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THE PALAEONTOLOGY AND PALAEOECOLOGY  
OF THE UPPER LEINTWARDINE AND  
LOWER WHITCLIFFE FORMATIONS,  
UPPER SILURIAN, OF LUDLOW, ENGLAND

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`All Ludlow rocks are similar, but some are more similar than others.`

J.D.Lawson, 25.8.84.

`We don't deal in truth, that's for lawyers and theologians. We deal in shades of grey.`

A.J.Boucot, 1983.

## CONTENTS

SUMMARY.....	1
ACKNOWLEDGEMENTS.....	2
1.INTRODUCTION.....	3
2.LOCATION OF COLLECTIONS.....	5
3.METHOD OF COLLECTION (LUDLOW ONLY).....	6
4.PREVIOUS WORK-LITERATURE SUMMARY.....	7
5.LITHOLOGY.....	8
6.PHOSPHATE PEBBLE BED AND ITS SIGNIFICANCE.....	11
7.FOSSIL PRESERVATION AND DISTRIBUTION.....	18
8.GEOCHEMISTRY.....	19
9.BIOCHEMISTRY.....	20
10.PALAEONTOLOGY IN THE WELSH BORDERLANDS SECTIONS (INCLUDING MICROPALAEONTOLOGY).....	21
11.PALAEONTOLOGY IN THE GOTLAND SECTIONS.....	25
12.EPIZOAN ECOLOGY AND SIGNIFICANCE.....	27
13.DISCUSSION AND CONCLUSIONS.....	29
14.APPENDICES.....	42
15.REFERENCES.....	51
PLATE.....	57
FIGURES.....	58
TABLES.....	95

## SUMMARY

The boundary of the Upper Leintwardine and Lower Whitcliffe Formations in the Upper Silurian (Ludfordian) of the Welsh Borderlands is examined in an attempt to explain the (sudden and gradual) faunal changes which occur. Faunal variations are both lateral and vertical. A transect across the depositional area from basin to shelf is examined in order to describe and explain lateral variations. Faunal abundances are examined using collections and information from published literature. Other aspects are considered e.g. biochemistry and geochemistry. Time and finance were found to be major limiting factors in this case, but there is some potential for future work in these disciplines.

Faunal variations occur at this level independently of lithological or obvious environmental changes. Comparison with rocks of similar age in Gotland reveals an absence of such variations, and a greater abundance and diversity of fauna. This is largely due to palaeogeographic differences. The presence of phosphate deposits throughout the Welsh Borderlands succession is indicative of unstable and discontinuous deposition, possibly linked to sea level changes. The depositional environment at the Leintwardine-Whitcliffe boundary is considered to be one of soft medium-fine grained sediment covered by a layer of living, dead, and fragmented shells. This cover was probably patchy, with areas of free soft sediment providing ecospace for infauna. The disturbance of shell cover and living organisms was caused by larger organisms walking, feeding and burrowing. Storms and currents provided only minor disturbance. Algae occurred as floating masses and as rooted forests, possibly utilising large bivalve or brachiopod shells as substrate, and probably supporting small epiplanktonic brachiopods and bivalves. Distribution of species tends to be dominated by one or two main species (Shaleria ornatella, Protochonetes ludloviensis etc). Most shells were quickly colonised by bryozoa unless buried quickly. Some organisms supported epifauna during life.

The disappearance of the dominant brachiopod Shaleria ornatella at the top of the Upper Leintwardine Formation is thought to be due to disease, selective predation, or changing current systems.

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## 1. INTRODUCTION

The Silurian rocks of the Welsh Borderlands have long been known for their well preserved succession of marine beds representing deposition in a range of environments from basinal to shallow shelf. These sediments contain characteristic and well defined faunas which form the basis of the Ludlovian stratigraphic nomenclature (Holland, Lawson and Walmsley 1963). Both gradual and abrupt changes occur within these faunas throughout the succession and across the area of Wales and the Welsh Borderlands. These changes are both vertical and lateral. Vertical changes occur at several levels throughout the Silurian, notably at the top of the Wenlock Limestone, and at the tops of the Elton, Bringewood, Leintwardine and Whitcliffe Formations (Fig.1). They have been the subject of many faunal analyses (e.g. Calef and Hancock 1974, Hancock *et al.* 1974, Lawson 1975, Cherns 1977, Watkins 1979, Antia 1981). This thesis is concerned with the changes at the boundary between the Upper Leintwardine and Lower Whitcliffe Formations of the Upper Ludlow Ludfordian Stage (Fig.2). This level is of particular interest because of the lack of any obvious lithological or environmental change. Faunal differences at other levels are more easily related to such changes.

Collections from several areas have been studied in detail, and information regarding other sections has been obtained from the literature (Fig.3). The problem under examination is two-fold - firstly, the nature of these changes i.e. which species appear or disappear and in what way, and secondly, the reasons for these changes. Any explanation of changing faunas must take into account the ecological conditions of the time, and the interspecies reactions that may have occurred. In the recent past, there has been much emphasis on the composition, structure, analysis and interaction of palaeontological `communities` and `associations` within this succession (e.g. Ziegler, Cocks and McKerrow 1968, Calef and Hancock 1974, Watkins 1979). This has, in many cases, resulted in the arbitrary division of the fauna into communities or associations, and the subsequent use of the groups thus formed as valid biological units. Individual species



have generally not been considered as separate units (except Cherns 1977). This omission is potentially serious in a succession containing largely disturbed assemblages. It is therefore proposed to treat each species as a separate palaeoecological unit, individually considering its palaeoecological requirements. For ease of discussion, species with similar ecological requirements will be grouped together, but this grouping does not imply cohabitation, contemporaneity or interspecific communication of any sort. Each group simply represents some organisms with similar ecological requirements to each other. Potential adverse ecological effects can then be ascertained and examined and an explanation for faunal disappearances attempted. An attempt is also made to take into consideration the many non-biological factors which may affect a fauna (cf. Scull et al. 1966).

Faunas of equivalent age from Gotland, Sweden (Fig.4) have also been examined. The Hemse Group and Eke Formation are roughly equivalent to the Upper Leintwardine and Lower Whitcliffe Formations in Britain (Fig.5). These faunas were selected for study because the Leintwardine species continue into definite Whitcliffe beds in carbonate facies. There is no series of faunal disappearances such as that shown in Figure 1. Collections from the Welsh Borderlands and Gotland were examined in similar ways and a comprehensive literature search for both areas was made, in order to ascertain the reasons for these differences. Lateral changes across the Welsh Borderlands are also considered.

## 2. LOCATION OF COLLECTIONS

Collections from the Welsh Borderlands fall into two groups:

1. Those from Mortimer Forest, Ludlow
2. Those from other localities throughout the Welsh Borderlands.

Mortimer Forest collections were made initially by J.D.Lawson with the intention of forming a representative collection of the Upper Leintwardine and Lower Whitcliffe Formations in this area. Subsequent additional collecting was carried out during the summer of 1984. The collections come from two sections cut and maintained by the Forestry Commission. These sections are numbered FC62 and 9X, which is also known as Overton Quarry (Fig. 6). The collection from FC62 includes part of the Lower Leintwardine Formation as well as the Upper Leintwardine and part of the Lower Whitcliffe Formations. Collections from other localities in the Welsh Borderlands were made by J.D.Lawson from May Hill, Pont Shoni and Aymestrey (Fig. 3). These were not supplemented by additional collecting due to inadequate financial resources for fieldwork. The section at May Hill was briefly visited and examined, however.

Gotland collections were made by J.D.Lawson from seven localities in the topmost Hemse Group and lowermost Eke Formation (Fig. 7). Each collection therefore represents approximately the same time level and the nature of the whole collection is fundamentally different from that made in the Welsh Borderlands. The collection was intended to be a sample of the type of fauna and lithology present in Gotland, and collecting was therefore not as precise as that carried out in Britain, specimens being collected from debris as well as outcrop.

### 3. METHOD OF COLLECTION (LUDLOW ONLY)

Due to the uneven and irregular distribution of fossils within the Upper Ludlow rocks, it was considered prudent to sample every layer when collecting. Each section in Mortimer Forest was labelled in two foot intervals A,B,C etc., the samples being numbered 62E (for example) or 9XE as appropriate. Within each two foot interval, every layer was hammered, and any fossils found were collected. Several larger pieces were subsequently split in the laboratory. Samples were numbered with British Geological Survey numbers prefixed Zw and have since been deposited with the BGS in Nottingham. In Overton Quarry, layers A and B form an outcrop in front of the main quarry face, and are therefore not continuous with C to N (Plate 1). From the faunal changes it is apparent that the Leintwardine/Whitcliffe boundary is crossed at level T/U in Section 62 and at level G/H in Section 9X. The Lower Leintwardine - Upper Leintwardine boundary in Section 62 is at level N approximately.

#### 4. PREVIOUS WORK - LITERATURE SUMMARY

The Silurian of Wales and the Welsh Borderlands has been extensively worked ever since Murchison published his Silurian System in 1839. In the past three decades the emphasis has been on thoroughly mapping the area and describing the faunal changes which occur. One of the first of these publications describes the rocks and their contained faunas around Builth (Straw 1937). Other areas were mapped and described during the fifties and sixties (Kirk 1951, Lawson 1955, Holland 1959, Walmsley 1959, Squirrell and Tucker 1960, Holland 1962, Whitaker 1962, Holland and Lawson 1963) culminating in the publication of a new biostratigraphical classification for the Ludlovian rocks of Wales and the Welsh Borderlands with the selection of a type area around Ludlow (Holland, Lawson and Walmsley 1963). Other areas were subsequently correlated with this classification (Phipps and Reeve 1967, Lawson 1973).

During this period, reasons for the faunal changes are generally not proposed or discussed (excepting Lawson 1960). The fashion for fossil communities appeared in the seventies and is reflected in the publication of several papers which attempt to divide the Ludlovian fossils into various communities (Calef and Hancock 1974, Watkins 1979). That some of these may be inaccurate is amply demonstrated by Lawson (1975). Excavation by the Forestry Commission of several cuttings and faces provided valuable exposures and more evidence of faunal changes (Cherns 1977, White and Lawson 1978, Antia 1981). The most recently discovered new exposures show some interesting faunal variations (White, Ellison and Moorlock 1984).

## 5. LITHOLOGY

The lithology of the Upper Silurian sediments in the Ludlow area has been described by Holland, Lawson and Walmsley (1963 : 116ff). The Upper Leintwardine Formation consists of 'irregularly bedded, light olive grey or pale olive, somewhat micaceous and calcareous, flaggy medium siltstones. These weather to pale yellowish brown or yellowish grey.' The Upper and Lower Leintwardine Formations are very similar with characteristic honeycomb weathering. The Lower Whitcliffe Formation comprises 'irregularly bedded, massive or thickly flaggy, more or less micaceous, somewhat calcareous, coarse to medium siltstones, with a large scale conchoidal or crudely blocky fracture. In colour they vary from medium grey in the fresh, more calcareous beds to shades of greenish grey and light olive grey. Weathering eventually produces a dusky yellow appearance.' In the field, therefore, it is difficult to distinguish between the Upper Leintwardine and Lower Whitcliffe Formations on the basis of lithology.

Twenty-five thin sections were made from both sections FC62 and 9X from levels on either side of the formation boundary. Examination of these confirms the field observation of lithological similarity between the two formations. The microscopic character of the rock may be described as follows:

Finegrained to very finegrained subhedral to anhedral equigranular quartz and feldspar crystals with overgrown or corroded margins sometimes set in a muddy or cryptocrystalline carbonate matrix. There is some feldspar twinning. Mica crystals are of biotite and green chlorite in roughly equal proportions with some muscovite. The biotite is strongly pleochroic brown to pale brown. Crystal size is variable and orientation is generally random. Some clustering and irregular distribution of micas occurs particularly where there is evidence of biogenic activity in the form of burrows or trails. This bioturbation is not visible in hand specimen. Burrows occur in both longitudinal and transverse sections. Rare shell fragments are present, both bivalves and brachiopods. Occasional larger

quartz crystals occur. Opaque minerals are common, but pyrite is rare. The amounts of quartz, feldspar and mica are reasonably constant throughout the succession, but the amount of carbonate varies considerably.

Laterally, the Upper Leintwardine lithology varies between the basin and shelf areas. Basinal areas such as Knighton, which have been studied in more detail with respect to lithology than shelf areas, contain smoothly bedded flaggy and shaly siltstones with calcareous bands and thin layers of iron oxide concentration. The Lower Whitcliffe Formation siltstones are thicker and irregularly bedded (Holland 1959). The succession at Builth contains both shelly and graptolitic facies in hard, thickly bedded dark blue-grey calcareous gritty mudstones (Straw 1937). The area from Pont Faen to Presteigne consists of striped flags with great lateral variation (Kirk 1951). Shelly and silt-banded flags with a nektonic fauna are interbedded with slumped siltstones containing a shelly fauna. These pass upwards into richly shelly flags in the southwest but are unfossiliferous in Radnor Forest. In general, the basinal area consists of laminated dark shaly siltstones with Monograptus leintwardinensis and siltstones with an Aegiria grayi - Neobeyrichia lauensis fauna indicating the Upper Leintwardine Formation. The Lower Whitcliffe Formation consists of the same calcareous siltstones with more massive bedding (Holland 1962).

The shelf area from Leintwardine south to the Malverns differs principally in its faunal content but some major lithological variations may be distinguished. The Leintwardine Formations (Upper and Lower) consist characteristically of flaggy calcareous siltstones with thin shelly limestones (Lawson 1960). On the western margin of the shelf, near Leintwardine and Aymestrey the Mocktree Shale facies is developed containing abundant Dayia navicula. At Aymestrey the Upper Leintwardine Formation is closer in character to the basin lithologies than the rocks found on the Whitcliffe at Ludlow (Lawson 1973), and consists of irregularly bedded flaggy siltstones. The Lower Whitcliffe Formation is similar but the bedding is more flaggy and thicker. At Leintwardine, jointing is common. The Upper Leintwardine

Formation consists of irregularly bedded yellowish grey micaceous siltstones, while the Lower Whitcliffe Formation differs only in an increase in sand sized particles and the presence of spheroidal weathering and some slumping (Whitaker 1962).

