones deposited from storm-generated currents which reach their peak frequency at a level between 40% and 60% up the sequence, but are always absent in the top 10–20% of the sequence (Brenchley, Newall and Stanistreet 1979). Finally, the top 1–3 m is always a bioturbated very fine brownish-weathering sandstone, characteristically containing cystoids. These features occur so consistently in each section that we believe they are good evidence for the synchroneity of each lithological horizon. The correlation so established allows the recognition of the Stage *5a/5b* boundary in the mid-western sections, where the Langåra Limestone–Shale Formation is developed as a lateral equivalent to the upper part of the Husbergøya Shale (text-fig. 2).



TEXT-FIG. 2. Stratigraphical profile from north-west to south-east across the Oslo–Asker area. The numbered vertical lines refer to the measured sections shown in text-fig. 1.

Although it is possible to recognize the $4d\,\gamma/5a$ boundary throughout the whole of the study area, there are subtle changes in facies towards the north-west, and neither the distinctive spreiten-bearing trace fossil horizon nor the cystoid-bearing sandstone can be traced north-westwards of locality 25. Consequently the top of the $5a$ cycle cannot be located with confidence, but we have tentatively placed it 2 m above the last thin sheet sandstone in the section to conform with other sections in the Asker district. Since the faunas on this north-west part of the area are also different from those to the south-east and lack both the stratigraphically valuable *Tretaspis* fauna and the *Hirnantia* fauna, it is not possible to make a firm correlation there on biostratigraphical evidence.

Throughout most of the area the faunas provide a basis for correlation with the type Ashgill sequence in Britain. The Husbergøya Shale has *T. sortita broeggeri* widespread in the topmost few metres of the formation, which Owen (1980) regarded as indicative of the topmost part of the Rawtheyan Stage. Since *Tretaspis* disappears within the bioturbated sandstone at the top of the Husbergøya Shale and is absent in the shales at the base of the overlying Langøyene Formation, it appears likely that this disappearance is of stratigraphical rather than of ecological significance. In Britain *Tretaspis* disappears abruptly at the top of the Rawtheyan (Ingham 1966). This placing of the Rawtheyan/Hirnantian boundary within a few centimetres of the top of the Husbergøya Shale is supported by the first appearance of a *Hirnantia* fauna at one locality in the uppermost few centimetres of the Formation, and the appearance more generally of that fauna in the lowermost few metres of the Langøyene Sandstone.

The relatively sparse faunas at the top of the Langøyene Sandstone Formation do not provide a basis for correlating this part of the sequence. However, the overlying shales contain graptolites, and have yielded a fauna from a locality 11 m above their base indicative of the lower *acuminatus* Zone (Howe 1982). This suggests that the upper boundary of the Langøyene Sandstone Formation probably lies within the *persculptus* Zone.

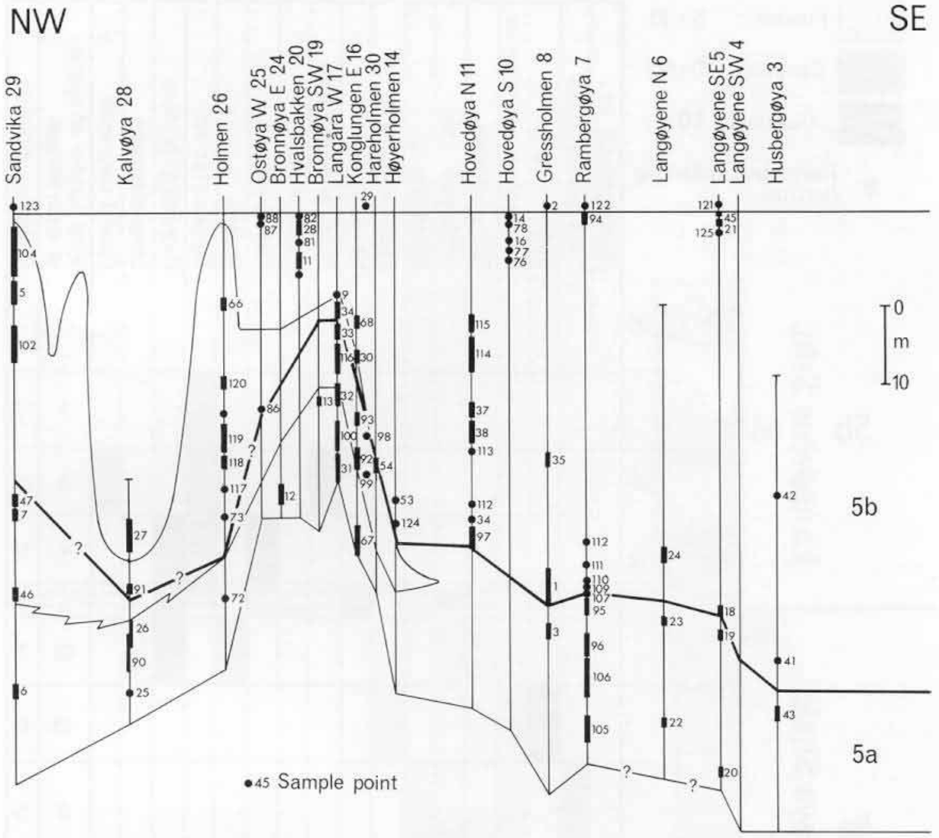
TERMINOLOGY AND SAMPLING METHODS

Throughout this account we have used the term 'assemblage' to mean the collected sample; 'association' refers to the recurrent association of taxa in a group of assemblages; and a 'community' is regarded as a biological association of taxa usually related to particular environmental conditions (Pickerill and Brenchley 1975).

The fossil assemblages described in this paper come mainly from argillaceous sediments, though a small proportion come from arenaceous sediments of the Langøyene Sandstone Formation. The fossils in the argillaceous sediments are generally disseminated through the bioturbated grey, calcareous silty mudstones of the Husbergøya Shale, the Langåra Limestone-Shale, or the lower part of the Langøyene Sandstone Formation, or may be found in the interbedded calcareous nodules or limestone beds of the last two units. Interbedded with the shales are thin sandstones, but these rarely contain fossils, and there are also a few thin bioclastic limestones in the west of the area which can be relatively fossiliferous. Most of the fossils occur individually rather than in clusters, though a few life assemblage clusters are recorded, and most fossils lie at variable angles to the bedding. Bedding plane samples are relatively rare. The faunas, though sparse, are diverse and include variable proportions of trilobites, brachiopods, bryozoans, gastropods, corals, orthocone nautiloids, etc. The trilobites usually occur as fragments, the gastropods and orthocones are often complete, whilst the brachiopods are commonly represented by some articulated valves in any one assemblage.

Disturbance of the shells prior to fossilization could have been the result of deep storm waves, wind-driven bottom currents, or bioturbation of the sediment. Bottom currents would have sorted the shell material into layers and produced bedding plane assemblages, so we believe the dispersed occurrence and variable orientation of the shells is possibly the result of wave stirring, but accentuated by the activity of burrowing organisms. We therefore regard most of the assemblages as essentially untransported or at most 'disturbed neighbourhood assemblages' (Scott 1974).

However, there are two groups of samples where shells may have been significantly moved, even though they are still indigenous to the area. In a few assemblages of the *Dalmanella* and *Hindella–Cliftonia* Associations, brachiopods, corals, and *Tentaculites* occur in thin- to thick-bedded sandstones representing a shoreface

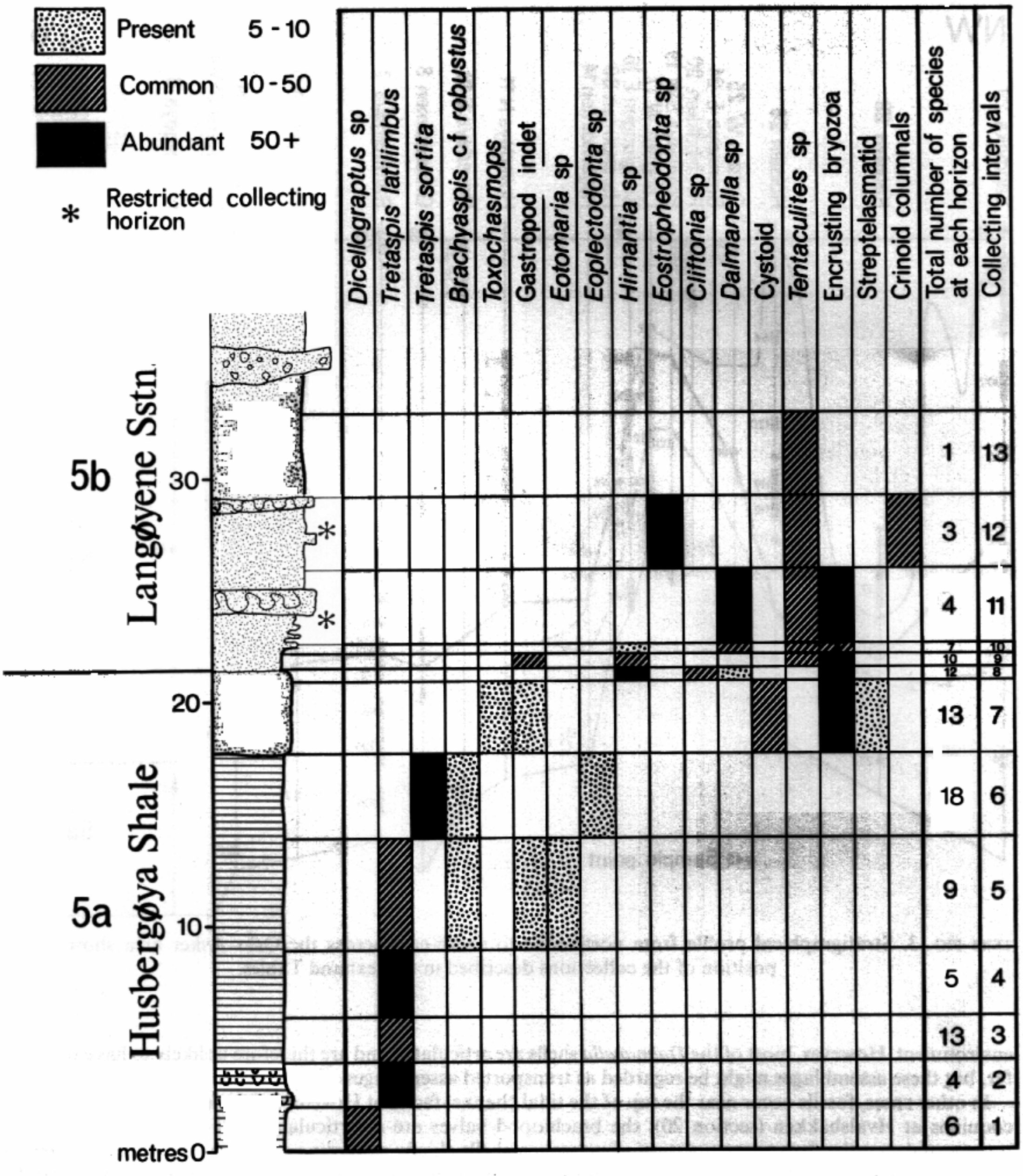


TEXT-FIG. 3. Stratigraphical profile from north-west to south-east across the Oslo–Asker area showing the position of the collections described in the text and Tables.

environment. However, most of the *Dalmanella* shells are articulated and are therefore unlikely to have travelled far, but these assemblages might be regarded as transported assemblages of local origin.

In other cases, fossils occur near the top of the tidal channel facies at Hovedøya (section 10) and in bioclastic coquinas at Hvalsbakken (section 20): the brachiopod valves are disarticulated and the faunas are clearly transported, but the dense accumulation of unbroken shells chiefly consisting of one or two dominant species suggests that the assemblage is indigenous to the area. In contrast, conglomeratic sediments filling the tidal channels have abraded corals and fossiliferous limestone clasts which are clearly allochthonous, and we have not considered these faunas in this account.

The very low density of fossils at most levels in the succession and the rarity of bedding plane assemblages has influenced our sampling methods. Bulk samples of a practical size (2–5 kg) have yielded very few fossils from these Ashgill sequences and therefore provide an incomplete sample of the fauna. Even persistent collecting from the outcrop has frequently yielded small samples which may be inadequate even to identify several of the taxa present. As an example, text-fig. 4 shows the results of collecting from the outcrop for two man hours per horizon in one section at Rambergøya. The thirty-four metres of the section yielded approximately fifty taxa, but of



TEXT-FIG. 4. The stratigraphical sequence at Rambergøya (section 7) showing the distribution of the commoner elements of the fauna in the sequence, and the diversity at each collecting interval.

these only six taxa occurred with more than fifty individuals within any one horizon, five other taxa were represented by between ten and fifty individuals, whilst all the other taxa yielded fewer than ten specimens. Note that in the Husbergøya Shale, in spite of a diversity as high as eighteen species per horizon, only *Tretaspis*, and at one horizon bryozoa, occurred as more than ten specimens. We have found that the ease with which fossils can be collected through the sequence is variable. This sometimes reflects the presence of a larger number of fossils but it also partially reflects the ease of collecting from the outcrop and the degree to which the shales have been decalcified. We have collected these relatively productive horizons (text-fig. 3) intensely, to a point where we find further collecting does not appear to significantly change the composition of the fauna, though we are aware that with such diverse assemblages further species are probably present. We have recorded field observations of the fauna in all the sections shown in text-figs. 2 and 3 to ensure that the less fossiliferous parts of the section are not found to contain a different fauna from that at the more richly fossiliferous levels. Further, we have systematically collected through two sections (7 and 17) to determine more rigorously whether our 'spot samples' were representative of broader stratigraphical levels. In nearly every case the spot samples contain the same fauna as the adjacent beds but are richer and have additional species. We therefore believe that the faunas from the sample-points shown on text-fig. 3 are a good reflection of the preserved biota, and may be used to analyse changing taxonomic composition and diversity in the succession.

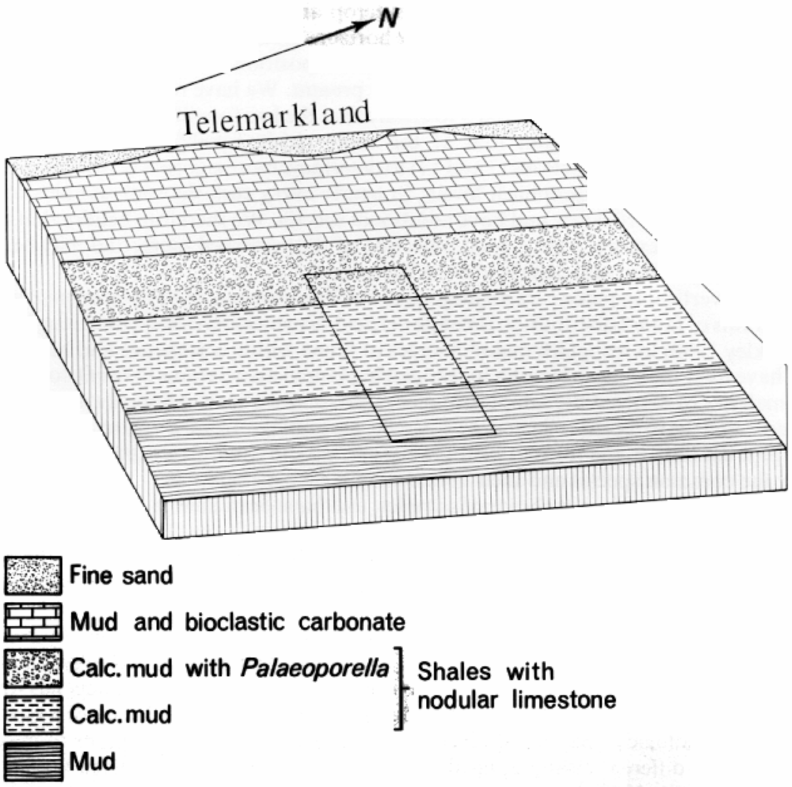
Samples collected in vertical sequence are analogous to the line transects used by modern ecologists (Djörjes 1971; 1972). Histograms of faunal distribution through vertical sequences have been used (e.g. by Hurst 1979*a*, *b*; Watkins 1979; Lockley 1980) to recognize major changes of fauna within a sequence and hence to define faunal associations. We have used the same principles in recognizing faunal associations in the Oslo region but, because of the relatively small size of many of the samples, and because some distinctive faunas are very restricted in their vertical distribution and have been collected as a single assemblage from a metre or two of section, it is inappropriate to plot the data in the form of histograms. We have instead presented them as a series of Tables (1-9) which show the common species and their abundance in each association.

Because we have been selective in our choice of samples, and have been unable to collect samples of the same size, we are unable to make quantitative statements about the density of faunas through the sequence, though an impression of varying density can be gained from text-fig. 4. The absolute values for the diversity of the assemblages are similarly affected by our sampling and should be used as a guide to the relative diversity of the assemblages.

In palaeoecological studies it is important to be aware of the limitations imposed on any conclusions by the nature of the sampling. The practical target population (Krumbein 1960) in palaeoecology is at its broadest 'the preserved part of the former biota'. However, the actual choice of target population depends upon the aims of the study. The aim may be to study the environmental distribution of a whole biofacies, or a particular group of fossils, it may be to test ecological theories of diversity, colonization, or equilibrium, or to make comparative studies of communities at different stratigraphical levels. The most commonly selected targets are 'the entire preserved biota' (e.g. Watkins 1979; Jaanusson, Laufeld and Sköglund 1979), or the preserved part of a single taxonomic group such as brachiopods or bryozoa (e.g. Williams 1976; Ross 1970), or the occurrence of individual genera or species (e.g. Broadhurst and Worsley 1975; Hurst 1978). Studies which restrict the target population often gain from more effective sampling, but lose by the restricted scope of the conclusions. We have selected the 'entire preserved biota' (apart from microfossils) as the target population, but we believe that brachiopods and trilobites are particularly well represented and identified in our faunal lists, whereas, for example, ostracodes are under-recorded, although we have tried to overcome this deficiency where possible by enlisting the aid of other specialists. It has not been possible to compare the completeness of our faunal records with previous lists because there are relatively few collections described from Stage 5 rocks in the Oslo-Asker district, and most of those that have been described are based on rather poorly localized museum collections. The taxonomy of fossils from the Oslo-Asker area is still under-studied, but Kiaer (1902) and Wright (1965) have recorded some brachiopods, Kiaer (1899), Wedekind (1927), Spjeldnaes (1964), and Neuman (1969) some corals, Strand (1934) has described the cephalopods, and the ostracodes were described by Henningsmoen (1954). The proetid trilobites were described by Owens (1970), and most of the other trilobites by Owen (1980; 1981). The echinoderms are being studied by Bockelie (in press) whilst the commoner elements of the brachiopod fauna are described in an accompanying paper (Cocks 1982). The authors of the species quoted may be found in these works. In this paper we take the term 'diversity' simply to mean the number of different taxa present in a collection from a single bedding plane.

Thus, we believe that the identifications of the commoner brachiopods and trilobites are sufficiently accurate to make conclusions about changes in the taxonomic composition and diversity of the assemblages, whereas the less precise information on the rest of the faunas allows the recognition of biofacies and broad changes in diversity, but does not allow conclusions about the detailed ecology of the communities.

The collections, apart from the brachiopods, are housed in the Paleontologisk Museum, Oslo and the holotypes of the new brachiopod species (described in Cocks 1982) are also stored there. The main part of the brachiopod fauna is stored in the British Museum (Natural History).

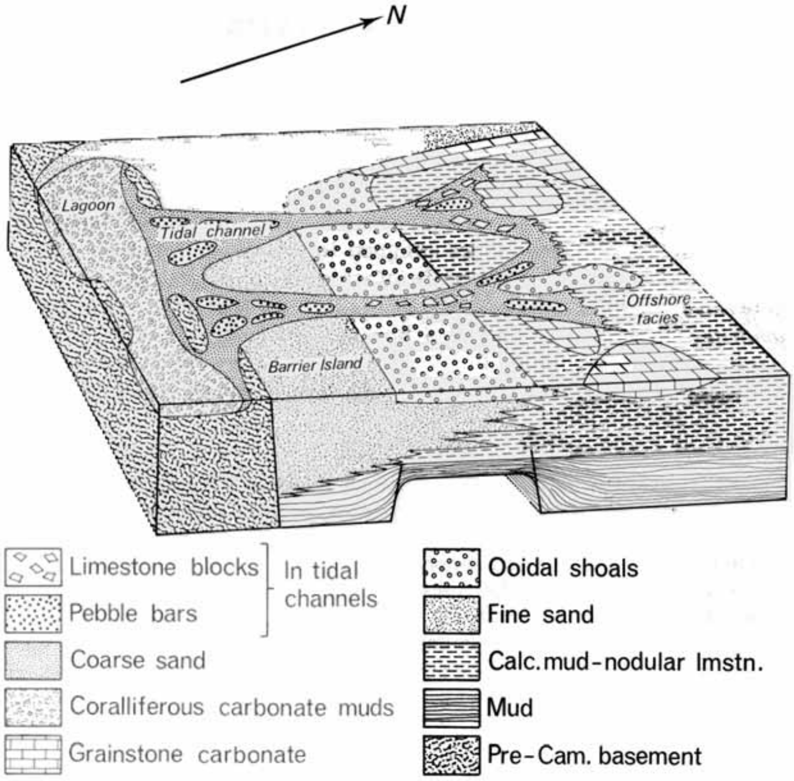


TEXT-FIG. 5. A reconstruction of the palaeogeography of the Oslo region in Stage 5*a* (late Rawtheyan) times. The rectangular grid approximately outlines the study area, which measures about 24 km by 16 km.

PALAEOGEOGRAPHICAL SETTING

The palaeogeography of the area in late Rawtheyan (Stage 5*a*) and earliest Hirnantian times consisted of fairly deep-shelf muddy environments established on a low eastward-facing palaeoslope (text-fig. 5). Into this low-energy environment storm-generated currents swept sand on rare occasions to form sheet sandstone beds within the generally argillaceous succession (Brenchley *et al.* 1979). The muddy sediments were more calcareous towards shore and this led to the development of the visually striking nodular limestones of the Langåra Limestone–Shale Formation. The nodules are diagenetic in origin but may reflect an originally higher content of biogenic carbonate mud within the sediment. The principal substrate throughout the area was silty mud and this is unlikely to have exerted a strong control on the ecology unless there were marked differences in its cohesion.