At May Hill, the lithologies of the two formations are almost identical, consisting of greyish olive flaggy calcareous siltstones (Lawson 1955). This description may also be applied to the sequences at Usk, Woolhope and the Malverns. At Usk, the siltstones vary in colour between light olive grey and pale yellowish brown and are slightly calcareous with thin seams of shelly limestone. The Lower Whitcliffe Formation contains thin bands of shale and hard blue-grey shelly limestones (Walmsley 1959). The Upper Leintwardine Formation at Woolhope consists of thinly bedded, dusky yellow siltstones with lenticular bands of limestones. Limestone bands are also present in the Lower Whitcliffe Formation (Squirrell and Tucker 1960). Both the Upper Leintwardine and Lower Whitcliffe Formations in the Malverns inlier contain bands of nodular limestone. The Lower Whitcliffe Formation is typically leached and weathered to rottenstone. In the south of the inlier the whole Upper Ludlow sequence is represented by forty feet of conglomeratic beds (Phipps and Reeve 1967). These conglomerates consist of subrounded pebbles of limestone and siltstone set in a siltstone matrix, and associated with a network of bryozoan colonies. They are otherwise poorly fossiliferous. Antia (1981) describes the Whitcliffe at Ludlow as comprising an interbedded sequence of bioturbated calcareous siltstones alternating with thin 'storm generated' siltstone and shell laminae.

## 6. PHOSPHATE PEBBLE BEDS AND THEIR SIGNIFICANCE

The boundary between the Upper Leintwardine and Lower Whitcliffe Formations is marked in several places (notably May Hill) by a thin layer of phosphate pebbles. This was described as a 'thin phosphatised fragment-bed' by Lawson (1955). The bed, which was examined during field work, consists of shelly fragments with small phosphate pebbles up to 1cm approx. maximum diameter. Pebbles are sub-rounded and sub-angular, and have an irregular distribution. This phosphatised layer has been noted in other places throughout the Welsh Borderlands. Kirk (1951) describes the Ludlovian-Downtonian succession of Brecon and Radnor as resembling that of Shropshire in its development of bone beds. The Lower Whitcliffe Formation in the Woolhope inlier contains small pebbles implying at least local erosion during sedimentation (Squirrell and Tucker 1960). The boundary of the Leintwardine and Whitcliffe Formations is marked by a phosphate bed in the southern part of the inlier and elsewhere by a thin argillaceous limestone with elongate siltstone pebbles. Lawson (1975:511) suggests that the phosphate pebble bed represents a break in deposition or slow deposition between the main stratigraphical units. At Aymestrey, the pebble bed is present nine metres above the base of the Upper Leintwardine Formation (Lawson 1973:262). There is also one developed at the base of the Upper Leintwardine Formation at Leintwardine (Whitaker 1962:334). This bed consists of pebbles of limonitised limestone and phosphatic material. According to Holland and Lawson (1963:278), the bonebeds developed in the Upper Leintwardine Formation near the Gorsley axis provide evidence of persistent instability along the shelf margin.

Phosphate deposits occur throughout geological history in a range of lithologies and have been the subject of intense analysis and theorising. They are of great significance in ecological terms although their method of formation is still under discussion. Most modern theories of phosphorite formation are modelled on that of Kazakov (1937) which involves direct inorganic precipitation of marine apatite from sea water (Burnett 1977). It is surmised that the ascent of phosphate-rich waters in areas



of upwelling involves a decrease in the partial pressure of  $\text{CO}_2$  and a rise in pH levels. This leads to supersaturation of sea water with respect to carbonate fluorapatite and direct inorganic precipitation. The observed association between the occurrence of marine phosphorites and upwelling led to the suggestion of a cause-effect relationship, and several examples were cited as evidence to support this. Goldberg and Parker (1960) describe the discovery of a piece of phosphatised wood from the Pacific sea floor, one of the rare examples of phosphatisation occurring at the present time. Phosphatisation occurred only in that portion of wood above the sediment-water interface implying that the phosphate is derived from the overlying sea water. The wood occurs in a productive area with respect to plant life and the overlying water has a low oxygen value. Goldberg and Parker suggest that the dissolved oxygen in the sea water reacted with the organic components of the wood causing a decrease in redox potential, pH and carbonate content. The high phosphate content of the water ensured deposition of apatite rather than calcium carbonate. Goldberg and Parker cite as evidence in support of their theory the fact that the wood has a high U/Th ratio, in accordance with that found in marine apatites.

According to McKelvey (1967) phosphorites are found in environments of strong upwelling associated with black shale, chert, dolomite, limestone and evaporites. Oceanic circulation brings phosphate from deep cold waters, where it is more abundant, to warmer surface waters where it is available to form phosphorites. The area off Peru and Chile is one of high organic productivity and according to Veeh *et al.* (1973) contains phosphorites dating from late Pleistocene to Recent, and currently forming ( $^{234}\text{U}/^{238}\text{U}$  dates). Phosphorite nodules occur in two narrow bands coinciding with the upper and lower boundaries of the oxygen minimum layer. Their major component is apatite rich in fluorine. Veeh *et al.* conclude that the formation of phosphorites off Peru has been more or less continuous from the late Pleistocene to the present and that reworking and continued enrichment have led to a preRecent age bias.

Publications during the seventies however, have disputed

Kazakov's hypothesis, and looked for other methods of phosphorite formation using evidence from the fossil record as well as re-assessing modern phosphorites. Baturin (1971) discusses stages of phosphorite formation in areas off southwest Africa and Chile, and proposes a cycle of stages which may be repeated to form layers of nodules. There are three stages involved in the cycle. The first involves biogenic deposition, the areas being rich in biogenic detritus which sinks and is preserved and incorporated into the sediment due to a low oxygen content. The second stage is diagenetic and the third is dynamic. A similar cycle was proposed by Baturin and Bezrukov (1979) in a general review of all modern phosphorites.

The first stage involves upwelling of dissolved phosphate onto the shelves. This may be the sole source of phosphate if there are no rivers or hydrothermal sources. This upwelling water is highly significant for biological productivity due to the enrichment of phosphate and other nutrients. Dissolved phosphate is used by phytoplankton and may be recycled often. Deposition on the sea-floor comprises the second stage and only occurs in particulate form. The phosphate brought up by the upwelling water is incorporated into living organisms and settles to the bottom as part of the organic detritus. It is then incorporated into the sediment. The third stage is the diagenetic redistribution of phosphate and the formation of nodules. This involves the mobilisation and redistribution of the geochemically active and mobile fraction of phosphate in the sediments. The high concentration of dissolved phosphate induces supersaturation with respect to calcium phosphate and results in precipitation on various surfaces such as diatoms, organic detritus and fish bones. It is suggested that precipitation is due to the patchy structure of the microenvironment. Lithification of the nodules induces compaction of the phosphate and self-purification by extrusion of non-phosphatic material. This leads to the simultaneous formation of silt-sand sized phosphate grains. The final stage involves the reworking of the nodules by water movement to form phosphorites. Baturin and Bezrukov conclude that fluctuating sea level is important for phosphorite formation in as much as it causes temperature variations. The formation of

phosphate is conditioned by warmer periods since these allow an extension of the shelf area and changes in the water temperature. This induces intensification of upwelling and an increase in biological productivity which in turn results in an accumulation of phosphate in shelf sediments. Low sea level facilitates reworking and accumulation.

The necessity of warm water for phosphorite formation and accumulation was suggested by Kolodny (1969) in a critique of Kazakov's hypothesis. Dating and analysis of modern sea floor nodules would suggest that they are presently being leached by sea water. No Recent phosphorite has been found to form in areas of present day upwelling according to Kolodny, who suggests that formation occurred in Miocene and Pliocene seas which may have been warmer. The conclusion is that there is a need to look for modern phosphorites in warm waters. Burnett (1977) suggests a link between periods of warming, low sea level, and phosphorite formation. The anoxic pore waters of the Peru-Chile shelf favour inorganic precipitation of apatite because of four characteristics:

1. High flux of dissolved inorganic phosphate
2.  $Mg^{++}$  depletion during diagenesis
3. High pH
4. Suitable nucleation sites (e.g. calcite crystals, feldspar crystals, skeletal material).

It was also noted that the dissolved phosphate content of pore waters in anoxic areas is higher than normal. If precipitation occurs out of anoxic pore waters, how is the phosphate converted into rocks? Burnett concludes that this occurs due to low sea-level, the fine-grained fraction being eroded away and causing the concentration of phosphorite into coarse-grained deposits and then into nodules. Evidence to support this idea comes from the Peru-Chile shelf where Quaternary phosphorite deposits formed during a period of major eustatic sea-level changes.

Other mechanisms for the formation of phosphorites have been proposed, and will be briefly discussed. Bushinsky (1964) proposes a shallow water origin for phosphorites based on several

criteria which include the smooth worn condition of the nodules due to rolling of nodules and associated pebbles, the presence of sand grains and the presence of thick walled benthic forams. By calculations Bushinsky determined that the source of the phosphorus was the rivers which flowed from the lowland coasts around areas of phosphorite deposition. Pomperdy et al. (1965) discuss phosphate exchange between sediments and overlying water in the inner continental shelf. The exchange is biologically controlled and takes place across the cell membranes of microorganisms. It occurs in the interstitial water of the sediments and is consequently very slow. In other situations, bacterial exchange may occur in the water above the sediments.

Phosphatised limestones on the South African continental margin are discussed by Parker and Seiser (1972). Mineralogical and geochemical evidence suggests that the lime mud matrix has been replaced by francolite. The mechanism proposed by the authors is that of submarine phosphatisation by permeating phosphate rich solutions. The contemporary phosphorite formation offshore of Peru and Chile is thought by Manheim et al. (1975) to be due to replacement of carbonate tests of Holocene benthonic forams in the interstitial waters of organic rich sediments. According to Manheim et al. there are four requirements for the formation of phosphorites:

1. Sediments rich in organic detritus
2. Water with low dissolved oxygen
3. Low rates of inorganic sedimentation
4. Low concentration of calcium carbonate in the sediment.

Piper and Codispoti (1975) have suggested that a significant change in global nutrient budgets may be required during periods of extensive phosphate accumulation. An increase in marine denitrification and a lowering of productivity results in an excess of phosphate accumulating in sea water until it precipitates as carbonate fluorapatite.

Phosphorite formation by reworking has been discussed by D`anglejan (1967) and Baturin (1970). The phosphorites of Baja California probably formed in an environment of shallow water

with a warm arid climate, low sedimentation and high productivity (D`anglejan 1967). The nodules occur at the sediment-water interface implying in situ formation by precipitation from sea water. Lateral facies changes may imply a penecontemporaneous marine transgression and the development of the deposit by reworking of previously formed phosphorites. It is likely that the apatite forms in situ by replacement of biogenous carbonate in foram tests. Baturin (1970) discusses phosphorite formation on the south west African shelf on the basis of three hypotheses- biogenic, chemogenic and volcanogenic. The area is in the southern arid climatic zone and has a small terrigenous supply. Cold upwelling water is enriched in phosphorus but depleted in oxygen. Most of this phosphorus is utilised by phytoplankton. Precipitation of calcium phosphate is likely to occur in interstitial water and is the result of several processes. The most favourable conditions for reworking bottom sediments and concentrating the phosphorite are created by sea level changes.

Baird (1978) uses the presence of a phosphatic pebble bed in shale to recognise a discontinuity probably due to submarine erosion in the Middle Devonian of New York. The pebble bed marks a sharp break between two different marine biotopes. The presence of marine strata above, below and laterally to the pebble bed indicates its origin to be subaqueous. In this it is similar to the pebble beds at May Hill and in other localities of the Welsh Borderlands. Submarine erosion may have been due to the overall shallowing and restrictions in space.

There seems to be a general consensus in the literature, amidst differing theories, that the formation of phosphorite deposits is encouraged and facilitated by warm seas, changes in sea level, and high organic productivity. Such factors are likely in the Welsh Borderlands at the time of deposition of the Leintwardine and Whitcliffe Formations. Organic productivity is unknown, but likely to have been high, judging from the abundance of fossil material preserved.

Phosphate deposits occasionally occur as bone beds and it is notable that such a deposit occurs at a higher stratigraphic

level i.e. the Ludlow Bone Bed at the boundary of the Upper Whitcliffe Formation and the Downton Castle Sandstone Formation. This and other bone beds have been the subject of many palaeoenvironmental and palaeontological analyses. A phosphate deposit must have a minimum of 4.5% phosphatic material to be called a bone bed (Antia 1979). The formation of bone beds is still unclear and they may be primary or secondary. Concentration of phosphatic fragments into a bone bed may be the result of changes in sea level dynamics. Regression of water level causes erosion of fine-grained material and a concentration of the coarse-grained fraction. This method seems possible in the Welsh Borderlands. The development of the pebble bed in certain areas and not in others is an indication of the instability and variability of the Upper Ludlow environment. Submarine erosion and instability may have had important consequences for the continuity of Silurian organisms, and may provide at least part of an explanation for the changing fauna.

## 7. FOSSIL PRESERVATION AND DISTRIBUTION

Within the sequence of monotonous Ludlovian siltstones, fossils are usually preserved as internal, external and composite moulds. There is also some original shelly material preserved especially in dalmanellids and Leptaena. Fossil distribution is uneven, fossils occurring in both bands and clumps. Watkins (1979) has divided fossil distribution into shell beds and clusters of conspecific populations. Shell beds are related to storm deposition and consist of laminated siltstone sheets of shelly fragments often difficult to identify. Shell beds represent the initially settling coarse fraction during mass silt transport. They comprise Watkins' 'transported assemblages'. Clusters of fossils occur in bioturbated sediment and comprise Watkins' 'disturbed neighbourhood assemblages', representing organisms which have been shifted from their life positions but not significantly moved or mixed ecologically. This distribution occurs throughout the Welsh Borderlands. At Woolhope, Squirrell and Tucker (1960) report that fossils occur in bands and lenticular bands, and that bands of comminuted shells also occur. The inlier at Usk contains fossils in decalcified layers of limestone, with many occurring covering bedding planes in sheets (Walmsley 1959). Antia (1981) suggests that shell laminae containing many shell fragments were probably caused by storms. Lawson (1973) mentions that fossils at Aymestrey occur in bands. At Leintwardine, fossils occur in decalcified layers or lenses as dark yellowish brown moulds of limonite (Whitaker 1962). Derived fossils appear at the base of the Upper Leintwardine Formation where there seems to be an unconformity. Some fossils are preserved in calcite. Leintwardine is unusual for its fauna of starfish and echinoids. In the Lower Whitcliffe Formation fossils are sporadically distributed and occur in layers or clusters. In the Upper Leintwardine Formation at May Hill, shelly limestone bands occur (Lawson 1955). In the Malverns inlier, Phipps and Reeve (1967) note that fossils occur as shell fragments in lenticles. At the type area of Ludlow, the thin shelly layers are often in a rotten, biscuity condition (Holland, Lawson and Walmsley 1963).