Soon after the start of Hirnantian times there were radical changes in the palaeogeography, which were probably initiated by differential block movement within the region, but emphasized by the significant late Ordovician glacio-eustatic regression. The early Hirnantian fault movements appear to have produced a tectonic high with a new ENE–WSW orientation (text-fig. 6), along which barrier islands became established with a seaward-facing shoreface towards the north. The sediments of the shoreface, of tidal channels, of oolite shales, and of the more offshore facies (text-fig. 6) are all well



TEXT-FIG. 6. A reconstruction of the palaeogeography of the Oslo region in Stage 5*b* (mid Hirnantian) times. Note the realignment of the facies belts along an ENE–WSW trend.

exposed in regressive sequence in the Oslo–Asker district, but the presence of land and lagoons along the tectonic high is deduced from the sediment transported into the tidal channels and preserved in the study area.

At the close of the Ordovician the palaeogeography changed once more. The rise of sea level which resulted from the initial melting phase of the Gondwana ice cap rapidly drowned the varied late Ordovician shallow marine facies and left a veneer of transgressive sediment followed by muds of a deep-shelf environment (Brenchley and Newall 1980). Following the transgression the regional eastward-facing palaeoslope was established once again and remained stable throughout at least the early part of Silurian times.

The faunal associations described in the following sections are related to the three phases of palaeogeographical development. The *Tretaspis* Association, *Onniella* Association, *Hirnantia* Association, *Hindella–Cliftonia* Association, and *Dalmanella* Association are all developed on the regional eastward-facing palaeoslope in Rawtheyan and early Hirnantian times. However, some *Hirnantia* assemblages are found in the shoreface sediments related to the later Hirnantian palaeogeography, and the *Holorhynchus* Association, *Thebesia* Association, *Brevilamnulella* Association, and *Monocraterion* Association are all related to this new palaeogeography. Finally, there are a small number of assemblages related to the end-Ordovician transgression.

THE FAUNAL ASSOCIATIONS

The Tretaspis *Association* (Table 1)

The association occurs as very sparse but moderately diverse assemblages dispersed through the mudstones of the Husbergøya Shale Formation. *Tretaspis* is consistently the commonest fossil and is represented by *T. latilimbus norvegicus*, except in the topmost three metres or so of the Husbergøya Shale, where *T. sortita broeggeri* (Pl. 86, fig. 1) is found. *Toxochasmops* sp., *Stygina latifrons extensa* (Pl. 86, fig. 5), and calymenid species are found in several assemblages and a total of at least twelve species of trilobite are found in assemblages assigned to this association (Table 1). In addition to trilobites there are several species of gastropods, of which loxonemataceans are the most common, and at least two bivalve genera are present. Bryozoa occur sporadically and in small numbers. The trace fossil *Chondrites* is ubiquitous and at a horizon low in the Husbergøya Shales there is a distinctive large trace fossil with spreiten (Pl. 85, fig. 5), referred to by Seilacher and Meischner (1965) as *Trichophycus*. Brachiopods are generally few in number and mainly occur in the middle and upper

TABLE 1. The *Tretaspis* Association. In this and the ensuing Tables 2–9 the numbers of specimens from each locality are shown. In animals with more than one fossil part, only the number of the more abundant part is included; for example, if 25 pedicle valves and 19 brachial valves of the same brachiopod species were found, then 25 would be shown in the table. The diversity simply indicates the total number of different species in a single collection. The numbers after each taxon in the 'Associated fauna' refer to the number of localities at which each was found: the absence of a number means that it was found at only one locality. Trace fossils and crinoid ossicles were not included in the counts. The localities are as shown on text-fig. 3.

	Localities											
	20	105	23	19	43	36	3	106	6	7	40	22
Trilobites												
Tretaspis latilimbus norvegicus	3	9						12	5			
T. sortita broeggeri			5	5	10	4	5			5		
Toxochasmops sp.									2			
Stygina cf. *latifrons extensa*				2			2					
calymenid								2	2	2	3	
Brachiopods												
Eoplectodonta oscitanda			3					3	3			4
Others												
loxonemataceans			5				6		3	2		
thin stick trepostomes				10+						8		2
Total number of specimens	4	12	19	22+	13	5	19	23	23	31	9	12
Diversity	2	4	9	6	4	2	8	7	11	13	3	5

Associated fauna includes:

Trilobites: *Brachyaspis* cf. *robustus* (2), *Cybeloides* sp., *Dionide* sp., *Dicranopeltis* aff. *polytoma*, *Lonchodomas* sp., *Sphaerocoryphe* sp., *Primaspis bucculenta* (2).

Brachiopods: *Epitomyonia* sp., *Leangella* sp., *Leptaena* sp., *Onniella kalvoya* (2), orthid indet., rhynchonellid? indet., *Strophomena*? sp., *Orbiculoidea* sp. porambonitacean?

Molluscs: bellerophontaceans (2), *Cymbularia pachygaster*, *Eotomaria* sp. aff. *eotomaria*, *Holopea*? sp. (2), *Palaeoneilo*? sp., *Praenucula*? sp.

Others: fenestellid bryozoa, *Serpulites* sp., *Climacograptus* sp.

Crinoid ossicles are rare.

Trace fossils include the ubiquitous *Chondrites* sp. *and Trichophycus*? sp.

Average number of specimens per locality: 16·0.
Mean diversity: 6·2.

part of the sequence containing the *Tretaspis* Association. The most characteristic brachiopod is *Eoplectodonta oscitanda*, but *Onniella kalvoya* is also recorded. These species are more typical of the *Onniella* Association (described below) and we regard some assemblages in the upper part of the Husbergøya Shale, where these species are more common, as belonging to a mixed *Tretaspis–Onniella* Association (see text-fig. 5).

Two species of cystoid, *Tetreucystis* sp. and *Eucystis* sp. (Bockelie, in press), are found in a bioturbated sandstone at the top of the Husbergøya Shale. This horizon is distinctive and we informally refer to it as the cystoid bed. The associated fauna belongs to the *Tretaspis–Onniella* Association.

The diversity of the assemblages in the *Tretaspis* Association is only moderate, but relative to the number of specimens collected is often high. From field observations we have found a maximum of eighteen taxa from one horizon (horizon 6, text-fig. 4). Samples collected from all the localities in the association, often from over ten man-hours' collecting, have yielded an average of 6·2 taxa from an average sample of 16·2 individual specimens.

The brachiopods in the *Tretaspis* Association are generally found both articulated and disarticulated and the trilobites are fragmentary. The fact that the fossils are found dispersed in the mudstones and are not sorted into layers indicates that they have probably not been transported, and it therefore seems likely that the fauna of the *Tretaspis* Association lived in the environment in which it is found, but that it might have been periodically disturbed by deep waves or transient bottom currents such as are recorded from modern continental shelves (e.g. Komar, Neudeck and Kulm 1972; Mooers 1976). Many of the fossils have also been disturbed by post-depositional organic activity, evident in the extensive bioturbation of the sediment.

The relative abundance of trilobites and gastropods and the ubiquitous presence of *Chondrites* in the association indicates a predominance of deposit-feeders amongst the preserved part of the fauna. However, filter-feeders are thinly represented by occasional brachiopods, crinoids, and bryozoa.

Stratigraphically the association occurs throughout most of the Husbergøya Shale, though there are some small changes in the fauna upwards through the sequence. In the lowermost two metres of the formation shelly faunas are rare or absent and instead diplograptids are found at a few localities. In the succeeding beds there is a sparse but diverse trilobite fauna and, above this, first brachiopods and then cystoids become successively more common, suggesting a slight progressive shallowing. The passage from beds with graptolites into beds with the *Tretaspis* Association indicates that the latter is at the deep end of the spectrum of benthic faunas. This conclusion is supported by the presence of the *Tretaspis* Association only in the east of the study area, whilst a richer, more varied fauna occurs at the same stratigraphical horizon in the west, which according to palaeogeographical interpretations was higher up the regional palaeoslope (Brenchley *et al.* 1979).

The Onniella *Association* (Table 2)

The *Onniella* Association is generally a low-density, high-diversity association and occurs as assemblages rather sparsely dispersed through the shales and nodular limestones of the Langåra Limestone–Shale Formation. The commonest elements of the fauna are brachiopods, but bryozoa are present in most assemblages and both simple rugose and tabulate corals are commonly present but rarely in abundance.

The characteristic brachiopods are *O. kalvoya* and *E. oscitanda*, which are each present in fourteen out of the fifteen assemblages included in the association. *Nicolella* sp. and *Leptaena* sp. are commonly present in small numbers and a thick stick bryozoan resembling '*Hallopora*' and hemispherical encrusting bryozoa are present in many localities. *Triplesia* sp., *Dolerorthis* sp., and *Sampo* sp. are found particularly in assemblages low in the stratigraphical sequence, while *Eospirigerina* is more common higher in the sequence. *Glyptorthis* sp., *Sampo* sp., *Orthambonites* sp., *Oxoplecia* sp., and *Platystrophia* sp. are moderately frequently found throughout the whole range of assemblages. Forty-eight genera of brachiopods have been recorded, but many of these are found only in small numbers at a few localities.

BLE 2. The *Onniella* Association

	Localities														
	31	67	12	25	75	72	26	32	6	7	27	46	47	48	73
Brachiopods															
Onniella kalvoya	8	3	46	14			11	6	14	17	24	5	1	19	8
Eoplectodonta oscitanda	5	1	4	2			16	3	5	3	2	4	3	6	2
Nicolella sp.	3	3	1	2					3	6		2		5	8
Leptaena sp.	2		6	4					2	1	5	1		2	5
Triplesia sp.	8		7												
Dolerorthis sp.	2		3	10					3				2		
Sampo sp.	2		3			2	8	4							
Eospirigerina sp.	2							8	3			6	6		2
Glyptorthis sp.				2				5			4	2	2		2
Orthambonites sp.				4	2		7		1					13	2
Oxoplecia sp.							2		2						1
Platystrophia sp.				2								2		14	
Trilobites															
Tretaspis askerensis	3														
Erratencrinurus (*Celtencrinurus*) *kiaeri*										4		8			
Others															
thick stick '*Hallopora*'				7			9	6	2	3	5	10	6	6	3
hemisphaeroidal trepostome	10	2		4							9	1	2	—0	
streptelasmatid corals	4			2				4		4					
Palaeoporella sp.												*	*		*
Total number of specimens	68	13	108	97	8	13	95	90	53	57	71	68	54	116	78
Diversity	17	7	21	28	7	10	29	34	21	16	16	32	22	26	27

Associated fauna includes:

Brachiopods: *Cliftonia* aff. *psittacina* (3), *Christiania* sp. (2), *Coolinia dalmani*, *Dicoelosia* sp. (2), *Diambonia* sp. (2), *Dinorthis* sp.? (2), *Drabovia* sp. (2), *Eochonetes* (2), *Eodinobolus* sp., *Eostropheodonta* sp. (2), *Epitomyonia* sp. (5), *Furcitella* sp. (2), *Gunnarella* sp., *Hesperorthis* sp., *Hindella cassidea* (4), *Hirnantia* sp., *Katastrophomena* sp. (2), *Kjaerina*? sp., *Kjerulfina*? sp. (2), *Kiaeromena*? sp. (2), *Kullervo*? sp., *Laticrura* sp. (2), *Leangella* sp. (5), *Mendacella* sp., *Oepikina* sp. (2), *Paucicrura* sp. (3), *Philhedra* sp. (2), *Plectothyrella*? sp. (2), *Parastrophina*? sp. (2), porambonitacean?, *Rostricellula* sp., *Stegerhynchus* sp. (2), *Skenidioides* sp. (5), *Strophomena* s.s. sp., Strophomenid indet., *Vellamo* sp.

Trilobites: *Acidaspis* cf. *asteroidea*, *Ascetopeltis bockelie*, *Astroproetus*? sp., *Brachyaspis* cf. *robustus*, calymenid (3), *Hadromeros* aff. *keisleyensis*, illaenid indet., *Lonchodomas* sp., *Panderia* sp., proetid indet., *Sphaerexochus* aff. *bridgei*, *Stenopareia* sp., *Toxochasmops* sp. (3).

Molluscs: bellerophontaceans, *Brachytomaria*? sp., *Cymbularia pachygaster*, *Globonema*? sp., *Helicelasma*? sp., *Holopea* sp., loxonemataceans, *Cuneamya*? sp., *Antiplectoceras*? *askerensis*, *Beloitoceras* sp., orthocones indet, *Spyroceras* cf. sp., A (Strand, 1933).

Bryozoans: *Corynotrypa schucherti* (3), *Callopora*? sp., encrusting cyclostome, flat stick trepostome.

Corals: halysitids (4), heliolitids (3), and favositids (3).

Others: *Opikella*? sp. (2), ostracodes indet. (2), *Serpulites* sp. (3), *Tentaculites* sp. (2), *Receptaculites* sp.

Crinoid ossicles are sporadically common, particularly in thin bioclastic beds.

Trace fossils include the ubiquitous *Chondrites* sp.

Average no. of specimens per locality: 64·0.

Mean diversity: 19·3.

Palaeoporella is common and *in situ* at these localities.

Amongst the thirteen trilobite genera, *Tretaspis askerensis* (Pl. 86, fig. 3) is found in small numbers at localities near the base of the Langåra Formation and *Erratencrinurus* (*Celtencrinurus*) *kiaeri* (Pl. 86, fig. 4) is found higher in the sequence; otherwise trilobites are generally rather rare.

Of the remainder of the fauna, compound corals, including halysitids, favositids, and heliolitids, are particularly obvious at some localities, especially those in Asker, but generally do not constitute a large number of individuals: we have also recorded the alga *Receptaculites* from two localities. Gastropods and bivalves are found in some assemblages, but in small numbers.

The most striking difference amongst the fossil assemblages is the presence or absence of the calcareous alga *Palaeoporella*. This forms dense clusters of calcareous tubes and locally must have formed an algal thicket on the sea floor. It is common in parts of the sequence in Asker from about 20 to 50 m in Stage 5 (Brenchley and Newall 1975), and is clearly *in situ* at some stratigraphical levels. To the south and east it is virtually absent and has been found only as rare fragments in the area around Langåra. Where *Palaeoporella* is well developed it is commonly found enclosed within large nodules. Collecting is generally more difficult at these levels, but brachiopods and other shells appear to be less abundant where *Palaeoporella* is dominant.

The diversity of the *Onniella* Association is high. We have recorded a diversity of thirty-four taxa from a collected assemblage and the average diversity from fifteen assemblages was 19·3, with a mean sample of sixty-four individuals. Although colonization of the sea floor can never have been dense, the presence of brachiopods, bryozoans, corals, and crinoids indicates a varied filter-feeding population. The deposit-feeding elements of the fauna, notably the trilobites and gastropods, are relatively reduced in numbers.

The sediments of the Langåra Formation are very similar to those of the Husbergøya Formation in that they are predominantly mudstones with interbedded sheet sandstones. The texture of the original substrate and the hydrodynamic conditions were apparently similar. The only significant difference is the abundance of diagenetic carbonate, which has formed the courses of nodular limestones in the Langåra Formation. The brachiopods in the assemblages are mainly disarticulated and the trilobites fragmentary, as in the *Tretaspis* Association. However, tabulate corals and *Palaeoporella* are commonly in growth positions.

The increased amount of carbonate in the succession, the greater percentage of sandstone, and the general palaeogeographical reconstruction (Størmer 1967; Brenchley and Newall 1980) all suggest that the *Onniella* Association occurred in a shelf environment, but shorewards and up the palaeoslope from the *Tretaspis* Association.

The Hirnantia *Association* (Table 3)

The *Hirnantia* Association *sensu stricto* is restricted to a few metres at the base of the Langøyene Sandstone (i.e. lowermost Hirnantian) and to one locality at the very top of the Husbergøya Shale and is confined to the eastern part of the Oslo–Asker area. The association is relatively rich in numbers of brachiopods and bryozoans and is moderately diverse. The characteristic brachiopods are *H. sagittifera* and *Dalmanella testudinaria*, which are always accompanied by the encrusting bryozoan *Ceramopora* (Pl. 86, fig. 6) and are usually associated with a thick stick bryozoan resembling *Hallopora*. *Cliftonia* aff. *psittacina* and *Eostropheodonta hirnantensis*, typical brachiopods of the *Hirnantia* fauna elsewhere, occur frequently here in this association but often in small numbers. The trilobite *Mucronaspis mucronata kiaeri* (Pl. 86, fig. 2) is to be found in very small numbers at most localities.

Twelve genera of brachiopods are recorded from assemblages belonging to the association, and five genera of trilobites. Bryozoans are common but appear to be restricted to a few genera. Amongst the rest of the fauna, *Tentaculites* sp., serpulids, and *Cornulites* sp. are quite commonly present, but corals and molluscs are rare. The association has an average diversity of 14·3 from an average sample size of 97·5 individuals.

The *Hirnantia* Association occurs in a unit a few metres thick consisting of interbedded shales and limestones with some sheet sandstones at the base of the Langøyene Sandstone. Not only is this horizon easily recognized lithologically but the large *Hirnantia* valves, commonly encrusted with bryozoa, make this a distinctive faunal horizon. The brachiopod fauna is partly disarticulated but contains about 50% of articulated valves, and appears to be a disturbed neighbourhood assemblage like those discussed previously. The enclosing sediment is mudstone or impure limestone, and appears to be little different in composition from the other shelf mudstones described earlier. The limestone beds consist of clay minerals and calcite in the form of microspar, and could be diagenetic in origin, but their lateral persistence suggests there might be an original carbonate mud component.

TABLE 3. The *Hirnantia* Association

	Localities			
		107	18	109
Brachiopods				
Dalmanella testudinaria	27	12	1	8
Hirnantia sagittifera	17	30	5	23
Cliftonia aff. *psittacina*	1	42		
Hindella cassidea	2		1	
Eostropheodonta hirnantensis		5	2	8
Trilobites				
Mucronaspis mucronata kjaeri	4	3		
Bryozoans				
hemisphaeroidal encrusting	7	40		17
thick stick '*Hallopora*' sp.		31		13
Others				
Tentaculites sp.				
Cornulites sp.		11		3
Total number of specimens	73	217	16	84
Diversity	15	20	10	12

Associated fauna includes:

Brachiopods: *Acanthocrania* sp., *Glyptorthis*? sp., *Lingula* sp. (2), *Leptaena* sp., *Orbiculoidea* sp., *Oxoplecia* sp., *Philhedra* sp.

Trilobites: *Calyptaulax* sp., *Illaenus* sp., *Platycoryphe* sp., *Toxochasmops* sp.

Others: *Globonema* sp., gastropods indet., bivalves indet, thin stick bryozoa, halysitids, *Serpulites* sp. (2), crinoids roots (2), *Barrandeocarpus* sp.

Average number of specimens per locality: 97·5.
Mean diversity: 14·3.

EXPLANATION OF PLATE 85

Fig. 1. Boundary between underlying Stage 4*d* γ beds (nodular limestone to left) and grey basal Husbergøya Shale Formation (to right); shore exposure at south-east Rambergøya, Oslo, Grid Ref. NM 965396.

Fig. 2. Sequence of vertical beds younging to the right; shore exposure at south-east Langøyene, Oslo, Grid Ref. NM 966384. Late Ashgill sandstones of the Langøyene Formation are overlain (from hammer head) by a 1 m transgressive sandstone and overlying nodular limestone with an *Onniella* Association, in turn overlain by the dark mudstones without shelly fauna of the basal Llandovery Solvik Formation.

Figs. 3, 4. The beaded trace fossil *Scalarituba*?, possibly representing infaunal feeding traces of a soft-bodied animal; different bedding planes near the top of the Langøyene Formation, south-east Langøyene.

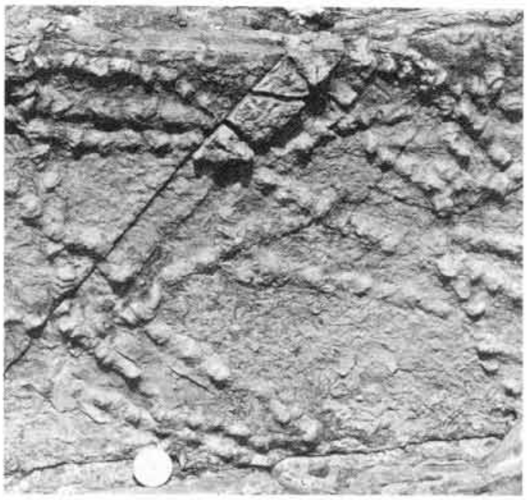
Fig. 5. The large spreite-bearing trace fossil *Trichophycus*?, showing the curved trace to the base of the burrows. This form occurs very commonly at levels about 3 m above the base of the Husbergøya Shale Formation; this example from Skjaerholmen, Grid Ref. NM 966370.

Fig. 6. Conglomerate including rugose corals (e.g. top right) as clastic particles and bored by *Tripanites* holes; 3-4 m from top of Langøyene Formation at south-east Langøyene.

1

2

3



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5

6

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This more calcareous horizon apparently represents a continuation of the regression which commenced in the late Rawtheyan and heralds the growth of the shoreface sequence a little higher in the succession. At this stage in the regressive development an inner shelf environment appears to be present (Brenchley and Newall 1980). The relationship of the *Hirnantia* Association with others is discussed in the next section.

The Hindella–Cliftonia *Association* (Table 4)

This association occurs through a few metres of sediment at the same stratigraphic level as the *Hirnantia* Association but is best developed in the western part of the area. The association is characterized by *Hindella cassidea*, *Cliftonia* aff. *psittacina*, and *Dalmanella testudinaria* with *Triplesia* sp. and *Eostropheodonta hirnantensis* as common associates. Thick stick bryozoa (?*Hallopora*) encrusting trepostomes and the streptelasmatid coral *Helicelasma* are also characteristic. The association is closely related to the *Hirnantia* Association s.s. but differs in lacking *Hirnantia* itself and being far richer in *Hindella* and *Cliftonia*.

TABLE 4. The *Hindella–Cliftonia* Association

	Localities								
	33	9	91	30	55	56	74	86	42
Brachiopods									
Hindella cassidea	24	30	4	22	3		1	3	6
Cliftonia aff. *psittacina*	18	110	1	22	5	14	14	5	
Dalmanella testudinaria	11	14	5	3	1	1	1		
Eostropheodonta hirnantensis	4	6	1	2		2			
Triplesia sp.	1		6	6					
Bryozoans									
Hallopora sp.	6	6		11	1				
Corals									
Helicelasma cf. *simplex*	8	50+		8					
Total number of specimens	133	259	20	100	11	19	17	8	6
Diversity	40	23	8	18	5	5	4	2	1

Associated fauna includes:

Brachiopods: *Coolinia dalmani*, *Dolerorthis* sp., *Drabovia* sp., *Eoplectodonta oscitanda* (2), *Eospirigerina* sp., *Eostropheodonta hirnantensis*, *Epitomyonia* sp., *Katastrophomena* sp., *Kullervo*? sp., *Lingula* sp., *Leptaena* sp. (13), *Nicolella* sp., *Onniella kalvoya*, *Orbiculoidea*? sp., orthid indet., *Parastrophina* sp., pentamerid indet., *Platystrophia* sp., porambonitacean indet., rhynchonellid indet., *Sampo* sp., *Skenidioides* sp., strophomenid indet., *Triplesia* sp., *Zygospira* sp.