## 8. GEOCHEMISTRY

In general, there is a lack of a co-ordinated approach when tackling problems presented by a succession of rocks such as those at Ludlow. This leads to a potential loss of valuable information which may be gained from other disciplines such as geochemistry. Such information may indicate changes in palaeoecology or palaeoenvironment which may provide answers to faunal problems. There is a need for a comprehensive geochemical analysis of the sections in Mortimer Forest. Due to restrictions of time and finance, such an analysis was not possible during the course of this project. There may be an indication of changing conditions preserved in the geochemical record of the sediment - in particular there may be useful information to be gained from the analysis of carbon, phosphate and clay content. Sediment geochemistry has been discussed by Degens (1965) and Degens and Reuter (1964). It appears that many techniques are successful mostly on younger and undisturbed sediments. However, there is some potential for future work, although detailed geochemical analysis is required (Anderson et al. 1958, Degens et al. 1961, Abelson et al. 1964).



## 9. BIOCHEMISTRY

Biochemical analysis of Silurian shells is difficult due to the obvious problem of age and the accompanying diagenetic changes which occur in both rock and fossil material. The substances found in the fossils themselves may be studied. This includes the mineralogy of calcite, and such chemicals as amino acids, first discussed by Abelson (1954). Shell mineralogy is generally considered to be a product of its environment, controlled in particular by factors such as salinity and temperature. Unfortunately, very well preserved shells are needed which have been unaffected by diagenesis, but there is some potential for palaeotemperature calculations in older material (Dodd, 1963, 1964). In a five part detailed study of brachiopod shell protein (Jope 1967-1973) various groups of proteins were isolated and classified. The best results came from Mesozoic and younger specimens. Ordovician species (Jope 1969a) did not give satisfactory results. There is, therefore, some potential for precise biochemical analysis on these fossils which may yield useful and interesting results.

## 10. PALAEOLOGY IN THE WELSH BORDERLANDS SECTIONS (INCLUDING MICROPALAEOLOGY)

All fossils collected were identified as far as possible (Murchison 1839, Davidson 1880, Cherns 1977, Siveter 1978) but with many of the comminuted shell layers, identification was not usually possible. Brachiopods and bivalves were identified to species level wherever preservation permitted. With many of the dalmanellids, however, distinction between Isorthis and Salopina was difficult. Other shelly fossils, e.g. trilobites and gastropods, were identified to generic level and then lumped together for the purposes of statistics, etc., since they form only a minor part of the fauna. Bryozoa were recorded simply as erect or encrusting forms. Many fossils were not preserved perfectly enough to allow precise identification, and in other cases, e.g. bryozoa, such identification would have been too time consuming in relation to the whole project, which was not intended to be an exercise in taxonomy.

After identification, fossils were recorded on index cards and counted, each fragment being counted as one specimen, unless obviously related to another fragment. Bryozoa were in some cases recorded as one colony, depending on their occurrence. Graphs of generic and specific abundances were then drawn for each section (Figs 8,9). These graphs, and the range charts which link all the information together, show various faunal changes across the Leintwardine-Whitcliffe boundary (discussed below). In order to study the vertical and lateral changes over an area within the Welsh Borderlands a literature search was undertaken (Straw 1937, Kirk 1951, Lawson 1955, Holland 1959, Walmsley 1959, Lawson 1960, Squirrell and Tucker 1960, Holland 1962, Whitaker 1962, Holland and Lawson 1963, Holland, Lawson and Walmsley 1963, Phipps and Reeve 1967, Lawson 1973, Antia 1981). This search involved the compilation of published faunal lists for several areas across the Welsh Borderlands encompassing a range of depositional environments. These lists were joined with data from several collections made by J.D. Lawson to produce a faunal distribution diagram (Fig. 11). It is clear from this diagram that there are two major types of faunal changes i.e.

vertical changes across the Leintwardine-Whitcliffe boundary and lateral changes across the depositional environment of basin to shelf. These changes are most apparent in the brachiopod fauna, while other shelly fauna, trilobites, for example, are less affected.

The main vertical changes at Ludlow include the sudden disappearance of Shaleria ornatella at the Leintwardine-Whitcliffe boundary and the sudden appearance and increase of Protochonetes ludloviensis through the Lower Whitcliffe Formation (Figs 8 vii, xxviii, 9vi, xxi). The dalmanellids, graptolites and trilobites are less common in the Lower Whitcliffe Formation, as is Aegiria grayi and Atrypa reticularis which peaks in the Upper Leintwardine Formation (Fig.8 xvi, ix, xiii, xix, xii, xxiii, Fig.9 xiii, x, xvii, ix, xxiii). Smooth ostracods are also less common in the Lower Whitcliffe Formation but peak just before the boundary in Levels 62S and 9XG (Fig.8 xvii, Fig.9 xv). At these levels they occur as sheets across bedding planes. Dayia navicula peaks at the boundary in Section 9X (Fig.9 iv) but appears in minor amounts in Section 62 (Fig.8 iv). Bivalves, orthocones, gastropods and worm tubes are more abundant in the Lower Whitcliffe Formation, in particular the bivalve Fuchsella amygdalina, of which several possible `life position` specimens have been found (Fig.8 xv, xxix, xxiv, Fig.9 xii, xix, xi, xxvii). These changes are present in other areas as seen in Figure 11, although due to inaccurate recording, slight changes may be hidden, as explained in the caption. Other species show an uneven distribution through the Mortimer Forest sections. Leptaena depressa peaks in the Upper Leintwardine Formation at level 9XE and then gradually declines (Fig.9 xvii). In Section 62 it is barely represented in the Upper Leintwardine at all (Fig.8 vi). Microsphaeridiorhyncus nucla, although present throughout the succession, peaks sharply at the boundary and then decreases in abundance (Fig. 8 i, Fig.9 i). The beyrichiid ostracods have a similar distribution pattern (Fig.8 xxv, Fig.9 xx). The bryozoa are the most ubiquitous of fossils but their distribution is not uniform. In Section 62, they peak at the boundary (Fig.8 xi), while in Section 9X there are two peaks, one at the boundary (Level G) and one at the top of the section in

Level N (Fig.9 viii).

Figure 11 represents a section taken from Knighton, in the deepest basinal area (Holland 1959) to the inner shelf region of May Hill, Usk and the Malverns. It is evident from this that lateral changes in the fauna are as pronounced as those vertical ones already described. There is a particular increase in the diversity of the shelly fauna (from basin to shelf) visible mainly in the diversity of brachiopods. Other groups such as the beyrichiid ostracods and the trilobites have a reasonably constant distribution. This may in part be linked to their mobility. Palaeoecology and the possible reasons for such changes are discussed in Section 13.

Micropalaeontological analyses of this part of the Upper Silurian have been carried out principally by Richardson and Lister (1969), Dorning (1981) and Aldridge (1975, 1979). The assemblage contains acritarchs, spores, dinoflagellates and conodonts. Previous publications have been mainly descriptive, concentrating on the taxonomy of the microfauna and generally ignoring any palaeoecology. Richardson and Lister (1969) discuss the nature of the miospore assemblage, which is generally less than 1% of the microfauna. Spores increase rapidly in the Downtonian but there are no characteristic faunas such as those found in the macrofossils - the miospores range right through the Upper Ludlow. Dorning (1981) uses acritarchs to recognise three associations with increasing depth - nearshore, offshore and deep water. According to this evidence the Leintwardine and Whitcliffe Formations represent gradually deepening and then shallowing environments. Dorning (pers. comm. 1983) recognises two distinct palynological assemblages at the Leintwardine - Whitcliffe boundary - those with abundant algal tissue and those without. Each assemblage has a distinct acritarch composition. Salinity at this time was probably abnormal, but it is unknown yet whether it was high or low. Aldridge (1976) links conodont distribution with macrofossil assemblages. It is not yet possible, however, to use conodonts as palaeoenvironmental indicators, instead, other fossils are used to give information about conodont palaeoecology. There are, however, some

parameters which may be worth considering e.g. the ratio of simple to complex microplankton, and the reduction in specific diversity of microplankton (Lister, pers. comm. 1983). These would both require sedimentological analysis.

It is obvious that there is considerable potential for a comprehensive micropalaeontological analysis of the Leintwardine - Whitcliffe section with respect to environmental and ecological information. That this has not been undertaken in the present study is due entirely to restrictions of time. It should be considered as important future research.

In Recent and Mesozoic sediments, it is possible to examine barren sediment for the presence of brachiopod fibres (the fibres of which the brachiopod shell is composed). This may then indicate the presence of brachiopods even though their macrofossils are not preserved. Such an examination was attempted on Silurian sediment from Mortimer Forest by Matthew Collins and revealed one brachiopod fibre in apparently unfossiliferous sediment. This has great potential for palaeontological analysis, but is difficult due to the small size of the fibres. It may be possible in the future to examine unfossiliferous sediment for these fibres, and to use their abundance as a measure of the abundance of brachiopods in that sediment.

## 11. PALAEOLOGY IN THE GOTLAND SECTIONS

The topmost Hemse Group and lowermost Eke Formation are considered to be roughly equivalent to the Leintwardine and Whitcliffe Formations in Wales and England (Fig.5). The nature of the collection meant that it was not possible to compile range charts for the distribution of fossils through time. Fossils were identified as in the Welsh Borderlands collection (Hede 1929, Kelly 1967, Bassett and Cocks 1977) and counted. Abundances were plotted on graphs to give an indication of the distribution of fossils throughout localities (Fig. 12). From these it can be seen that most fossils are well distributed and abundant in most localities. Exceptions to this include Figure 12 xxii-xxix which represent single specimens (three cornulitids in xxiii) from locality 36. Additional faunal abundances were obtained from a literature search (Hede 1929, Bassett and Cocks 1974, Stel and de Coö 1977) contributing to the diversity of the Gotland fauna. A faunal distribution diagram was drawn up for comparison with the Welsh Borderlands (Fig. 13) - this only includes fauna identified in the collections and found in the Welsh Borderlands. Many species, particularly brachiopods, are unique to Gotland, and to plot them all on a distribution diagram would be too time consuming and of limited value.

A detailed comparison and interpretation of the two areas (Gotland and the Welsh Borderlands) will be undertaken in Section 13, but some points should be mentioned here. It is apparent that both the diversity and abundance of the fauna from Gotland are greater than in the Welsh Borderlands (Fig. 12, Table 1). This is even more striking considering the fact that the amount of bulk rock sampled in Gotland is approximately half that sampled in the Welsh Borderlands. Several genera are unique to Gotland e.g. Boucotinskia spp and the tentaculitids. The emphasis of the fauna is also strikingly different with S.ornatella the dominant fossil in Gotland and M.nucula in the Welsh Borderlands (Tables 2,3). It should also be noted that the faunal changes characteristic of the Welsh Borderlands section do not occur in Gotland. According to Stel and de Coö (1977), S.aff.ornatella continues on throughout the Burgsvik and on into

the Hamra-Sundre Beds. Other genera are absent from the Gotland section, including the graptolites, annelids and Lingula, although Stel and de Coö record Lingula in the Burgsvik Beds. Corals, crinoids and stromatoporoids are very abundant and much more diverse than in the Welsh Borderlands.

## 12. EPIZOAN ECOLOGY AND SIGNIFICANCE

The term `epizoa` includes all organisms which live on or within the external surface of any other organism (host), whether dead or alive, regardless of their relationship with the host organism, which may or may not be parasitic, and which in many fossil examples remains uncategorised. Epizoa have generally been ignored in palaeoecological analyses, but are potentially useful tools in several respects.

1. They may provide information about the life functions and interactions of both themselves and their host organism(s). They thus represent one of the few situations in which such information is available in the fossil record.
2. Epizoa have been used as evidence in determining life positions (Hurst 1974, Spjeldnaes 1984). In order to do this, it must first be reasonably established that encrustation occurred during the life of the host, by examining growth lines and contact areas. It may then be inferred for example that a brachiopod with a cornulitid on its pedicle valve lived with its pedicle valve uppermost.
3. Spjeldnaes (1984) has determined a shade-loving fauna of epizoa based on occurrences on leptaenid brachiopods and corals. Although this technique has limitations, epizoa may be used to a certain extent in environmental determinations.
4. According to Watkins (1981, pers.comm. 1983) epizoan numbers can be used to determine Ludlovian rates of sedimentation. This is done by counting the numbers of encrusted and non-encrusted shells and determining their relative proportions. Slower rates of sedimentation would be expected to produce more encrusted shells and vice versa. A count for the sections from Mortimer Forest produces a ratio of 1:50 encrusted to non-encrusted shells. This is fairly low and would seem to indicate a moderate to high rate of sedimentation during Leintwardine and Whitcliffe times.

Table 4 shows the numbers and types of epizoan bearing organisms (after Watkins 1981). Figures refer to the number of hosts, not the number of epizoa. Bryozoa are the most abundant epizoa, settling on a wide range of host organisms with a slight



preference for orthoconic nautiloids. This reflects their abundance throughout the sections as non-encrusting organisms. Most of the bryozoan epizoa are encrusting or lamellar forms which probably used empty shell fragments as a substrate after the death of the occupants. On some of the orthocones, however, encrustation occurs around the shell indicating that epizoan attachment occurred during the life of the host. This would have provided the bryozoa and other normally sessile organisms with the advantages of movement i.e. plentiful food supply, wide gamete dispersal areas, ability to escape burial etc. There are also some stick or erect forms of bryozoa occurring as epizoa, which may possibly have used the shell as a substrate during the life of the host. This is possible in the cases of specimens Zw5488 (on S.ornatella), Zw5557 (on M.nucula) and Zw5709 (on L.depressa). Latex moulds were made of these specimens.

Orthocones are popular hosts for other epizoa too, possibly due to their large surface area which enables several epizoa to co-exist without collision or interference. Cornulitids have been found as epizoa but none so beautifully orientated towards their host's commissure as that described by Holland (1971). Two free living specimens were also found. According to Richards (1971), solitary cornulitids living during the Silurian were commensal. Certainly no evidence of parasitism was found in the ten cornulitids from the Mortimer Forest sections. Boring epizoa such as Vermiforichnus, discussed in detail by Cameron (1969) may have been parasitic but preservation in general is so unclear as to leave epizoa-host relationships in some doubt. This doubt also extends to any consideration of mode of life, particularly as time of encrustation cannot be established.

It is interesting and puzzling to note that in both sections from Mortimer Forest the numbers of epizoa present increase by more than 100% across the Leintwardine-Whitcliffe boundary. If rates of sedimentation are increasing, as has been proposed both here and elsewhere (Watkins 1979), then the opposite would be expected. However, the numbers involved are so small in both cases (5 to 11 in FC62 and 7 to 18 in 9X) that this may not be of any importance.