Trilobites: *Dicranopeltis* aff. *polytoma*, *Harpidella* (s.l.) *occidentalis* (2), *Mucronaspis mucronata kiaeri* (2), *Panderia* sp., *Stenopareia* sp. (2), *Toxochasmops* sp.

Molluscs: bellerophontaceans (2), *Globonema* sp., *Holopella* sp (2), Loxonematacea, platyceratid, *Pleurotomaria*? sp., *Ambonychia* sp., *Cuneamya*? sp., *Beloitoceras* cf. *heterocurvatum*.

Bryozoans: *Hallopora*? sp., hemisphaeroidal trepostome (4), phylloporinid cryptostome, *Rhabdonesonida* sp. (2), thin stick trepostome (2).

Corals: *Grewinkia*? sp., *Leolasma* sp., *Streptelasma* sp. (2).

Others: *Tentaculites* sp. (2), *Receptaculites* sp. (2).

Crinoid ossicles are sporadically common, particularly in thin bioclastic beds.

Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 63·7.

Mean diversity: 11·6.

The total diversity of brachiopods recorded from the assemblages of this association is twenty-eight, though many of these are found in small numbers at only one or two localities. Bryozoans are common and relatively varied, as are streptelasmatid corals. A varied but sparse fauna of trilobites (six genera) and gastropods (five genera) is present. The preservation of the fauna is that of a disturbed neighbourhood assemblage, apart from locality 33, where a bed containing brachiopods in life position was collected. The diversity of fauna is very variable, ranging from forty to two, with an average, from eight localities, of 15·6 from an average number of 63·7 individuals per locality. The predominance of brachiopods, bryozoans, and corals indicates that the preserved part of this fauna was a filter-feeding assemblage. However, deposit-feeding gastropods are present, and trilobites sporadically found.

The enclosing sediment is like that of the *Hirnantia* Association in being predominantly argillaceous, but is even more calcareous and includes one limestone bed which is up to 1 m thick. Sheet sandstones are absent from these sediments. An inner shelf environment appears to be represented, with the more calcareous aspect indicating a nearer-shore, shallower situation than that of the coeval *Hirnantia* Association s.s.

The Dalmanella *Association* (Table 5)

This association is a very much reduced representative of the *Hirnantia* and *Hindella–Cliftonia* associations. It is strongly dominated by *Dalmanella testudinaria*, and all the other brachiopod genera (total ten) occur sporadically and in small numbers. Other faunal elements are not abundant, though thick stick bryozoa (?*Hallopora*) and encrusting trepostomes are sometimes present. Three genera of trilobites, *Tentaculites* sp., and crinoid debris are also recorded. The highest diversity recorded is twelve and the average diversity from seven localities is 4·9.

The *Dalmanella* Association occurs in mudstones immediately above the *Hirnantia* Association in a regressive sequence, so it is reasonable to assume that it occupied a slightly shallower environment

TABLE 5. The *Dalmanella* Association

	Localities							
		41	15	53	54	124	39	34
Brachiopods								
Dalmanella testudinaria	28	21	11	35	5	11	8	24
Cliftonia aff. *psittacina*		2			1			3
Hindella cassidea					1			
Lingula								
Leangella aff. *cyclindrica*		4						
Eoplectodonta oscitanda		4						
Bryozoans								
Hallopora? sp.		3	2					30
hemisphaeroidal trepostome					4			21
Total number of specimens	36	41	21	36	12	11	8	81
Diversity	6	12	8	2	5		1	7

Associated fauna includes:

Brachiopods: *Eospirigerina* sp., *Hirnantia* sp. (2), *Nicolella* sp., orthid indet. (2).
Trilobites: illaenid indet, *Mucronaspis mucronata kiaeri*, *Toxochasmops*.
Other: gastropod indet. *Tentaculites* sp.

Crinoid ossicles are found in small numbers at a few localities.
Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 30.
Mean diversity: 5·3.

on the inner shelf. The only reservation to this conclusion is that *Leangella* and *Eoplectodonta*, which are typical of the deeper-water *Onniella* Association, occur at two localities even though they were absent from the preceding *Hirnantia* Association.

Trematis–Bivalve *Assemblages*

Elements of the *Hirnantia* fauna *sensu lato*, notably *Hirnantia* and *Eostropheodonta*, together with *Plectothyrella* and *Hindella*, are found at a few localities (e.g. 37, 18, 38) in the more sandy sequence overlying the beds with the *Hirnantia* association s.s. At localities 37 and 38 these elements occur rarely and are associated with many specimens of an unusually large inarticulate brachiopod, *Trematis norvegica*, and an abundant bivalve fauna chiefly consisting of modiolopsids, but also including at locality 38 '*Pterinea*' and ?*Cuneamya*. Streptelasmatid corals are also found at this level. These *Trematis*-Bivalve faunas appear to occur at the level where the inner shelf mudstone facies passes into the predominantly sandy facies of the lower shoreface. The actual fauna collected from locality 37, at north Hovedøya, was 32 pedicle valves and 26 brachial valves of *T. norvegica*; 35 specimens, all articulated with both valves and apparently in life position, of the modiolopsid bivalve; 10 large conulariids; 3 articulated *Hindella cassidea* and one disarticulated pedicle valve; one articulated specimen each of *Hirnantia*, *Eostropheodonta*, and *Leptaena*; and a further disarticulated brachial valve of *Eostropheodonta*; a total of 85 specimens with a diversity of 7.

The Holorhynchus *Association* (Table 6)

This association is found only in the north-west part of the study area, where it occurs above beds with an *Onniella* Association, near the top of the Langåra Limestone–Shale Formation. Through about 8 m of section *Holorhynchus giganteus* dominates the fauna, being generally dispersed through the silty mudstones but sometimes being sufficiently densely packed to form shell banks. We have made three collections from near Sandvika (section 29) which, together with field observations from locality 26 at Holmen, show the fauna to be fairly homogeneous. *H. giganteus* is nearly always the dominant form in the association, but *Eoplectodonta rhombica* is well represented and *Onniella* sp. and *Leptaena* sp. are usually present. Thick stick bryozoans are usually quite common, and both streptelasmatid and tabulate corals are normally present. Thirteen genera of brachiopods are recorded from the assemblages in the association, which is a marked reduction from the underlying

EXPLANATION OF PLATE 86

Fig. 1. *Tretaspis sortita* (Reed) *broeggeri* Størmer, latex cast of a cranidium × 3, PMO 103963 from uppermost Husbergøya Formation at Hovedøya.

Fig. 2. *Mucronaspis mucronata* (Brongniart) *kiaeri* (Troedsson), cranidium × 4, PMO 101549, from 1·6 m. below the top of the Husbergøya Formation at south-west Rambergøya, Grid Ref. NM 961394.

Fig. 3. *Tretaspis askerensis* Owen, cranidium × 6, PMO 100657, from near the base of the Langåra Limestone–Shale Formation, Holmenskjaerest, Asker, Grid Ref. NM 838363.

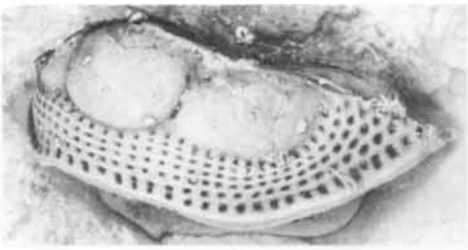
Fig. 4. *Erratencrinurus* (*Celtencrinurus*) *kiaeri* Owen, cranidium × 2·5, PMO 11291, from Langåra Limestone–Shale Formation, Nybörg, Asker.

Fig. 5. *Stygina latifrons* (Portlock) *extensa* (Reed), cranidium and thorax moult in Salter's position, × 2·5, PMO 97018, from whithin 1 m below the top of the Husbergøya Formation, Husbergøya, Grid Ref. NM 961375.

Fig. 6. The cystoporate bryozoan *Ceramopora* encrusting a *Hirnantia* shell, BB 93948, latex cast × 2, from top 15 cm of Husbergøya Formation, Rambergøya west, Grid Ref. NM 962394.

Fig. 7. The meandering trace fossil *Helminthopsis* from the Langøyene Formation, north Hovedøya, Oslo, Grid Ref. NM 967416.

Fig. 8. Burrows of *Monocraterion* in parallel laminated sandstones of the lower shoreface, Langøyene Formation, west Rambergøya, Grid Ref. NM 960394.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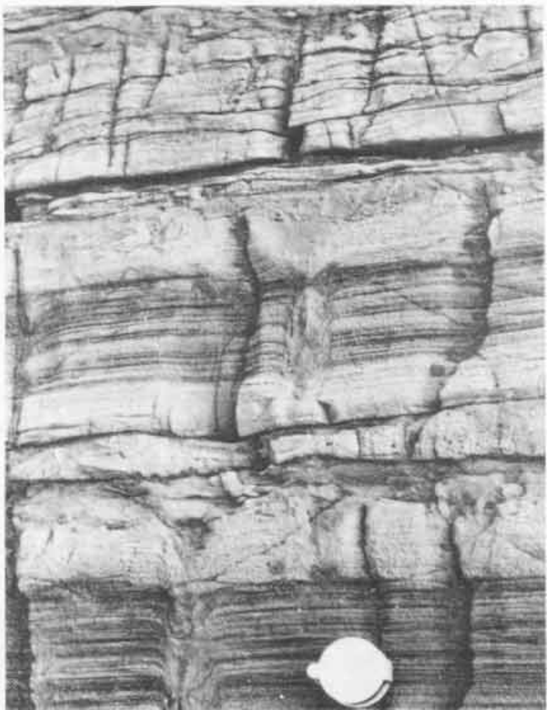
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TABLE 6. The *Holorhynchus* Association

	Localities		
	5	106	44
Brachiopods			
Holorhynchus giganteus	31	95	15
Eoplectodonta rhombica	15	10	13
Onniella sp.	4	10	1
Leptaena sp.	2	2	2
Dolerorthis sp.	4	3	
Nicolella sp.	1		3
Bryozoans			
Hallopora? sp.	2	15	2
Corals			
streptelasmatid	2	24	
halysitid	2	3	
heliolitid		3	1
favositid		10	3
Bivalves			
modiolopsid indet.	1		
Total number of specimens	84	205	38
Diversity	17	21	8

Associated fauna includes:

Brachiopods: *Eospirigerina* sp., *Hesperorthis* sp., *Katastrophomena* sp., *Leangella* aff. *cylindrica*, *Paucicrura* orthid indet., pentamerid indet., *Sericoidea*? sp.

Molluscs: gastropods indet., pleurotomariacean, nuculid? bivalve, *Similodonta*? sp., *Discoceras*? sp. indet.

Bryozoans: Hemisphaeroidal trepostome, thin stick trepostome, encrusting net bryozoan.

Other: *Receptaculites* sp.

Crinoid ossicles are rare.

Trace fossils include the ubiquitous *Chondrites* sp.

Average number of specimens per locality: 109.

Mean diversity: 15·3.

Onniella Association. The sediment in which the *Holorhynchus* Association is found is less calcareous than that lower in the sequence but is more silty, and this probably reflects the shallower situation of the *Holorhynchus* Association.

The Thebesia *Association* (*Channel-fill faunas*) (Table 7)

This association is mainly dominated by the rhynchonellid *Thebesia scopulosa*, often with *Hindella*, *Comatopoma*, and *Leptoskelidion loci*, and occurs in the upper horizons of the tidal channel at Hovedøya (section 10), and in a more restricted form at the top of sandstones filling a channel at Langøyene locality 125, section 5. Corals are associated with the brachiopods in some beds, with *Palaeophyllum* being particularly abundant at Hovedøya, and streptelasmatid corals and bryozoa being sporadically present and common on some bedding planes.

Those tidal channels which were cut through the shoreface sandstones in the south of the area, or through mudstones in the north-west of the area, tend to be wide and filled with a varied suite of allochthonous sediments. In contrast, the channels which were cut through lithified oolitic limestone

TABLE 7. The *Thebesia* Association and other Channel-fill Faunas

	Localities					
	76	77	16	78	14	125
Brachiopods						
Thebesia scopulosa	97	14		65	15	
Hindella cassidea	26	25		17	4	
Comatopoma sp.	3	1	1	12		4
Leptoskelidion loci	24	7		8	3	
Corals						
Palaeophyllum sp.				20+		
streptelasmatid corals		2		7		
Bryozoans						
thin stick trepostome				5		
thick stick trepostome	2		3			5
hemisphaeroidal trepostome			18			
Total number of specimens	169	52	36	151+	23	11
Diversity	9	6	8	19	4	4

Associated fauna includes:

Brachiopods: *Dalmanella* sp., *Dolerorthis*? sp., *Eostropheodonta* sp., *Hesperorthis*? sp., *Kjaerina*? sp., *Onniella* sp., orthid indet., *Philhedra* sp., *Stegerhynchus*? sp., strophomenid indet.

Trilobite: *Mucronaspis* sp.

Molluscs: *Holopella*? sp., pleurotomariacean, orthocones indet.

Corals: *Sarcinula* sp., favositid

Other: cornulitid.

Crinoid ossicles are sporadically common amongst the bioclastic debris.

Trace fossils include *Chondrites* sp. and varieties of *Planolites* spp.

Average number of specimens per sample: 73·7.
Mean diversity: 8·1.

in the central belt shown in text-fig. 7 (Brenchley and Newall 1980) were narrow and were filled with a sequence of different sediments. The Hovedøya Channel is lined with fallen blocks of oolitic limestone covered by sandstone, and this shows evidence of high current-velocities. The channel was finally filled by bioclastic sediments with brachiopod coquinas and coral-rich beds. The brachiopods in the coquinas have a mixture of articulated and disarticulated specimens and the corals occur as substantial colonies. The faunas appear to be disturbed, though essentially *in situ*, assemblages, and they lived within channels which had been first partly filled and then become relatively inactive, allowing local colonization of the sea floor. This is well illustrated at locality 125 (section 5, Langøyene), where conglomerates which infill a broad channel have a surface at the top where the limestone clasts are bored by *Tripanites* sp. (Pl. 85, fig. 6), suggesting a stabilization of the pebble fill. Overlying the conglomerates are sandstones with *Comatopoma* sp. and bryozoans.

The Brevilamnulella *Association* (*Coquina fauna*) (Table 8)

At two general localities very near the top of the Ordovician, one in the central belt and the other in the north-west part of the study area, there are coquinas dominated by the pentameracean *Brevilamnulella kjerulfi*. Throughout most of the central belt the uppermost Ordovician is represented by oolitic limestones (text-fig. 8) which contain few fossils, and none that are untransported. However, at Hvalsbakken (section 20, text-fig. 1) there is a development of up to 9 m of bioclastic limestone containing some ooids, which might either be a local facies variant of the ooidal shoals or alternatively might lie within a channel cut into the oolite. These bioclastic limestones contain abundant *Brevilamnulella*, together with a small number of other brachiopods, and rare tabulate and rugose corals and bryozoans in some beds. The valves of *Brevilamnulella* are predominantly disarticulated but unbroken, and because of the dense and virtually monospecific accumulation of shells it seems likely that the assemblages, though transported, are of local origin.

The second occurrence of the *Brevilamnulella* fauna is found at the northern margin of the study area at two places near Sem Vatern (Grid Refs. NM 799364, NM 800364,) where it is abundant in several beds in calcareous siltstones near the top of the Ordovician sequence at each locality.

The *Brevilamnulella* Association has a low diversity and in terms of brachiopods is nearly monospecific in some beds. However, at Hvalsbakken some bedding planes have yielded *Brevilamnulella* in association with two species of corals and two types of bryozoans. The association appears to represent a localized but successful colonization of the very late Ordovician sea floor.

TABLE 8. The *Brevilamnulella* Association (Coquina Fauna)

	Localities					
	80	11	81	82	69	70
Brachiopods						
Brevilamnulella kjerulfi	37	70	8	14	25	72
Rostricellula? sp.		3	1			
Bryozans						
Hallopora sp.	4	3	2			
Corals						
Streptelasmatid	4		1	2		
Total number of specimens	46	78	14	26	28	73
Diversity	4	3	6	8	2	2

Associated fauna includes:

Brachiopods: *Eoplectodonta oscitanda*, *Eospirigerina* sp., *Hesperorthis*? sp., *Hindella* sp. (2), *Leptaena* sp., *Onniella* sp.

Others: pleurotomariacean, single rugose corals indet., heliolitid, *Palaeoporella* sp.

Crinoidal ossicles occur in some of the bioclastic beds.

Average number of specimens per sample: 44·2.
Mean diversity: 4·2.

The Monocraterion *Association*

The Langøyene Sandstone Formation yields very few body fossils except from localities near the base and a few localities in the transgressive facies at the top. However, trace fossils are intermittently common through the sandstone sequence, and are particularly common in the lower part where the sandstones are thinly bedded. *Monocraterion* sp. (Pl. 86, fig. 8) is common at several horizons in the eastern part of the study area, and *Planolites* and *Chondrites* occur where there are thin mudstone partings between sandstone beds. Traces, probably referable to *Helminthopsis* sp. (Pl. 86, fig. 7) also occur on some bedding planes. Coarse sandstones and conglomerates filling tidal channels form a major part of the middle and upper part of the formation, and these sediments generally have no ichnofauna. However, sandstones overlie channels in some places near the top of the succession and these contain a very distinctive, large, beaded, infaunal trace (Pl. 85, figs. 3, 4) which was called *Scalarituba* by Seilacher and Meischner (1965, p. 615).

Where the Langøyene Sandstone contains more interbedded shale beds, as at Hovedøya, the trace fossil fauna is particularly varied and includes *Chondrites*, *Planolites*, *Monocraterion*, *Nereites?* sp., *Phycodes*, *Teichichnus*, *Helminthopsis?*, *Diplichnites*, and a trace similar to *Thalassinoides* (see *Monocraterion–Teichichnus* Association on text-fig. 7). Brenchley and Newall (1975) have interpreted this more shaly facies as forming offshore from the more sandy shoreface facies to the south (see text-fig. 8).

Faunas of the Silurian Transgressive Sequence

The Stage 5 sequence ends with a thin transgressive sand sheet, containing a diverse *Onniella* assemblage (Table 9), chiefly including smaller forms; this sheet is present over most of the Oslo district. The sand forms the lower part of a distinctive couplet, of which the upper part is a nodular limestone about 60 cm thick with a sparse fauna of *Eospirigerina* and other brachiopods, illaenid trilobites, and orthocones. To the east of the area, at Hovedøya, Rambergøya, and nearby localities, this couplet is succeeded by dark shales (Pl. 85, fig. 2) with no shelly fauna, although some bedding planes have abundant graptolites. Howe (1982) has reviewed these graptolites and notes the presence of very early Llandovery *acuminatus* Zone forms 11 m above the base of the dark shales at Ormøya, indicating that the time, if any, unrepresented by rock near the Ordovician–Silurian boundary in the area is minimal. To the west of the area there are no dark shales, and the Llandovery transgression did not deepen the water beyond depths colonized by shelly benthos. For example, a locality near Sandvika (Grid Ref. NM 851403) yielded a diverse assemblage of the Llandovery *Clorinda* Community in a continuous section 7 m above the top of the *Holorhynchus* Beds, as did a temporary road section near Holmen (Grid Ref. NM 836363). At another locality, at Konglungen (Grid Ref. NM 850347), a rich assemblage dominated by *Triplesia* was collected in position of growth 2 m above the base of Stage 6. Similar early Silurian faunas are widespread and have been described from Britain (Ziegler, Cocks and Bambach 1968; Cocks and Toghill 1973) from both sides of the Iapetus Ocean.

TABLE 9. The *Onniella* Association in Transgressive Facies

	Localities		
	21	87	94
Brachiopods			
Eoplectodonta oscitanda	16	17	
Leangella aff. *cylindrica*			
Paucicrura sp.	4		13
Onniella kalvoya		17	
Dolerorthis sp.	5	1	
Bryozans			
thin stick trepostome	1	2	2
Hallopora?	13		3
Total number of specimens	103	48	36
Diversity	17	9	13

Associated fauna includes:

Brachiopods: *Cliftonia* aff. *psittacina*, *Dalmanella testudinaria*, *Dicoelosia* sp., *Laticrura* sp., *Leptaena* sp., *Leptoskelidion loci*, *Lingula* sp., orthid indet., *Rostricellula* sp., *Skenidioides* sp., *Stegerhynchus*? sp., *Thebesia scopulosa*.

Trilobites: *Decoroproetus exevus*, *Stenopareia* sp.

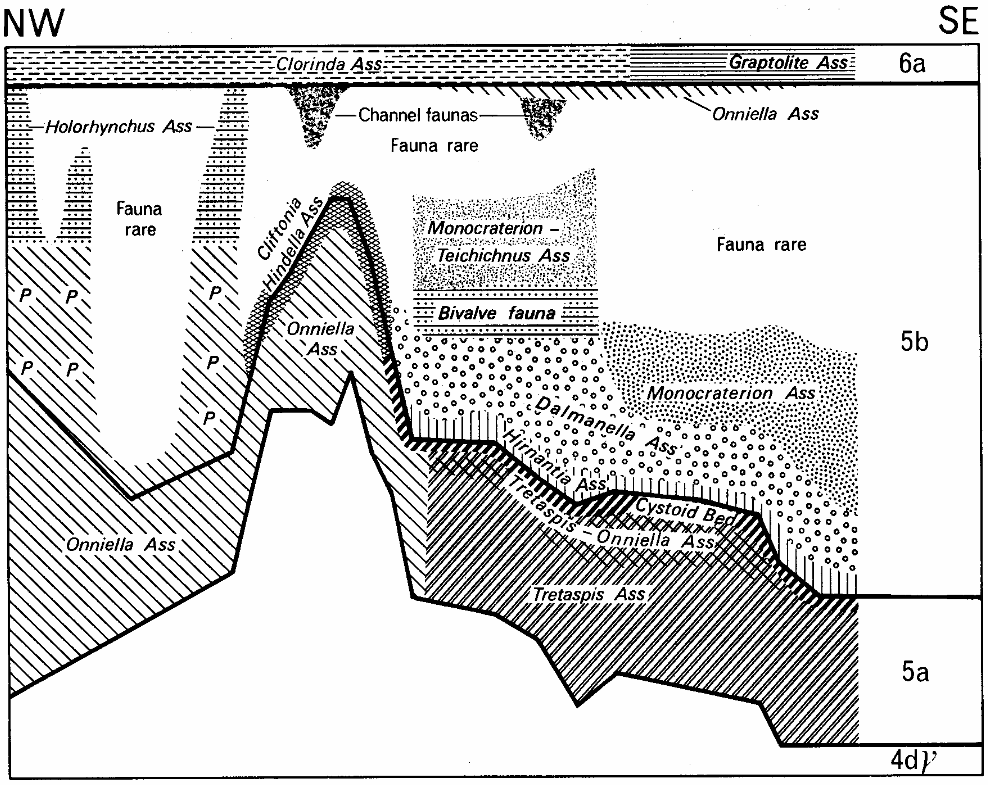
Others: hemisphaeroidal trepostomes (2), orthocones indet.