## 13. DISCUSSION AND CONCLUSIONS

As Figure 1 shows, sudden faunal changes are common throughout the Upper Silurian sediments of the Welsh Borderlands. It is clear when comparing Figures 1 and 11, however, that these changes are emphasised when only the brachiopod and other benthonic fossils are examined. The changes are less pronounced when the fauna is taken as a whole (Fig. 11). Cherns (1977:400) comments on these changes thus:

‘The vertical and lateral faunal variations depend upon environmental conditions. For example, D.navicula remains concentrated in the more distal areas of the shelf, while S.lunata, which enters the fauna earlier in the SE inliers, appears to prefer more proximal shelf conditions. The migration north and west of the typical Whitcliffe Beds assemblages of P.ludloviensis, M.nucula and S.lunata during the Leintwardinian suggests that there was progressive environmental change across the shelf. However, the opposite trend for S.wilsoni, which dies out lower in the succession in the shelf edge and Ludlow areas, to be replaced by S.ornatella, shows that each species responded individually and differently to the evolving palaeogeography. The top LLB [Lower Leintwardine Beds] and ULB [Upper Leintwardine Beds] shelf fauna has an abundance of the large strophomenids S.ornatella and L.depressa plus A.reticularis all of which appear adapted for resting freely on a substrate, in fairly quiet conditions and with little sedimentation. In contrast, the middle LLB shelly limestones of Perton have a concentration of ribbed, plicated, pedically attached forms - S.wilsoni, M.nucula, H.elegans - which are well-adapted for more turbulent conditions. Hence, the distributions of the brachiopod species in the LLB are thought to be of ecological, rather than stratigraphical significance.’

The final sentence applies equally well to the distribution of brachiopod species in the Upper Leintwardine Formation. This study has attempted to discover the actual ecological controls on all the Leintwardinian species, not only on the brachiopods. Obviously, there have been difficulties in doing this, not only because of the nature of the fossil record itself, but also

because of the monotony and lack of obvious sedimentary features of the lithology. The continuity of the lithology across the Welsh Borderlands has been described in Section 5. The variations which occur in the amounts of calcareous material present in the sediments do not relate to any obvious faunal change. The most noticeable lithological difference at the level of the Leintwardine and Whitcliffe Formations is that between the sediments of the basin and shelf. The greater silt content of the basin is reflected in the reduction of the shelly fauna seen on the shelf (Fig. 11).

However, the presence of numerous phosphate horizons throughout the succession and the large deposit of conglomerate in the Malverns inlier suggest a changeable and unstable depositional environment. From an examination of the literature (Section 6) it seems reasonably certain that a depositional environment of warm seas and changing sea levels is required for the formation of phosphate pebble deposits. High organic productivity may also be necessary, but is difficult to assess in fossil examples. Palaeogeographic reconstructions place the British Isles (the southern part) at between ten and twenty degrees south of the equator during Ludlovian times (Fig. 14). At this time, the Iapetus Ocean in Britain was in its dying phases and closing rapidly. It was a time of tectonic activity and such disturbances may affect sea levels. They may also be reflected in the biological conditions (Ziegler 1970, McKerrow and Ziegler 1972). Shallowing seas and possible periods of drying out seem likely to have occurred and to have left their imprint in the sediment as phosphate deposits. Such conditions affect salinity, food supply, temperature and light supply. The importance of this with regard to changes in fauna is discussed below.

Fossil preservation gives a further indication that the depositional environment of Leintwardine-Whitcliffe times was not monotonous and without disruption. Shelly laminae interpreted as storm deposits (Watkins 1979) imply that the environment was subjected to periodic disturbance and reworking. This may have had local effects on the faunal and floral populations but is unlikely to have resulted in the extinction of major and

widespread groups.

The faunal changes which occur in the Upper Leintwardine and Lower Whitcliffe Formations have been described in Section 10. Before attempting to explain these changes, it is useful to examine similar disappearances at the boundary of the Lower and Upper Leintwardine Formations. One of these involves the brachiopod Sphaerirhynchia wilsoni which declines and disappears rapidly in the topmost Lower Leintwardine Formation (Cherns 1977:211). Some species show a slight preference for certain facies e.g. D.navicula appears to have been tolerant of the silty environment of the distal shelf region and therefore to sedimentation (Cherns 1977:228), and shows a preference for silty lithologies (Cherns 1977:227). Others, however (e.g. H.elegans), show no relationship between facies type and abundance (Cherns 1977:231). Palaeoecological analyses carried out on Lower Leintwardine assemblages indicate 'a local derivation for fossils from a mosaic faunal settlement pattern in a shelf environment' (Cherns 1977:390).

Faunal variations which occur throughout a section in either a vertical or lateral sense may be due to either biological or non-biological factors. Biological factors include changes in predator abundance, food supply, the nature of interspecific reactions and the onset of disease. These may be reflected in the fossil record but may be open to several forms of interpretation. For example, an increase in predator abundance may lead to more predators as fossils, but such an observation may equally be due to a preservational artefact, or a change in current direction. It is therefore difficult to recognise biological factors at work through the fossil record. Non-biological factors include changes in water depth, salinity, temperature, substrate, turbidity, rate of sedimentation, current direction, amount of light and oxygen supply. Substrate change is recognisable by a grain size change or a compositional change, recorded in the mineralogical components of the sediment. Such features should be easily visible in thin section but are apparently absent in the Ludlow succession (Section 5). Localised substrate changes, however, may not be so well

preserved. The disappearance of a patch of shelly cover may mean the disappearance of a species which has lost its means of anchorage, but the event may not be recorded at all in the fossil record. Turbulence may be recognised by the presence of sedimentary structures - however, these are rare in the succession at Ludlow.

Other factors may be inferred from the record e.g. depth change may be inferred from the sedimentary structures or from the nature of the fauna (thin shells, presence of algae etc.). Increase in sedimentation rate can be inferred from epizoa (see Section 12) or may be related to shallowing. Some factors such as temperature and salinity changes are not easily recognisable in the record. It is therefore important when assessing the palaeoecological conditions of a given geological section to consider together all the factors and variations which may have played a part in shaping the living community and in affecting its preservation or lack of it.

In an attempt to assess the importance of the various palaeoecological factors in vertical faunal changes, each species or group of species (e.g. bryozoa) was treated as a separate palaeoecological unit and its requirements were assessed (Cameron 1969, Schopf 1969, Ryland 1970, Cherns 1977, Hurst and Watkins 1978, Watkins 1978, Hewitt and Watkins 1980, Fursich and Hurst 1981, Mikulic and Watkins 1981, Watkins 1981). For ease of discussion, species or groups with similar ecological requirements were put together (Table 5). This table does not imply that all members of a group have the same tolerance level to various conditions, only that their ecological requirements and dislikes are similar enough to facilitate discussing them together. Several factors affect species regardless of their individual palaeoecological needs, and can therefore be said to affect all groups to the same extent. Such factors include disease, salinity and temperature changes, lack of light and starvation. These factors are generally not evident in the fossil record.

Group A (Table 5) includes all infaunal organisms, many of which

are soft-bodied and therefore not reflected to any great extent in the record. The presence of phosphate lined burrows indicates the existence of some worms, although their numbers are probably greatly underestimated. The burrowing inarticulate brachiopod Lingula (which is present throughout the succession) has been studied in detail by Cherns (1979) from several specimens in life position. The genus forms only a minor part of the fauna in the present study. It is likely that infaunal organisms preferred slow sedimentation rates in order to avoid burial. There is a slight increase in the amount of worm tubes present in the Lower Whitcliffe Formation. This may be a preservational artefact, but may be linked to the decrease in epifaunal brachiopods which cleared the sediment of much of its shelly cover.

Semi-infaunal organisms, composing Group B, also form a relatively small part of the fauna. Members of this group can withstand some sedimentation and a slight amount of turbulence. These organisms are common in shallow shelf areas and increase in the Lower Whitcliffe Formation. This may be due to the availability of space, both actual and ecological, provided by the decrease of the brachiopods. According to Watkins (1978), bivalve abundance is greatest at extremes of the environmental gradient i.e. in both the highest energy (endo-byssate forms) and lowest energy (nuculoids) environments. This indicates a wide range of tolerance to ecological conditions.

Epifaunal organisms fall into Groups C and D according to whether they prefer high or low energy environments, with a subsidiary group E which contains organisms requiring a hard site for attachment. (These organisms are cementing brachiopods, and form a very minor part of the fauna. Their lifestyle and ecology are largely unclear, but it is thought that they have a wide tolerance of conditions.) Group C organisms prefer higher energy environments where the water may be shallow, and must be within the photic zone. Crinoids belong to this group, and also bryozoa, which have been shown to prefer rough water, growing larger in more turbulent conditions (Schopf 1969, Ryland 1970). According to Cherns (1977:271) the growth form of bryozoa is 'environmentally adapted, relating to current action,

availability of substrate, sedimentation rate, temperature and depth. Stronger larger forms are found in the basal conglomerate beds, and in the Aymestry Limestone facies. The former deposits are thought to represent turbulent conditions. The generally larger size in calcareous facies may indicate that less turbid conditions were preferable. The decreased abundance and size of branching colonies towards the shelf edge could result from intolerance for silty, soft bottom conditions. Members of this group are intolerant of turbidity and high sedimentation rates, being particularly susceptible to silting up. This is shown in A.reticularis by its higher abundance in calcareous facies in the Lower Leintwardine Formation, the smaller size of individuals in the shelf edge areas, and its absence from areas with laminated siltstone lithology (Cherns 1977:223). Both the bryozoa and the brachiopod M.nucula decrease gradually throughout the Lower Whitcliffe Formation but are otherwise notable for their widespread distribution. Their general decline may be due to an overall increase in turbidity throughout Lower Whitcliffe times, related to an increase in sedimentation rates in a restricted and shallowing sea.

Group D organisms prefer a quieter environment, many of them possessing structures which would be damaged in rough water e.g. the spines of P.ludloviensis and the long trail of L.depressa. This group contains S.ornatella, the disappearance of which marks the boundary between the Upper Leintwardine and Lower Whitcliffe Formations. According to Cherns (1977:202) 'the distribution pattern indicates that S.ornatella may be intolerant to sedimentation and turbidity. Its high concentration in the shelf sequences, and decrease in size and abundance westwards could be explained thus.' The disappearance of S.ornatella and also that of L.depressa could be explained by an increase in sedimentation rates in the Lower Whitcliffe. However, the disappearance of S.ornatella is so sudden, and the appearance and increase of P.ludloviensis at the same level is so rapid, that some other explanation must be sought. Cherns (1977:195) suggests that the 'persistence of P.ludloviensis during transitions from marine to non-marine facies relates to a high tolerance for shallow, silty and sandy conditions in more proximal shelf environments.' This

tolerance may have given the species an advantage over S.ornatella in an unstable and changing environment. S.ornatella was so successful during the Upper Leintwardine however, that some factor must have acted adversely upon it, to cause its disappearance. This factor may have been disease, and the mechanism of takeover may have been similar to the case of red and grey squirrels in modern times.

Grey squirrels were introduced by man into territories already occupied by red squirrels. This in itself was not enough to cause a change. Disease, however, caused only the red squirrels to be severely restricted in numbers, or to die out completely. The grey squirrels were unaffected by disease and were thus able to fill the ecological niches left by the reds. They were so successful in this that the reds found it difficult or impossible to recover their former abundances and in some areas disappeared completely (Matthew Collins, pers. comm.). Thus disease or selective predation may have caused the demise of S.ornatella and facilitated the takeover of P.ludloviensis. Another explanation for this major faunal change involves the changing current directions postulated by Watkins (1979) to explain the sudden appearance of S.ornatella at the base of the Upper Leintwardine Formation. If a change in current direction brought in exotic larvae from an area away from the shelf, it is equally possible that the currents reverted to their original patterns, or changed to a different pattern, thus stopping the supply of S.ornatella larvae. This sudden absence would have created settling space for other larvae, notably that of P.ludloviensis which experiences a sudden increase in abundance. The successful takeover of P.ludloviensis may have been facilitated by the presence of spines along its hinge line. The environment of the Whitcliffian was one of high sedimentation (Watkins 1978:42). It is possible that the spines and the curvature of P.ludloviensis helped to raise it further above the sediment than S.ornatella would have found possible, and thus enabled it to escape sedimentation for a time, at least.

Group D also includes the dalmanellids. These brachiopods (S.lunata and I.orbicularis/clivosa) are very similar in external



morphology, and during the present study, they have generally not been distinguished, but have been recorded simply as 'Isorthis sp.' or 'dalmanellids'. Other workers have, however, separated them, due to their different vertical distributions. Thus it is useful to note that 'the two species have very similar forms, and by inference, have comparable modes of life. The vertical replacement of Isorthis by S.lunata supports this conclusion' (Cherns 1977:211).

The final group includes all motile animals, swimmers, crawlers, grazers etc. Some members of this group, especially the cephalopods, may escape localised conditions e.g. an influx of sediment by swimming away from them. Trilobites and ostracods gradually decline throughout the Lower Whitcliffe Formation, whereas cephalopods and gastropods are more common. The presence of food is one of the most important factors governing motile animals so it is therefore necessary to identify possible food sources. Many ostracods are believed to have been planktonic and therefore at the mercy of the ocean currents. Others swam actively and fed on smaller organisms which formed part of the plankton, therefore effectively behaving in a similar way to their planktonic cousins. Trilobites also had different methods of feeding but being essentially benthic, an increasing rate of sedimentation may have had an adverse effect on them. It is also possible that their apparent decline is due to preservational bias. Gastropods are generally grazers, though a few are carnivorous. All are generally benthic, unless living on algal forests which may raise them within the water column. There may have been an increase in algal vegetation during the Lower Whitcliffe due to the shallowing and linked increase in current activity. Cephalopod increase may be linked to bivalve increase if it is assumed that bivalves formed a major part of their diet. The individuals found tend to be larger than those in the Upper Leintwardine, thus indicating that they are older and more mature and therefore found the environment more sympathetic to their needs.

Sudden changes in faunal composition such as those discussed from the Upper Ludlovian of the Welsh Borderlands may in some cases be

due to the presence of opportunistic species, or of species which at some stage in their history behave in an opportunistic way (Levinton 1970, Watkins 1979). Levinton (1970) cites seven points by which opportunistic species may be recognised in the fossil record.

1. Random orientation and lack of size sorting of specimens in individual beds, but a tendency for dominant species to occur in size group aggregations.
2. Distribution over a limited area, beyond which the horizon is unfossiliferous.
3. Aggregation of individual species in clusters, especially if a species is sessile, or stationary infaunal.
4. Presence of the species in thin but widespread isochronous horizons indicating brief invasions.
5. Species is found abundantly in several otherwise distinct faunal assemblages.
6. Species appearing in great abundance in a facies with which it is not usually associated.
7. A species numerically dominates an assemblage by 85-100% by numbers.

Of these, criteria 2,3,4, and 7 are recognisable in the distribution of S.ornatella in the Ludlow area. Watkins (1979) has plotted species of brachiopods according to their abundances and has determined that S.ornatella, in the Upper Ludlow at least, is an opportunistic species.