Crinoid ossicles are common at each of the three localities.

ENVIRONMENTAL DISTRIBUTION OF THE ASSOCIATIONS

The vertical and lateral distributions of the faunal associations are shown on a stratigraphical profile in text-fig. 7. The vertical sequence of faunas reflects the progressively shallower conditions evolving during the latest Ordovician glacio-eustatic regression, whilst the lateral changes reflect the lateral differences in bathymetry throughout the region. A comparison between text-figs. 7 and 8 shows that the faunal associations are closely related to the varied late Ordovician environments, and range from the *Tretaspis* Association in a relatively deep shelf environment to the *Monocraterion* Association developed on the lower and middle shoreface.

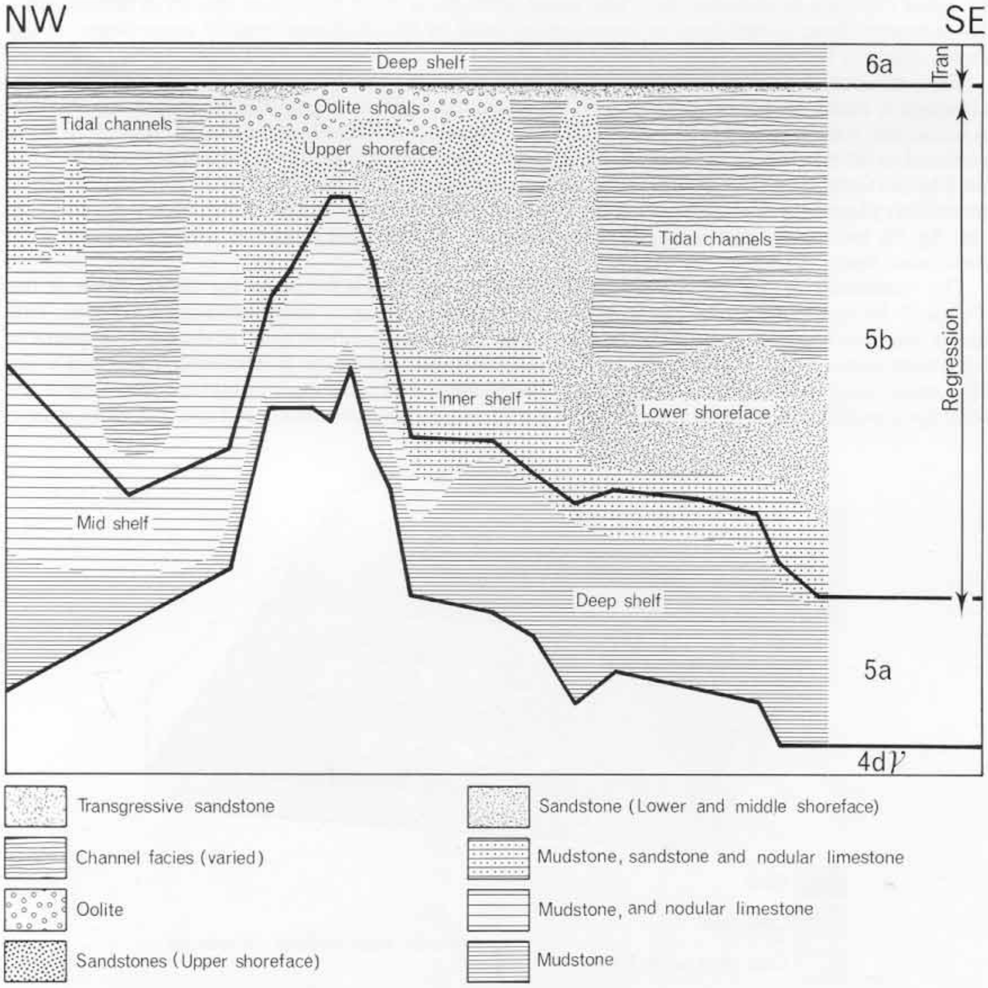
The faunal associations in Stage 5*a* (later Rawtheyan) of the study area were all situated in a shelf environment (text-fig. 9), with the highly diverse *Onniella* Association in the more calcareous muds towards the shore, and the sparser and less diverse *Tretaspis* Association further down the palaeoslope. It is difficult to make an estimate of absolute depth for the associations or to identify their specific location on the Ordovician shelf. The absence of lamination within the silty argillaceous sediments suggests they were not generally affected by bottom currents, but the disarticulation of a substantial proportion of the bivalved specimens suggests that there may have been some stirring of the muddy sediments. We have suggested earlier that this might be the effect of deep waves during



TEXT-FIG. 7. Stratigraphical profile from north-west to south-east across the study area (cf. text-figs. 2 and 3) showing the stratigraphical distribution of the faunal associations.

storms. Since the Oslo–Asker district lay a substantial distance (300 km +) east of the platform margin it is very probable that it was protected from the most severe of the oceanic swells, and storm-wave base would have been at a relatively shallow depth. Bottom sediment stirring can occur to depths of 125 m or more on high-energy coasts, but occurs at considerably shallower depths on low-energy coastal margins (Komar 1979), and therefore a depth less than 100 m might be regarded as likely for the *Tretaspis* Association.

An alternative estimate of maximum depth can be made because the late Ordovician regression apparently exposed the whole area, which is suggested to have involved a sea level change of no more than 100 m (Brenchley and Newall 1980), and so we again regard this as the likely maximum depth for



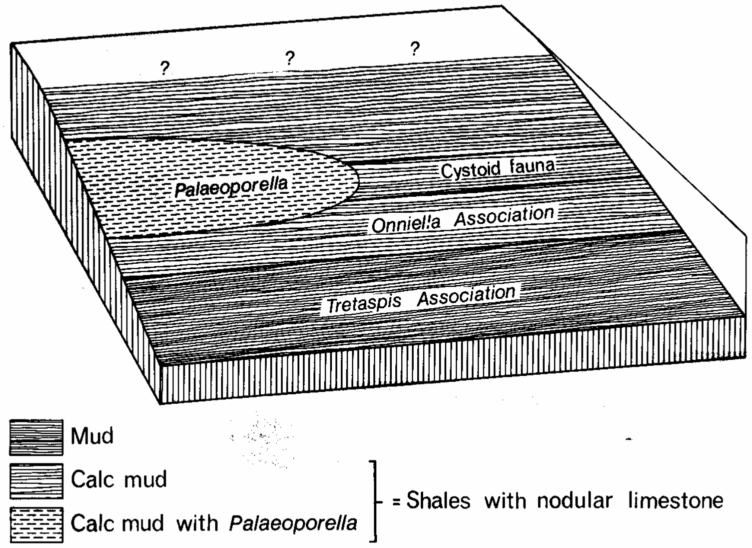
TEXT-FIG. 8. Stratigraphical profile from north-west to south-east across the study area (cf. text-figs. 2, 3, 7) showing the distribution of sedimentary environments.

the *Tretaspis* Association. The transition down the palaeoslope from the *Onniella* Association to the *Tretaspis* Association involves a shift from brachiopod-, bryozoan-, and coral-dominated filter-feeding faunas to trilobite- and gastropod-dominated deposit-feeding faunas, which probably reflects the decrease in food supply with both increase in depth and distance from shore.

The Stage 5*b* (Hirnantian) associations range from mid-shelf to middle-shoreface environments (text-figs. 7 and 10). The *Hirnantia* fauna *sensu lato* lived in a shelf environment, but we are able to subdivide that fauna into a *Hindella–Cliftonia* Association and a nearer-shore *Hirnantia* Association *sensu stricto*. A third, closely related, *Dalmanella* Association possibly lived in an intermediate situation, but this cannot be clearly demonstrated since the three associations do not occur in a single vertical succession. In addition to the rather low-diversity *Dalmanella* Association, there are a few assemblages which are found in the sandy sediments of the lower shoreface and which are dominated by either *Cliftonia* or *Hindella*, with very small numbers of other subsidiary species of macrofauna. We interpret these assemblages as representing some of the shallower benthic assemblages in the clastic facies of the area.

The precise environment position of the *Holorhynchus* Association is difficult to establish because, although it occurs in a shelf environment shallower than the stratigraphically underlying *Onniella* Association, it does not occur in a stratigraphical sequence with the *Hirnantia* fauna. *Holorhynchus* is confined to the north-west of the study area, and its distribution is patchy in a manner resembling the shell banks formed by large pentamerids such as *Pentamerus* and *Kirkidium* in the Silurian. We have tentatively placed the *Holorhynchus* Association at a depth similar to that of the *Hirnantia* faunas in text-fig. 10, but suggest that it may have lived closer to a carbonate shoreline, where food may have been more freely available.

The shallowest of the benthic associations with body fossils found in the clastic facies is the *Trematis*-Bivalve Association, characterized by *Trematis norvegica* and modiolopsid bivalves. This fauna has been found at only two localities, where the transition from shelf to shoreface appears to have been relatively gradual. In such situations the Bivalve association is succeeded stratigraphically by a trace fossil fauna with *Monocraterion*, *Teichichnus*, and other horizontal burrows. Where the shelf-to-shoreface transition was more rapid the *Trematis*-Bivalve Association and *Teichichnus* have



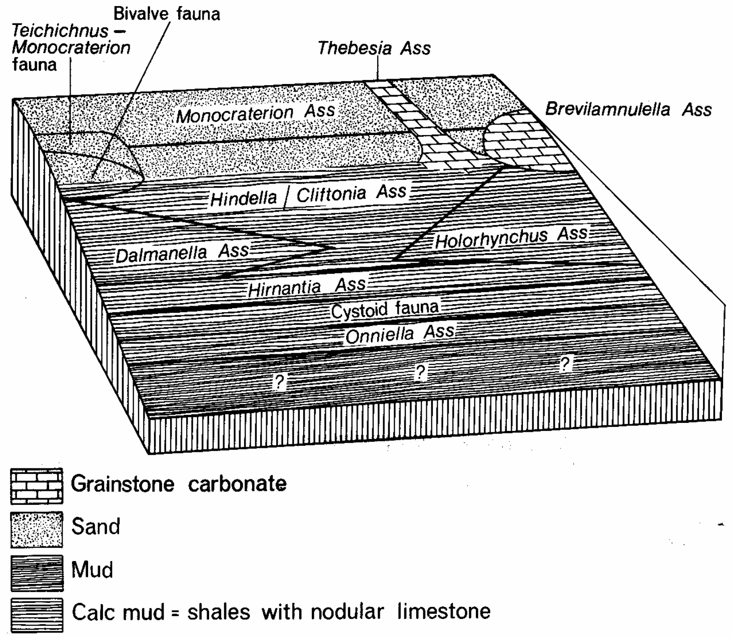
TEXT-FIG. 9. A reconstruction of the distribution of late Rawtheyan faunal associations in the Oslo–Asker area.

not been found (text-fig. 7). The transition from bioturbated muds and silts of the inner shelf to sands of the shoreface is unlikely to have occurred at a depth greater than 20 m (cf. Sanders and Kumar 1975) and was probably considerably less.