It has been implicit in the discussion so far that fossils occur in or near their life positions. Discussions and evidence from modern shelf communities (Matthew Collins, pers.comm.1985) indicate that this is a reasonable assumption. Watkins' disturbed neighbourhood assemblages (see Section 7) represent the most common type of preservation in the succession - clusters of shells in various orientations, sometimes spreading out over bedding planes, sometimes in discrete groups. At one time the main source of disturbance of marine shells was thought to be physical - principally current action. It is now recognised, however, that most disruption is biogenic (Antia 1981, Collins pers.comm.1985) and caused by burrowing, walking etc. by larger organisms such as arthropods. Disturbance during periods of

strong current activity is minimal and amounts to distances of centimetre scale only. Watkins` disturbed neighbourhood assemblages are therefore considered to be reasonably accurate representations of living associations, but not necessarily of life positions or biological communities. Shelly laminae thought to be produced by storms (Watkins 1979) were probably formed by transport from beach areas or by in situ breakage.

In the modern shelf environment studied by Collins (pers.comm.1985) the nature of the substrate has provided some interesting insights. The upper layer of the sediment consists of coarse shelly fragments which provide pedicle attachments sites for brachiopods, byssal sites for bivalves etc. This layer remains coarse despite the continual input of finer sediment from the water column. The fine sediment apparently filters down between the shelly fragments without burying them. Burial therefore only occurs episodically, as a result of a sudden input of sediment, for example during a storm. It is likely that the substrate during the Upper Ludlow was similar with a fine-grained sediment bottom unevenly covered with shell debris. The debris supported various brachiopods and possibly some algae, while other species rested in areas of softer sediment. Disturbance was probably quite high, from walkers, such as trilobites and other arthropods. Disarticulation studies on brachiopods have shown that they can undergo several months continual battering without breakage or disarticulation (Collins pers.comm.). It is possible, therefore, that disarticulated brachiopods in the Ludlovian succession were the victims of cephalopods or arthropods, either as prey or as obstacles in a walkway.

Figure 11 shows a transect from basin to shelf across the Welsh Borderlands from Knighton to the Malverns. The lateral changes - increase in diversity and abundance of shelly fauna (brachiopods, bivalves, trilobites etc) - can be related to the ecological changes associated with the differences between basin and shelf. The basinal environment has less light, deeper and quieter water and less food in the lower regions. The sediment surface is below the photic zone and may be anoxic in places. There is little sessile epifauna such as that found in the shelf and the

faunal emphasis is on motile animals such as cephalopods. The shelf regions, however, are progressively shallower, with more light, more currents and more food. There are likely to be attachment sites on the sediment surface in the form of shelly debris, allowing the settlement of epifauna. The increase in light and food supply allows the diversification of a shelly fauna which was restricted in basinal areas. Other increases include oxygen availability and temperature. Biological factors may affect both basin and shelf equally (e.g. disease), but non biological factors vary considerably in effect, being linked to each other to a certain degree.

Taking all the evidence together, it is possible to arrive at a description of conditions during Upper Leintwardine and Lower Whitcliffe times which offers some explanations for the various faunal variations. During the deposition of the Upper Leintwardine Formation, a fine-grained sediment bottom was covered with shell debris from dead bivalves and brachiopods, possibly washed down from shallower beach waters, and algae. Soft sediment was available for infaunal and semi-infaunal organisms. Storms were of normal occurrence. Disturbance of organisms was common from walking arthropods, predators etc. It seems likely that during deposition of the Lower Whitcliffe Formation there was an increase in sedimentation rate linked to shallower and more turbulent water. The prevailing current system may have switched direction. S.ornatella died out because of this, or because of disease or selective predation. This allowed P.ludloviensis to fill its niche through the advantage of its spines and shell curvature enabling it to escape sedimentation. Bivalves became more abundant because the increasing sedimentation put restrictions on the brachiopods and freed more ecological niches. Algae occurred both as floating masses and rooted forests, possibly supporting small epiplanktonic brachiopods or bivalves and ostracods. The distribution of species tended to be in small conspecific clusters, while the fauna was dominated by one or two main species (e.g. S.ornatella, M.nucula, P.ludloviensis). Most shells would be colonised by bryozoa after death, unless buried quickly. Some organisms, however, support epifauna during life

e.g. cephalopods and some brachiopods.

Many of the differences between this situation and that of the Gotland fauna can be ascribed to the palaeogeography and palaeolatitude of the Baltic. The area around Gotland and part of mainland Sweden and continental Europe is considered to have been less than ten degrees south of the equator (Scotese et al. 1985), and under a shallow carbonate depositing sea (Stel and de Co0 1977). According to Laufeld and Bassett (1981) deposition in Gotland during the Ludlovian was dominated by carbonate sedimentation and reef formation, indicating a shallow, epicontinental sea at low latitudes. Algae throughout the succession indicate that deposition occurred within the photic zone, at probably less than 100m (Laufeld and Bassett 1981:26). Facies vary both laterally and vertically. The milder climate was obviously more favourable to life than the cooler seas of the Welsh Borderlands. This can explain the greater faunal diversity found in the Gotland section, but there is also a difference in faunal emphasis that needs explanation (Tables 2,3).

The dominance of S.ornatella in Gotland may be due to warmer temperature and slow sedimentation rate. The prevailing ocean currents may have been more stable than in the Welsh Borderlands. The species does not appear to behave as an opportunistic species in Gotland, although it does numerically dominate the fauna in places. In general, the most abundant fauna in Gotland are those which prefer clear, calm water with little sedimentation or turbulence. Those species which tolerate disturbance and silty environments flourish better in the Welsh Borderlands (e.g. P.ludloviensis, bryozoa and bivalves). M.nucula is dramatically rare in the Gotland section. This may be due to a lack of competitive ability, i.e. it cannot compete successfully for ecospace with other brachiopod species, but only thrives when they are unsuccessful. It may equally be due to a preference for cooler waters. Orthocones are also rare in Gotland - possibly the water was too shallow for them, or a lack of bivalves as food may have proved a limiting factor. The fact that many species carry on uninterrupted throughout the Upper Silurian indicates that the Baltic environment was more stable in terms of

temperature, water depth and ocean currents. It is noticeable that graptolites, annelids and Lingula are absent from the Gotland collection. Infauna are presumably restricted because of the lack of free soft sediment due to biohermal takeover and carbonate debris. This may affect other organisms such as orthocones (see above) and predatory gastropods. Graptolites may be absent as a result of current direction (if planktonic), preservational bias, or because of a dislike of shallow water, preferring the cooler, deeper waters of such areas as the Welsh Basin. Corals are absent in the Welsh Borderlands due to the silty nature of the environment. The temperature may have affected them, although they are present in the Bringewood Beds (Aymestry Limestone facies) so this seems unlikely. It is interesting in terms of evolution to note that L.depressa in the Welsh Borderlands is represented by L.rhomboidalis in Gotland, a very similar and probably closely related species.

The fauna and palaeoecology of both the Silurian of the Welsh Borderlands and the Silurian of Gotland are now very well known and reasonably understood. There are some gaps in knowledge, however, which need to be filled in order to complete the information available for this period. These gaps include detailed geochemical and palynological analyses of both sections, particularly the British one. Such analyses may serve to answer the few remaining questions about Silurian faunas of the Welsh Borderlands and Gotland.

FOSSIL/LEVEL	A	B	C	D	E	F	G	H	I	J	K	L	M	N
<u>Shaleria ornatella</u>	24.42	50.50	48.84	6.30	0.88	1.95	1.46	-	-	-	-	-	-	-
<u>Microsphaeridiobryoncus nucula</u>	18.74	7.00	6.40	27.56	28.32	43.41	38.25	35.82	14.53	36.15	32.50	12.16	6.70	14.00
<u>Protochonetes ludloviensis</u>	1.26	3.00	2.33	0.79	0.88	-	0.21	-	24.42	6.15	-	31.76	59.62	10.70
<u>Aegiria grayi</u>	5.05	1.00	0.58	1.57	-	2.93	4.78	-	-	14.62	15.00	-	-	-
<u>Shagamella ludloviensis</u>	3.37	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Bryozoa</u>	7.37	7.50	8.14	7.87	8.85	11.71	6.44	11.94	5.81	8.46	6.67	6.08	7.69	22.00
<u>Isorthis spp</u>	1.68	1.00	1.74	-	-	-	-	-	-	-	-	-	-	-
<u>Beyrichiids (total)</u>	2.53	0.50	-	-	0.88	3.90	3.33	2.99	1.74	4.62	1.67	-	0.96	-
<u>Dalmanellids (total)</u>	20.21	15.50	19.77	22.83	14.16	6.34	1.66	23.88	10.47	5.38	8.34	3.38	1.92	1.34
<u>Leptaena depressa</u>	0.63	3.00	1.74	8.66	30.09	2.44	0.42	-	0.58	-	-	-	-	-
<u>Bivalves (total)</u>	0.63	2.00	1.16	1.57	4.42	1.46	1.25	4.48	4.65	7.69	15.83	33.78	16.35	32.67
<u>Orthocones indet.</u>	0.63	-	-	-	-	0.98	0.42	-	-	-	4.16	4.73	1.92	12.67
<u>Alrypa reticularis</u>	1.26	2.50	5.23	10.24	3.54	2.44	-	1.49	-	-	-	-	-	-
<u>Salopina lunata</u>	3.58	2.50	-	-	0.88	-	-	1.49	-	1.54	1.67	1.35	-	2.67
<u>Dayia navicula</u>	2.32	0.50	-	-	-	-	-	7.46	19.77	1.54	2.50	2.70	-	-
<u>Gastropods (total)</u>	0.63	-	-	0.79	0.88	0.98	0.21	1.49	-	3.08	1.67	2.70	0.96	1.34
<u>Neobeyrichia laevis</u>	1.47	-	-	0.79	-	1.46	2.49	-	-	-	0.83	-	-	-
<u>Smooth ostracods</u>	2.11	-	-	-	4.42	15.61	35.76	8.96	15.12	7.69	5.83	-	-	-
<u>Monograptids indet.</u>	0.21	-	-	6.30	0.88	-	-	-	-	-	-	-	-	-
<u>Trilobites (total)</u>	0.42	1.50	1.74	1.57	-	2.93	2.91	-	-	-	2.50	0.68	-	-
<u>Ptilodictya lanceolata</u>	-	1.00	1.16	-	-	-	-	-	-	-	-	-	-	-
<u>Cornulites serpularius</u>	-	1.00	-	-	-	0.49	-	-	-	-	-	-	-	-
<u>Howellella elegans</u>	-	-	1.16	-	-	0.98	-	-	-	-	-	-	2.88	-
<u>Orbiculoidea furcata</u>	-	-	-	0.79	0.88	-	-	-	-	-	-	-	-	-
<u>Crinoid ossicles</u>	-	-	-	2.36	-	-	0.42	-	-	-	-	-	-	-
<u>Worm tubes</u>	-	-	-	-	-	-	-	-	2.33	4.00	0.83	0.68	0.96	2.67
<u>Lisogula lata</u>	-	-	-	-	-	-	-	-	0.58	-	-	-	-	-

APPENDIX A. SECTION 9X, HORTIMER FOREST. FAUNA IN PERCENTAGES.

FOSSIL/LEVEL	A	B	C	D	E	F	G	H	I	J	K	L	M	N
<u>Shaleria ornatella</u>	116	101	84	8	1	4	7	-	-	-	-	-	-	-
<u>Microsphaeridiorhyncus nucula</u>	89	14	11	35	32	89	184	24	25	47	39	18	7	21
<u>Protochonetes ludloviensis</u>	6	6	4	1	1	-	1	-	42	8	-	47	62	16
<u>Aegiria grayi</u>	24	2	1	2	-	6	23	-	-	19	18	-	-	-
<u>Shagamella ludloviensis</u>	16	-	-	-	-	-	-	-	-	-	-	-	-	-
Bryozoa	35	15	14	10	10	24	31	8	10	11	8	9	8	33
<u>Isorthis spp</u>	8	2	3	-	-	-	-	-	-	-	-	-	-	-
Beyrichiids (total)	12	1	-	-	1	8	16	2	3	6	2	-	1	-
Dalmanellids (total)	96	31	34	29	16	13	8	16	18	7	10	5	2	2
<u>Leptaena depressa</u>	3	6	3	11	34	5	2	-	1	-	-	-	-	-
Bivalves (total)	3	4	2	2	5	3	6	3	8	10	19	50	17	49
Orthocones indet.	3	-	-	-	-	2	2	-	-	-	5	7	2	19
<u>Atrypa reticularis</u>	6	5	9	13	4	5	-	1	-	-	-	-	-	-
<u>Salopina lunata</u>	17	5	-	-	1	-	-	1	-	2	2	2	-	4
<u>Davia navicula</u>	11	1	-	-	-	-	-	5	34	2	3	4	-	-
Gastropods (total)	3	-	-	1	1	2	1	1	-	4	2	4	1	2
<u>Neobeyrichia lauensis</u>	7	-	-	1	-	3	12	-	-	-	1	-	-	-
Smooth ostracods	10	-	-	-	5	32	172	6	26	10	7	-	-	-
Monograptids indet.	1	-	-	8	1	-	-	-	-	-	-	-	-	-
Trilobites (total)	2	3	3	2	-	6	14	-	-	-	3	1	-	-
<u>Prilodictya lanceolata</u>	-	2	2	-	-	-	-	-	-	-	-	-	-	-
<u>Cornulites serpularius</u>	-	2	-	-	-	1	-	-	-	-	-	-	-	-
<u>Howellella elegans</u>	-	-	2	-	-	2	-	-	-	-	-	-	-	-
<u>Orbiculoidea rugata</u>	-	-	-	1	1	-	-	-	-	-	-	-	3	-
Crinoid ossicles	-	-	-	3	-	-	2	-	-	-	-	-	-	-
Worm tubes	-	-	-	-	-	-	-	-	4	4	1	1	1	4
<u>Lingula lata</u>	-	-	-	-	-	-	-	-	1	-	-	-	-	-

APPENDIX B. SECTION 9X, NORTIMER FOREST. FAUNA IN ACTUAL FIGURES.



FOSSIL/LEVEL	AE	G	H	I	J	K	L	H	R	O	P	Q	R	S	T	U	V	W	X
<u>Microsphaeridiothyncus nucula</u>	14.06	7.26	3.60	8.60	-	1.67	-	50.0	27.27	8.87	12.68	24.39	15.00	7.23	36.76	42.07	28.43	15.56	9.50
<u>Orbiculoidea rugata</u>	0.19	0.56	-	-	-	1.67	-	-	1.82	-	-	2.44	5.00	-	-	-	-	1.12	-
<u>Salopina lunata</u>	4.75	-	4.32	2.15	-	-	-	-	-	7.39	-	-	-	-	0.36	0.61	-	2.23	-
<u>Dayia navicula</u>	10.09	13.41	12.23	-	-	-	-	-	7.27	4.93	-	-	-	-	1.47	1.22	4.06	1.12	-
<u>Sharamella ludloviensis</u>	28.32	8.38	4.32	2.15	-	-	-	-	3.64	3.94	-	-	-	-	-	-	-	-	-
<u>Shalaria ornata</u>	16.04	47.49	30.94	48.39	33.34	1.67	-	10.00	7.27	0.49	22.54	4.88	-	0.21	0.74	-	-	-	-
<u>Leptaena depressa</u>	2.38	2.79	7.19	2.15	-	1.67	-	10.00	3.64	-	-	-	-	-	-	-	-	-	-
<u>Serpulites longissimus</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
J.de C.Soverby	-	-	-	-	-	1.67	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Isorthis sp2</u>	1.18	1.68	1.44	-	-	-	-	-	-	0.99	-	2.44	-	-	0.74	-	-	-	-
<u>Bryozoa</u>	2.57	5.03	10.79	11.83	-	8.34	-	10.00	18.18	5.91	15.49	16.64	5.00	3.18	12.50	10.98	5.08	15.56	3.17
<u>Ascidia grayi</u>	0.19	-	-	-	-	-	-	-	-	9.85	-	-	-	-	0.74	-	-	-	1.36
Monograptids indet.	0.19	-	2.16	2.15	33.34	63.34	100.0	10.00	-	-	-	-	-	-	-	-	-	-	-
<u>Lingula lewisii</u>	0.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Bivalves (total)</u>	3.37	4.47	4.32	2.15	-	-	-	10.00	16.36	3.94	-	7.32	10.00	-	0.74	1.22	5.58	20.00	3.62
<u>Dalmanellids (total)</u>	14.85	1.68	12.23	3.23	-	-	-	-	1.82	12.81	9.86	9.76	20.00	3.47	1.47	2.44	1.52	2.23	0.45
<u>Smooth ostracods</u>	-	2.79	4.32	8.60	-	-	-	-	3.64	-	-	-	-	-	68.79	18.75	20.73	8.12	0.45
<u>Cornulites serpularius</u>	-	2.23	-	-	-	-	-	-	-	0.49	-	-	-	-	-	-	-	1.12	-
<u>Trilobites (total)</u>	-	0.56	1.44	7.53	-	3.34	-	-	-	2.96	7.04	9.76	5.00	0.58	1.84	1.22	2.03	-	-
<u>Strophonella suglyphg(Hisinger)-</u>	0.56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Monograptus leintwardinensis</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lapworth	-	-	0.72	-	-	15.00	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Sphaerirhynchia wilsoni</u>	-	-	-	1.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(J.Soverby)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Orthocones indet.</u>	-	-	-	-	33.34	1.67	-	-	1.82	0.99	-	-	10.00	-	0.36	3.05	1.52	15.56	2.26
<u>Beyrichiids indet.</u>	-	-	-	-	-	-	-	-	5.45	5.91	9.86	-	15.00	8.67	11.76	8.54	-	3.34	4.98
<u>Neobeyrichia laeensis</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	1.16	-	3.05	-	-	-
<u>Cranions implicata</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(J.de C.Soverby)	-	-	-	-	-	-	-	-	1.82	-	-	-	-	-	-	-	-	-	-
<u>Protoconostes ludloviensis</u>	-	-	-	-	-	-	-	-	-	30.05	18.31	21.95	15.00	6.65	11.03	3.66	42.13	13.34	71.50
<u>Strophomenids indet.</u>	-	-	-	-	-	-	-	-	-	0.49	1.41	-	-	-	-	-	-	-	-
<u>Lingula lata</u>	-	-	-	-	-	-	-	-	-	1.41	-	-	-	-	-	-	-	-	-
<u>Atrypa reticularis</u>	-	-	-	-	-	-	-	-	-	1.41	2.44	-	-	-	-	-	-	-	-
<u>Worm tube</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.36	-	0.51	6.67	-
<u>Gastropods (total)</u>	1.19	1.12	-	-	-	-	-	-	-	-	-	-	-	0.36	1.22	1.02	2.33	2.71	-

APPENDIX C. SECTION 62, NORTHERN FOREST. FAUNA IN PERCENTAGES.

FOSSIL/LEVEL	AE	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
<u>Microsphaeridiorhynchus nucula</u>	71	13	5	8	-	1	-	5	15	18	9	10	3	25	100	69	56	14	21
<u>Orbiculoidea rugata</u>	1	1	-	-	-	1	-	-	1	-	-	1	1	-	-	-	-	1	-
<u>Salopina lunata</u>	24	-	6	2	-	-	-	-	15	-	-	-	-	-	1	1	-	2	-
<u>Dayia navicula</u>	51	24	17	-	-	-	-	4	10	-	-	-	-	-	4	2	8	1	-
<u>Shagamella ludloviensis</u>	143	15	6	2	-	-	-	2	8	-	-	-	-	-	-	-	-	-	-
<u>Shaleria ornatella</u>	81	85	43	45	1	1	-	1	4	1	16	2	-	1	2	-	-	-	-
<u>Leptaena depressa</u>	12	5	10	2	-	1	-	1	2	-	-	-	-	-	-	-	-	-	-
<u>Serpulites longissimus</u>	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Isorthis spp</u>	6	3	2	-	-	-	-	-	2	-	1	-	-	-	2	-	-	-	-
Bryozoa	13	9	15	11	-	5	-	1	10	12	11	6	1	11	34	18	10	14	7
<u>Aegiria gravi</u>	1	-	-	-	-	-	-	-	20	-	-	-	-	-	2	-	-	-	3
Monograptids indet.	1	-	3	2	1	38	1	1	-	-	-	-	-	-	-	-	-	-	-
<u>Lingula lewisii</u>	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bivalves (total)	17	8	6	2	-	-	-	1	9	8	-	3	2	-	2	2	11	18	8
Dalmanellids (total)	75	3	17	3	-	-	-	1	26	7	4	4	12	4	4	3	2	1	-
Smooth ostracods	-	5	6	8	-	-	-	2	-	-	-	-	-	238	51	34	16	-	1
<u>Cornulites serpularius</u>	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-
Trilobites (total)	-	1	2	7	-	2	-	-	6	5	4	1	2	5	2	4	-	-	-
<u>Strophonella euglypha</u>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Monograptus leintwardinensis</u>	-	-	1	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Sphaerirhynchia wilsoni</u>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orthocones indet.	-	-	-	-	1	1	-	1	2	-	-	2	-	1	5	3	14	5	-
Beyrichiids indet.	-	-	-	-	-	-	-	3	12	7	-	3	30	32	14	-	3	11	-
<u>Neobeyrichia laucensis</u>	-	-	-	-	-	-	-	-	-	-	-	-	4	-	5	-	-	-	-
<u>Craniops implicate</u>	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<u>Protochonetes ludloviensis</u>	-	-	-	-	-	-	-	-	61	13	9	3	23	30	6	83	12	158	-
Strophomenids indet.	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
<u>Lingula lata</u>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
<u>Atrypa reticularis</u>	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
Worm tube	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	6	-	-
Gastropods (total)	6	2	-	-	-	-	-	-	-	-	-	-	-	1	2	2	2	6	-

APPENDIX D. SECTION 62, HORTIMER FOREST. FAUNA IN ACTUAL FIGURES.

FOSSIL/LOCALITY	22	23	26	28	35	36	41
Bivalves	-	5.41	0.28	0.39	-	0.22	-
Trilobites	9.13	8.11	1.42	9.02	2.82	3.19	13.21
Dalmanellids	0.87	5.41	8.25	8.24	4.52	2.60	11.32
<u>Shaleria ornatella</u>	0.14	43.24	23.61	-	32.46	31.80	45.28
<u>Atrypa reticularis</u>	5.65	2.70	4.69	1.18	4.62	6.22	-
Bryozoa	0.58	2.70	1.00	3.14	2.77	3.63	7.55
Tentaculitids	-	2.70	-	0.78	0.77	-	-
<u>Neobeyrichia lauensis</u>	-	5.41	7.25	-	0.98	3.19	3.77
Smooth ostracods	-	21.62	0.85	0.78	3.39	16.98	-
<u>Dayia navicula</u>	72.61	2.70	15.79	1.18	5.44	9.49	3.77
<u>Protochonetes ludloviensis</u>	0.43	-	0.71	0.78	3.85	7.49	-
Colonial corals	0.14	-	1.71	-	0.46	1.41	1.89
<u>Aegiria grayi</u>	8.70	-	1.28	47.45	0.05	1.56	-
Beyrichiids	0.72	-	31.15	27.06	36.31	8.52	7.55
<u>Leptaena rhomboidalis</u>	-	-	0.28	-	0.46	-	-
<u>Boucotinskia spp</u>	0.87	-	0.28	-	0.05	0.07	1.89
<u>Leptaena spp</u>	-	-	0.57	-	0.10	2.15	-
Solitary corals	-	-	0.85	-	0.26	0.15	1.89
<u>Howellella elegans</u>	-	-	-	-	0.41	0.22	1.89
Gastropods	0.14	-	-	-	0.10	0.37	-
Stromatoporoid	-	-	-	-	0.05	-	-
Serpulid	-	-	-	-	-	0.07	-
<u>Cornulites spp</u>	-	-	-	-	-	0.22	-
<u>Morinorhyncus crispus</u>	-	-	-	-	-	0.07	-
<u>Calcibeyrichia torosa</u>	-	-	-	-	-	0.07	-
<u>Lingula sp</u>	-	-	-	-	-	0.07	-
<u>Microsphaeridiorhyncus nucula</u>	-	-	-	-	-	0.07	-
<u>Orbiculoidea sp</u>	-	-	-	-	-	0.07	-
Orthocone	-	-	-	-	-	0.07	-

APPENDIX E. GOTLAND COLLECTION. FAUNA IN PERCENTAGES.

FOSSIL/LOCALITY	22	23	26	28	35	36	41
Bivalves	-	2	2	1	-	3	-
Trilobites	63	3	10	23	55	43	7
Dalmanellids	6	2	58	21	88	35	6
<u>Shaleria ornatella</u>	1	16	166	-	632	429	24
<u>Atrypa reticularis</u>	39	1	33	3	90	84	-
Bryozoa	4	1	7	8	54	49	4
Tentaculitids	-	1	-	2	15	-	-
<u>Neobeyrichia lauensis</u>	-	2	51	-	19	43	2
Smooth ostracods	-	8	6	2	66	229	-
<u>Dayia navicula</u>	501	1	111	3	106	128	2
<u>Protochonetes ludloviensis</u>	3	-	5	2	75	101	-
Colonial corals	1	-	12	-	9	19	1
<u>Aegiria grayi</u>	60	-	9	121	1	21	-
Beyrichiids	5	-	219	69	707	115	4
<u>Leptaena rhomboidalis</u>	-	-	2	-	9	-	-
<u>Boucotinskia spp</u>	6	-	2	-	1	1	1
<u>Leptaena spp</u>	-	-	4	-	2	29	-
Solitary corals	-	-	6	-	5	2	1
<u>Howellella elegans</u>	-	-	-	-	8	3	1
Gastropods	1	-	-	-	2	5	-
Stromatoporoid	-	-	-	-	1	-	-
Serpulid	-	-	-	-	-	1	-
<u>Cornulites spp</u>	-	-	-	-	-	3	-
<u>Morinorhyncus crispus</u>	-	-	-	-	-	1	-
<u>Calcibeyrichia torosa</u>	-	-	-	-	-	1	-
<u>Lingula sp</u>	-	-	-	-	-	1	-
<u>Microsphaeridiorhyncus nucula</u>	-	-	-	-	-	1	-
<u>Orbiculoidea sp</u>	-	-	-	-	-	1	-
Orthocone	-	-	-	-	-	1	-

APPENDIX F. GOTLAND COLLECTION. FAUNA IN ACTUAL FIGURES.

## APPENDIX G.

Distribution of fauna in Gotland from collections and published faunal lists. Sources are Hede 1929, Bassett and Cocks 1974, Stel and de Coö 1977. No abundance data published, therefore fossils are marked as present (P) or absent (A) only.

SPECIES ETC.	Hemse/ Eke	Burgsvik	Hamra	Sundre
ALGAE (TOTAL)	P	P	P	A
ANNELIDS (TOTAL)	P	P	P	A
BEYRICHIIDS (TOTAL)	P	P	P	P
BIVALVES (TOTAL)	P	P	P	P
BRACHIOPODS				
<u>Aegiria grayi</u>	P	A	A	A
<u>Anastrophia deflexa</u>	P	A	P	P
<u>Antirhynchonella linguifera</u>	P	A	A	A
<u>Atrypa marginalis</u>	P	A	A	A
<u>A. reticularis</u>	P	P	P	P
<u>Atrypella prunum</u>	P	A	A	A
<u>Atrypina barrandii</u>	A	A	P	A
<u>Boucotinskia spp.</u>	P	P	P	P
<u>Brachyprion spp.</u>	P	P	P	P
<u>Coelospira pusilla</u>	P	P	P	P
<u>Coolinia pecten</u>	P	A	A	A
<u>Craniops implicata</u>	P	P	P	A
<u>Cyrtia exporrecta</u>	P	A	A	A
<u>Dalejina hybrida</u>	P	A	A	A
Dalmanellids (TOTAL)	P	P	P	P
<u>Dayia navicula</u>	P	P	A	A
<u>Desquamatia spp.</u>	P	A	P	P
<u>Dicoelosia biloba</u>	P	A	A	A
<u>Dictyonella capewellii</u>	P	A	A	A
<u>Didymothyris didyma</u>	P	A	A	A
<u>Ferganella diodonta</u>	P		A	A
<u>Glassia obovata</u>	P	P	A	A
<u>Glassina laevinscula</u>	P	A	A	A
<u>Gypidula galeata</u>	P	A	A	A

SPECIES ETC.	Hemse/ Eke	Burgsvik	Hamre	Sundre
<u>Hesperorthis gotlandica</u>	P	A	A	A
<u>Homeospira baylei</u>	P	P	P	P
<u>Howellella elegans</u>	P	P	P	P
<u>Janius barrandi</u>	P	A	A	A
<u>Kirkidium knightii</u>	P	A	A	A
<u>Kozlowskiellina deltidialis</u>	P	A	A	A
<u>Lepidoleptaena spp.</u>	A	P	P	P
<u>Leptaena rhomboidalis</u>	P	P	P	P
<u>Leptaena spp.</u>	P	P	P	P
<u>Leptostrophia filosa</u>	P	A	P	A
<u>L. impressa</u>	P	P	P	A
<u>Lingula spp.</u>	P	P	A	A
<u>Linoporella punctata</u>	A	A	P	P
<u>Lyssatrypa ?sulcata</u>	P	A	A	A
<u>Microsphaeridiorhyncus nucula</u>	P	P	P	P
<u>Nucleospira pisum</u>	P	A	A	A
<u>Orbiculoidea spp.</u>	P	A	P	A
<u>Plectambonites ?inconstans</u>	P	A	A	A
<u>Plectotreta lindstroemi</u>	P	A	A	A
<u>Protochonetes ludloviensis</u>	P	P	P	A
<u>P. striatellus</u>	P	P	P	P
<u>Ptychopleurella bouchardi</u>	P	A	P	P
<u>Resserella canalis</u>	P	A	A	A
<u>Rhynchotreta cuneata</u>	P	A	A	A
<u>Shaleria ornatella</u>	P	A	A	A
<u>S. aff. ornatella</u>	P	P	A	A
<u>Skenidium lewisii</u>	P	A	A	A
<u>Sphaerirhyncia wilsoni</u>	P	P	P	P
<u>Spiratrypa spp.</u>	A	A	P	P
<u>Spirifer elevatus</u>	P	P	P	P
<u>S. schmidtii</u>	P	A	A	A
<u>Spirigerina quinquecostata</u>	A	P	P	P
<u>Striispirifer plicatellus</u>	P	A	A	A
<u>S. striolatus</u>	P	P	P	P
<u>Strophomena crispa</u>	P	A	A	A
<u>S. orbigny</u>	A	A	P	P

SPECIES ETC.	Hemse/ Eke	Burgsvik	Hamre	Sundre
<u>Strophonella euglypha</u>	P	P	A	A
<u>S.funiculata</u>	P	A	A	A
<u>Whitfieldella spp.</u>	P	A	P	P
BRYOZOA (TOTAL)	P	P	P	P
CEPHALOPODS (TOTAL)	P	P	P	P
CORALS (TOTAL)	P	A	P	P
CRINOIDS (TOTAL)	P	P	P	P
GASTROPODS (TOTAL)	P	P	P	P
GRAPTOLITES (TOTAL)	P	A	A	A
OTHER OSTRACODS	P	P	P	P
SPONGES (TOTAL)	P	A	A	A
STROMATOPORIDS (TOTAL)	P	P	P	P
TENTACULITIDS (TOTAL)	P	A	A	A
TRILOBITES (TOTAL)	P	P	P	P

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PLATE 1. Overton Quarry (Section 9X), Mortimer Forest, Ludlow,  
showing labelling of beds in two foot intervals.