The shallowest faunas in the carbonate environment are those of the *Brevilamnulella* Association, which are found intimately associated with ooidal tidal shoals. These faunas lived either in the more stable parts of the shoals which could be colonized, or in shallower channels within the oolites. The *Thebesia* Association is certainly found within tidal channels cut through the oolites, but, judging by the presence of substantial coral colonies, the faunas probably colonized the channels when they were relatively inactive and had been partially drowned during a transgressive episode.

At the very end of the Ordovician the shallower marine clastic and carbonate environements were rapidly inundated during the transgression, reflecting the first phase of the melting of the Gondwanan icecaps (Brenchley and Newall 1980). The *Thebesia* faunas in the tidal channels might have developed during the very earliest phase of this transgression. However, the faunas of the *Onniella* Association are much more widespread, and are found in the thin veneer of bioturbated sand which blanketed much of the Oslo–Asker area. These are first succeeded by sparse faunas including *Eospirigerina*, often in reworked carbonates, and then by faunas of more typically Silurian aspect, such as the *Clorinda* faunas of the west and the graptolites to the east, a distribution which reflects the local re-establishment of the eastward-facing palaeoslope in early Llandovery times.

The distribution of the associations in relation to their environments indicates that they occupied fairly specific parts of the late Ordovician shelf, and to this extent were depth-related. The texture of the substrate can have had little influence on the distribution of the faunas because most of the associations are found in silty mudstones of similar grain size. The chief variation amongst the shelf sediments lies in the amount of carbonate present, which is reflected today in the abundance of



TEXT-FIG. 10. A reconstruction of the distribution of Hirnantian faunal associations in the Oslo–Asker area.

limestone nodules. It is possible that early cementation of the carbonate gave some sediments a greater cohesion, and thus affected the substrate favourably for colonization by an epifauna, but there is no evidence that contemporary cementation proceeded far enough to give rise to hardground surfaces. Where unstable sandy substrates were developed on the shoreface, these were almost wholly devoid of shelly epifauna and were populated only by an infaunal burrowing benthos, represented particularly by the trace fossil *Monocraterion*.

The role of food resources in partitioning the benthos is always difficult to assess; however, the faunas of the study area are found in shales with nodular limestones, and the nodules generally decrease in abundance with distance from shore. The $\delta^{13}C$ values in the nodules are close to zero (J. Gluyas, pers. comm.), which suggests that, although they are of diagenetic origin, they developed from original biogenic carbonate. Biogenic carbonate mud is likely to have been formed either from algae or microplankton, and may therefore represent potentially high food levels available for macrofauna. Conversely, the poor development of carbonate nodules in the sediments containing the *Tretaspis* Association might reflect the lower resource levels available to this deeper-water fauna.

TABLE 10

	Brachiopod diversity			Trilobite diversity			Total diversity
	max	min	average	max	min	average	average
Tretaspis Association	3	0	1·2	7	1	3·7	6·2
Onniella Association	18	4	12·7	5	0	1·5	19·3
Hirnantia Association	9	5	6·5	3	1	2·0	14·3
Hindella–Cliftonia Association	25	1	6·3	5	0	1·2	11·6
Dalmanella Association	8	1	4·0	2	0	0·4	5·3
Holorhynchus Association	9	5	7·7	0	0	0	15·3
Thebesia Association	9	4	5·8	1	0	0·2	7·8
Brevilamnulella Association	7	1	3·2	0	0	0	4·2
Transgressive *Onniella* Association	13	5	8·0	3	0	1·0	13·0

The estimated total diversity, in particular the diversity of the brachiopod fauna (apart from the relative lack of brachiopods in the deepest-water *Tretaspis* Association), varies with depth and distance from shore (Table 10). The nearshore associations, such as the *Brevilamnulella*, *Dalmanella*, and *Trematis–Bivalve* associations, and the *Hindella–Cliftonia* assemblages found in sandy sediments, all have rather low diversities; and mean diversity reaches a peak in the *Onniella* Association. It is the filter-feeding elements of the associations which determine this pattern, because if the deposit-feeders alone are considered, then the maximum diversity is reached in the deeper-shelf *Tretaspis* Association. This pattern of diversity, with low mean values nearshore, a mid-shelf peak, and then declining values with greater depth, is similar to that found in other studies of Lower Palaeozoic faunas (Calef and Hancock 1974; Hurst 1979*a*; Lockley 1980). The increasing values away from shore are best explained by the stability-time hypothesis of Sanders (1969), whilst the drop in density and diversity towards the outer part of the shelf was probably the result of relatively low levels of food supply which apparently affected Lower Palaeozoic communities much more severly than modern ones, perhaps caused by the relatively ill-ventilated state of seas at that time (Leggett *et al.* 1981).

COMPARISON WITH OTHER ASHGILL FAUNAS

Comparison of the Oslo associations with those from other contemporary sequences is hampered by the absence of studies through the faunal succession elsewhere. However, there are many assemblages known from one or two detailed localities in many areas of late Ashgill age, in particular the many descriptions of *Hirnantia* faunas in recent years. These include faunas from Poland (Temple 1965), Bohemia (Marek and Havlíček 1967), Morocco (Havlíček 1971), England and Wales (Temple 1965; Cocks and Price 1975; Hiller 1980), Ireland (Wright 1968), Canada (Lespérance and Sheehan 1976; Cocks and Copper 1981), the United States (Amsden 1974), Kazakhstan (Appollonov, Bandaletov and Nikitin 1980), China (Rong 1979), and South Africa (Cocks *et al.* 1970), and the fauna has also been briefly reported from other areas such as Belgium and Burma. In Scandinavia the *Hirnantia* fauna has previously been recognized in Sweden by Bergström (1968), and Sheehan (1979) has discussed its palaeoecology. By contrast, faunas of Rawtheyan age have not been fully described from an ecological standpoint from anywhere, and their systematics only partially revised, for example the brachiopods from North Wales (Hiller 1980) and the trilobites from Kildare, Ireland (Dean 1970–1978). However, lower Ashgill (Pusgillian and Cautleyan) palaeoecological studies have been made on material from the United States (e.g. Bretsky 1970) and Canada (Copper 1978), but these are in the Richmondian, which does not appear to be directly comparable with the Oslo–Asker region either in the taxa present or in the composition of its ecological associations. The *Orthambonites–Leptestiina* and *Onniella–Skenidioides* Associations reported by Harper (1979) from Girvan, Scotland, appear to include forms which occur in our *Onniella* Association, and it is also relevant to note that Harper is able to divide his Hirnantian faunas from the High Mains Sandstone Formation into two, which he terms *Eostropheodonta–Hindella* and *Hirnantia–Hindella* Associations.

The Oslo–Asker faunas are also quite different from those found in the carbonate mounds of Rawtheyan age (and thus contemporary with the lower part of our study area) which are developed in several places in the Anglo-Baltic area, particularly in Kildare, Ireland; Keisley, northern England; and Boda, Sweden. Other bioherms, such as that at Portrane, Ireland, are of earlier ages in the Ashgill. Smaller reefs are also known from near Oslo, for example the one of probable Rawtheyan age at Ullerntangen, Ringerike, but, despite the variety of ecological niches available in such bioherms and the large and diverse number of species which occur in them, there are very few species in common between these habitats and those of the more open shelf and shoreface deposits of the Oslo–Asker area.

The variable shallow-water deposits and faunas from our area are seldom preserved in rocks of late Ashgill age. In particular, the *Monocraterion* Association and the Channel-fill (*Thebesia* Association) and coquina (*Brevilamnulella* Association) faunas are preserved nowhere else, except on the North American craton (Amsden 1974), and it is a surprise to find such apparently specialized and widely dispersed faunas with such close similarities in composition and taxa. However, faunas dominated by *Holorhynchus* are known from several areas, notably in the Ulkuntas Beds of Kazakhstan (Sapelnikov and Rukavishnikova 1975), where the associated fauna, especially of corals and brachiopods, appears to be much more diverse than in Oslo–Asker. As in Oslo–Asker, the precise stratigraphical relationships of the *Holorhynchus*-bearing beds and those with the *Hirnantia* faunas are difficult to establish, and their detailed age (although undoubtedly late Ashgill) and ecological position appear uncertain. *Holorhynchus* has also been identified in the late Ashgill Porkuni Beds of Estonia.

Although the identification and correlation of mid-shelf and shallower-water faunas of Hirnantian age is now well established, problems still remain in the recognition of deeper-water faunas. Now that the *persculptus* Zone is known to represent at least the later part of the Hirnantian, it is possible to identify some deeper-water faunas as being Hirnantian in age. These include the shells and trilobites known from the so-called *Atrypa flexuosa* Limestone at the base of the Skelgill Beds in the Lake District of northern England (Marr and Nicholson 1888). That Limestone yields forms which can be reidentified as including *Kinnella*, *Ravozetina*, *Paromalomena*, and other genera which, although occurring with *Hirnantia* faunas elsewhere, are absent from the Oslo–Asker area. This suggests that the *Hirnantia* fauna *sensu lato* (i.e. the *Hirnantia* community of Cocks and Price 1975 occurred in a fairly wide range of depths on the shelf. Our work in the Oslo Region and that by Harper (1979) near Girvan, Scotland, shows that the *Hirnantia* fauna was partitioned into fairly discrete associations which probably reflect several environmentally controlled communities. Some genera, notably *Hirnantia*, *Eostropheodonta*, *Plectothyrella*, and possibly *Dalmanella*, although exhibiting an environmental preference for an inner shelf environment, were eurytopic and apparently thrived over a wider depth range than was usual for other brachiopod genera in Lower Palaeozoic times.

The composition and community structure of the world-wide *Hirnantia* faunas are seen to vary widely; some, e.g. the Bohemian assemblage, have as many as half of the taxa present consisting of endemic forms, yet other assemblages have no endemic species. Some assemblages have a relatively high diversity, with over thirty species of macrofauna recorded from them, and others have no more than five or six species in total, with perhaps only two or three abundantly represented (for a review of work up to that time see Cocks and Price 1975, pp. 720–723). The Oslo–Asker area is distinctive in showing most of the range of diversity in the different localities from which we have collected: the diversity of our *Hirnantia* faunas (including the *Hindella–Cliftonia* and *Dalmanella* Associations as well as the *Hirnantia* Association *sensu stricto*) differs from between two and thirty-four different species collected from each of the various localities. It is therefore probable that the variability in the diversity of the *Hirnantia* faunas recorded from various parts of the world is not necessarily caused by the more fundamental factors of geographical situation, but reflects partly the environmental location of the fauna and partly the variable conditions for colonization found on the local shallower shelf or lower shoreface. The stratigraphical appearance of the *Hirnantia* fauna seems to be closely correlated with the Hirnantian glacio-eustatic sea level changes. However, the suggestion that the *Hirnantia* fauna is a cold-water fauna (Sheehan 1979) should be treated with some caution in view of its great latitudinal spread which includes the circumpolar occurrences of what are now South Africa and Libya to the tropics of Canada, and its close association in the Oslo–Asker sequence with oolites which are usually associated with warm waters. Nevertheless it does seem that the late-Ordovician glacio-eustatic changes were connected with substantial changes in the community structure of the fauna, and with extinction of many species at the end of the Ordovician.

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