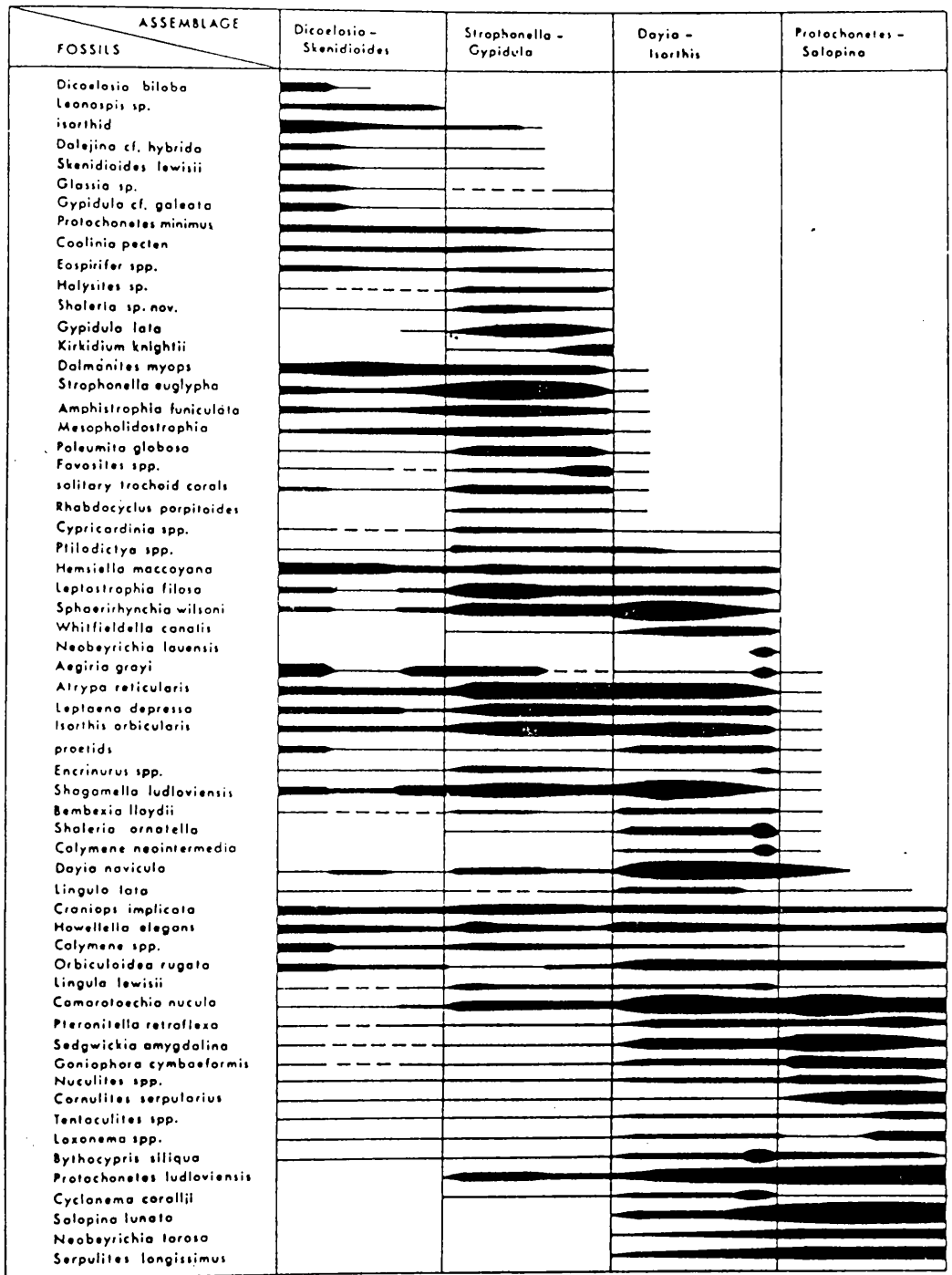


FIG.1. Range chart of benthonic fossils in the Welsh Borderlands Ludlovian, from Lawson 1975.

Series	Stage	Local division	Thickness in feet (approx.)	Lithology
LUDLOVIAN (approximately 1,000 to 1,300 ft.)	WHIT- CLIFFIAN	Upper Whitcliffe Beds	100	Flaggy calcareous siltstones with shelly limestone bands
		Lower Whitcliffe Beds	80	Irregularly bedded, massive or thickly flaggy calcareous siltstones
	LEINTWAR- DINIAN	Upper Leintwardine Beds	5 to 18 (thicker eastwards)	Flaggy calcareous siltstones
		Lower Leintwardine Beds	100	Thinly flaggy calcareous siltstones
	BRINGE- WOODIAN	Upper Bringewood Beds	40 to 150 (thinner eastwards)	Irregularly flaggy or nodular silty limestones
		Lower Bringewood Beds	160 to 200 (thicker eastwards)	Flaggy calcareous siltstones with limestone nodules
	ELTONIAN	Upper Elton Beds	150 to 250	Well bedded, flaggy calcareous siltstones with flaggy limestone bands
		Middle Elton Beds	150 to 350 (thinner eastwards)	Conchoidally fracturing, shaly and thinly flaggy, muddy siltstones
		Lower Elton Beds	100 to 150	Irregularly bedded, shaly and flaggy, calcareous silty mudstones
	WENLOCKIAN	Wenlock Limestone	200 to 450 (thinner eastwards)	Flaggy silty limestones alternating with calcareous silty shales, 50-60 ft. of nodular limestone at top
Wenlock Shales		approx. 1,000 seen	Thinly flaggy, calcareous silty mudstones or calcareous silty shales	

FIG.2. Stratigraphy of the Ludlovian of the Welsh Borderlands, from Holland, Lawson and Walmsley 1963.



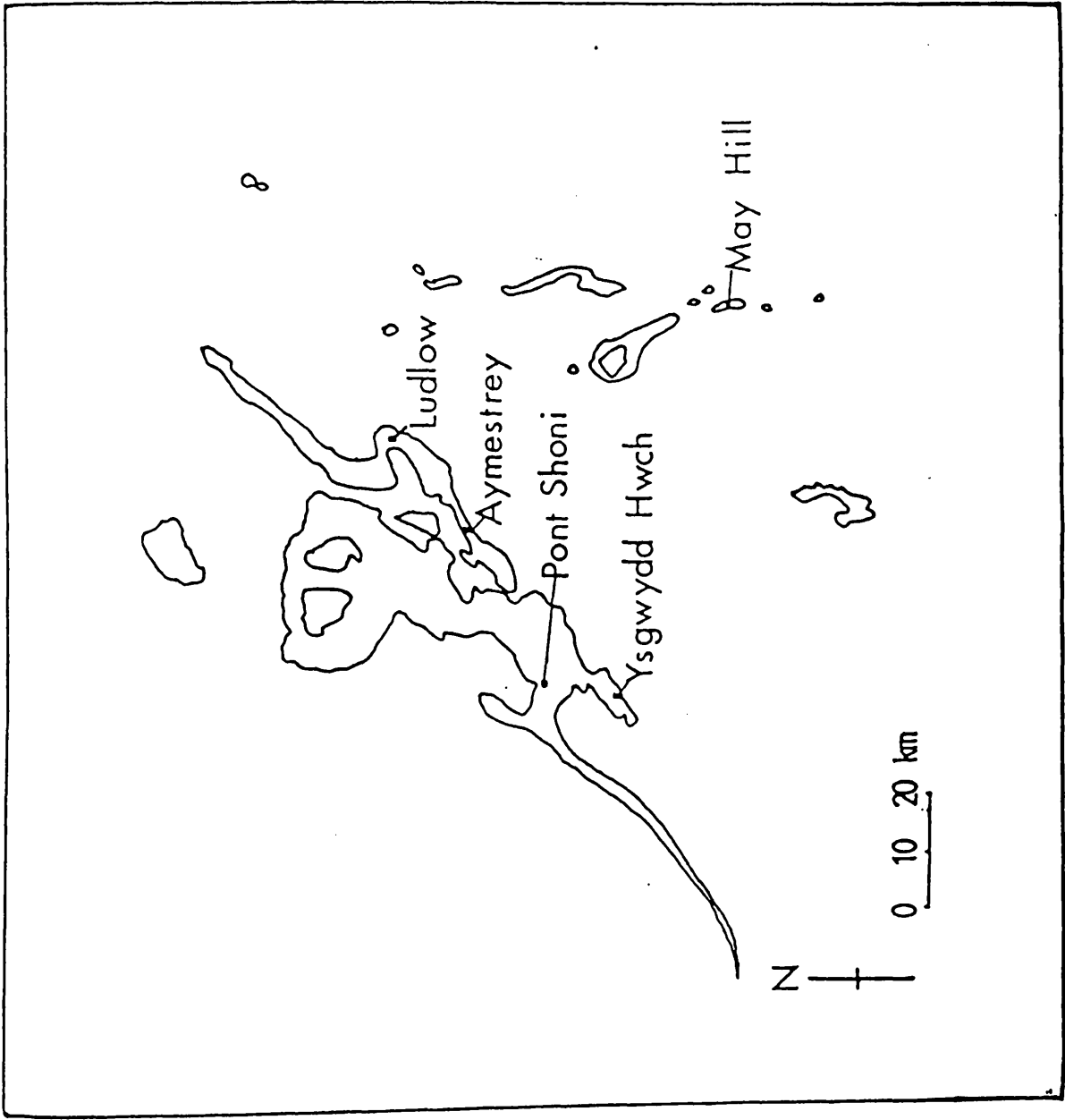


FIG.3. Collection points in the Welsh Borderlands.

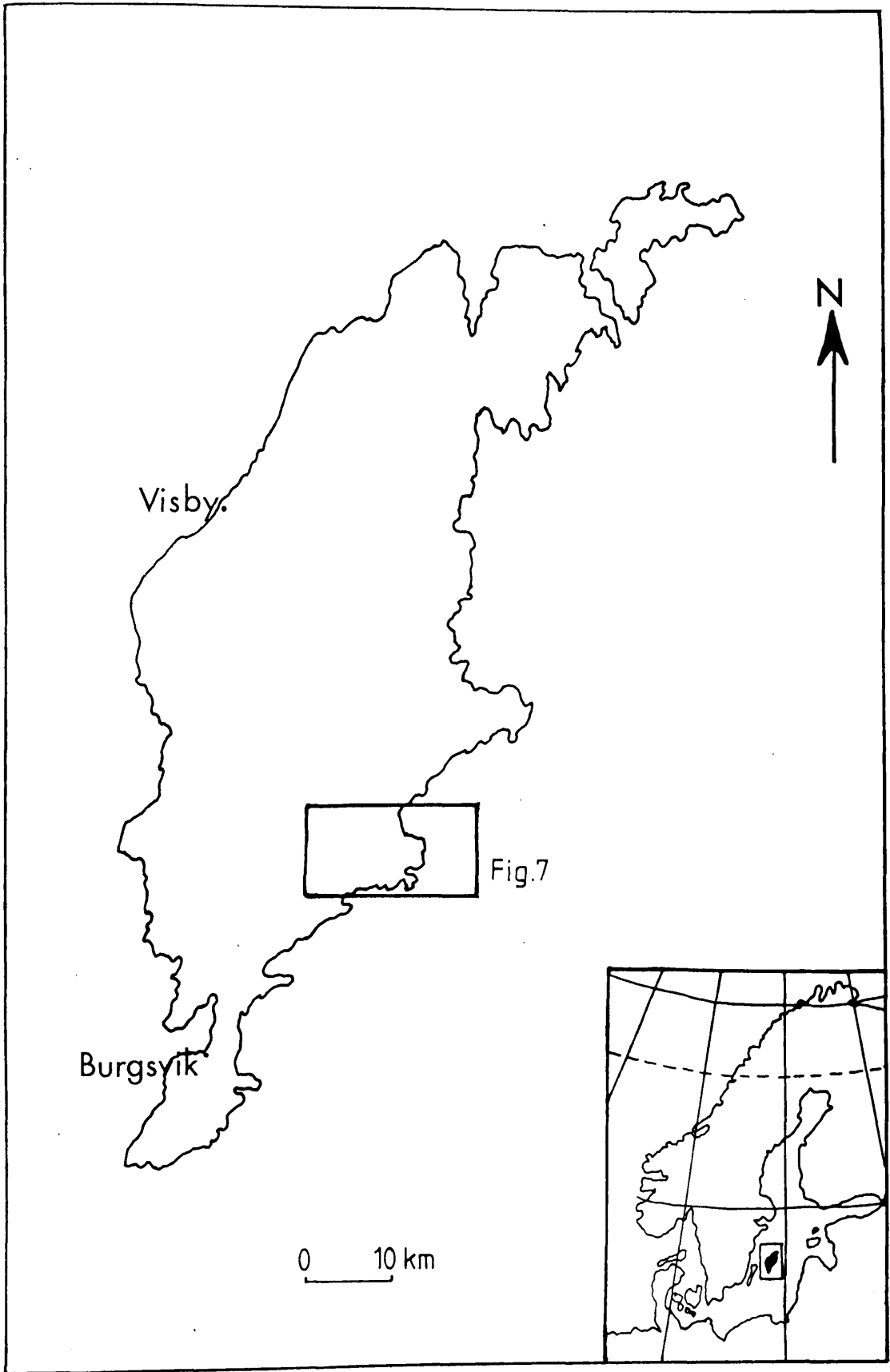


FIG. 4. Location map of Gotland, Sweden.

L U D L O W	WHITCLIFFIAN		SUNDRE
			HAMRA
			BURGSVIK
	LEINTWARDINIAN	<u>M.leintwardinensis</u>	EKE
	BRINGEWOODIAN	<u>M.tumescens</u>	HEMSE
ELTONIAN	<u>M.scanicus</u>		
	<u>P.nilssoni</u>		

FIG.5 Stratigraphic correlation between Gotland and Britain, showing graptolite zones (after Laufeld and Jeppsson 1976).

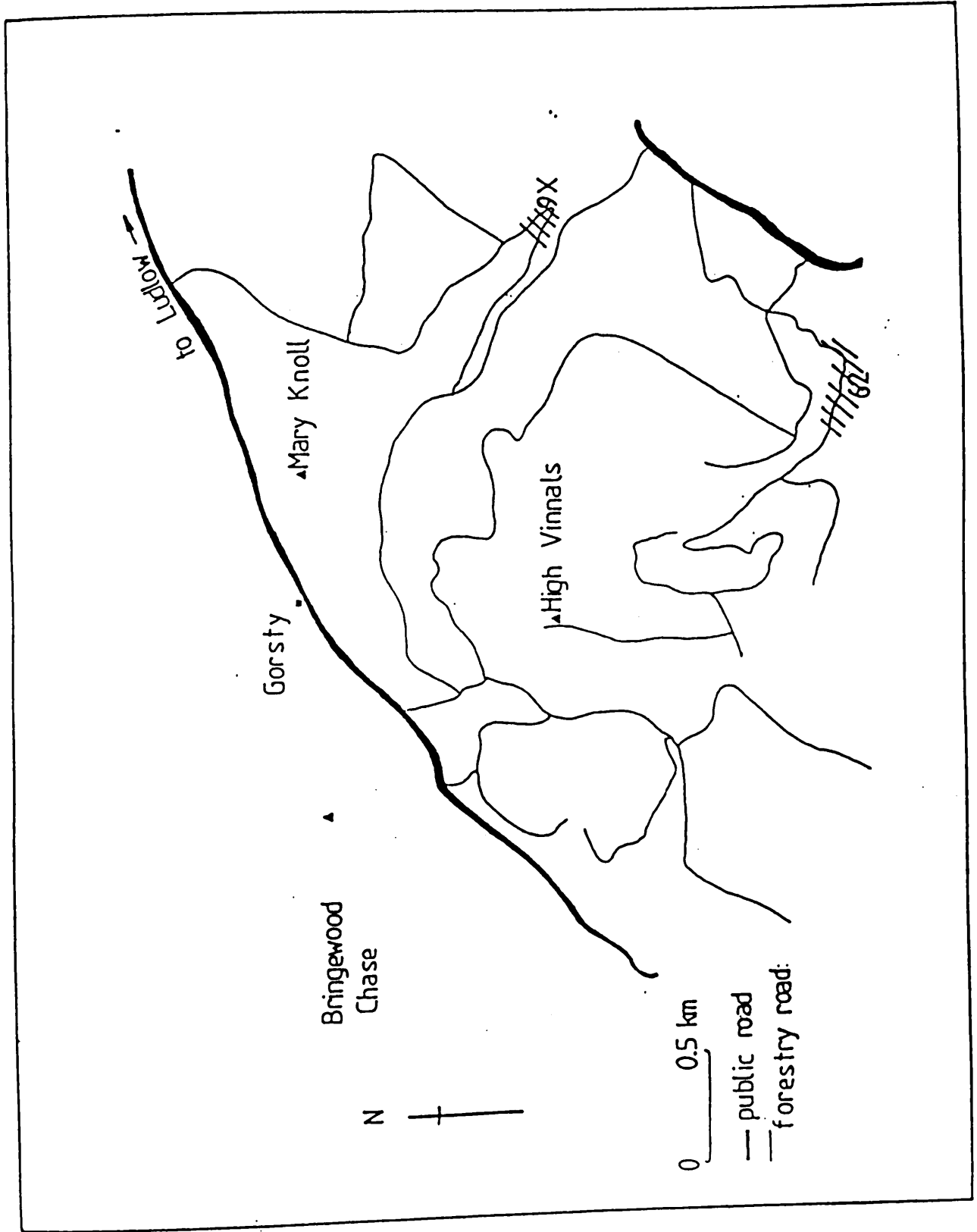


FIG.6. Collection points in Mortimer Forest, Ludlow.

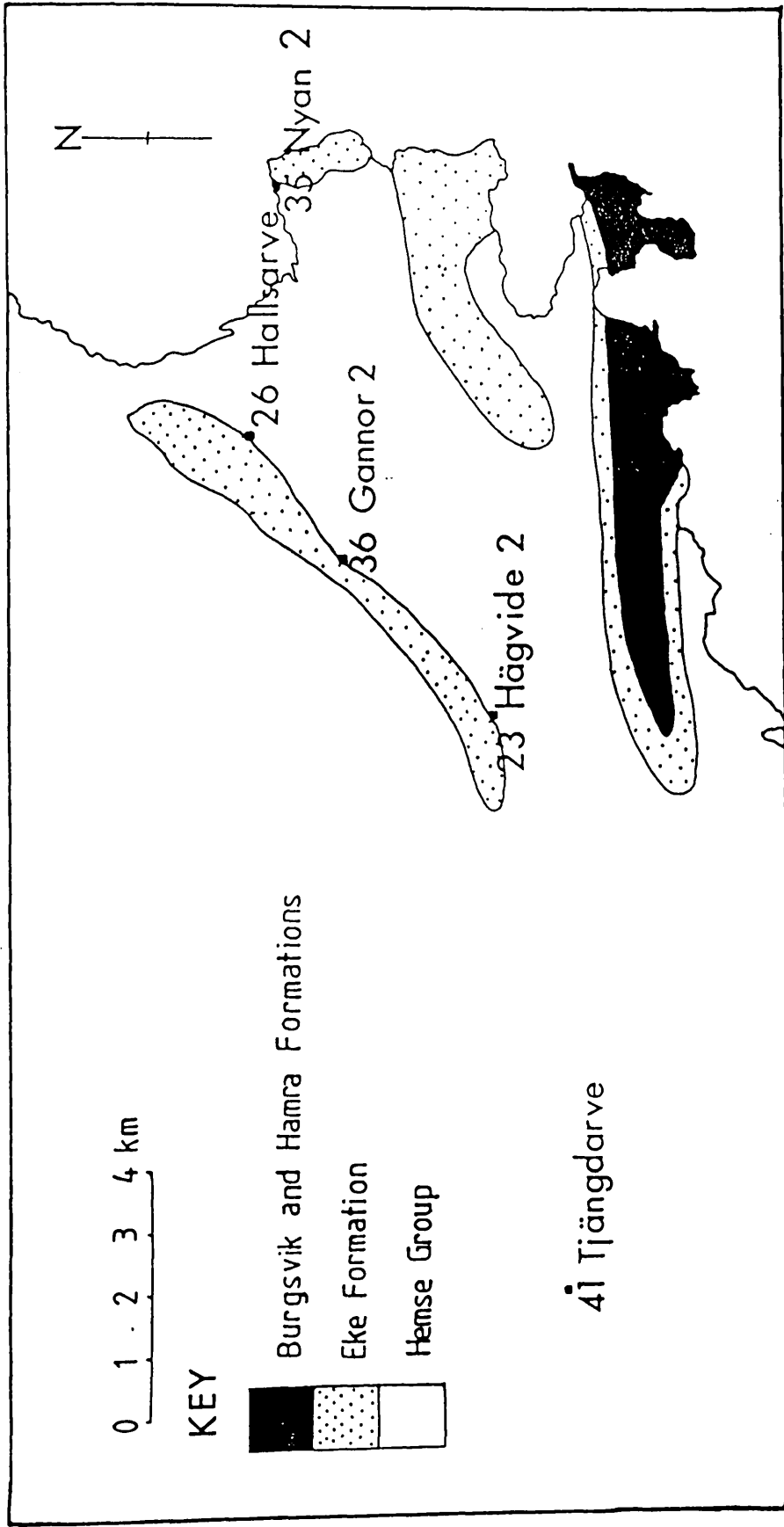
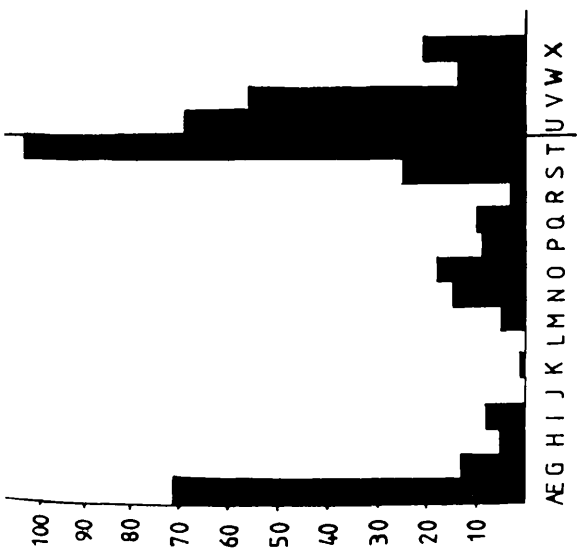
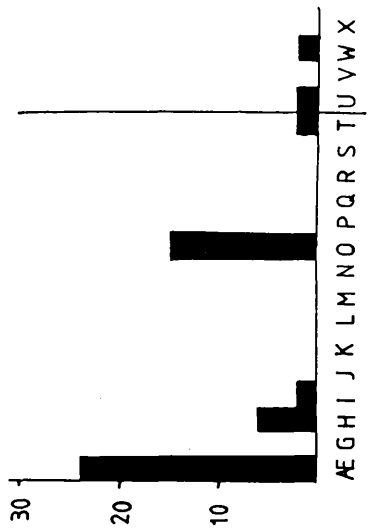


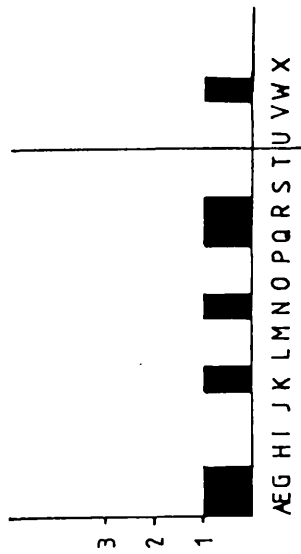
FIG. 7. Collection points in Gotland.



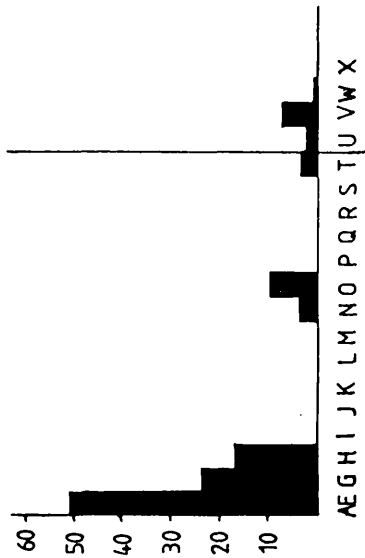
i) *Microsphaeridiorynchus nucula*



iii) *Salopina lunata*



ii) *Orbiculaidea rugata*



iv) *Daya navicula*

FIG.8 (i-xxx ). Frequency plots for Montimer Forest 62. Vertical axes=frequency. Horizontal axes=collecting levels.

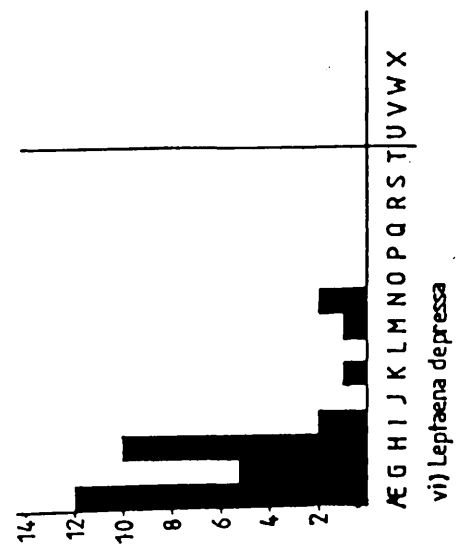
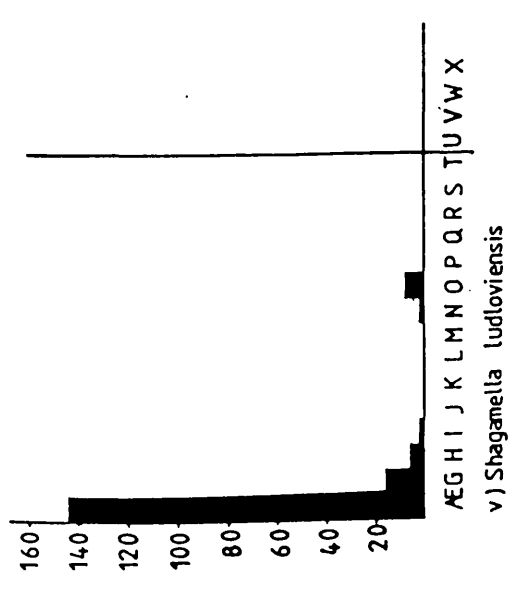
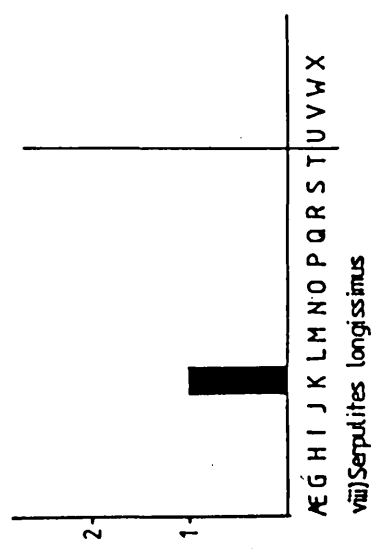
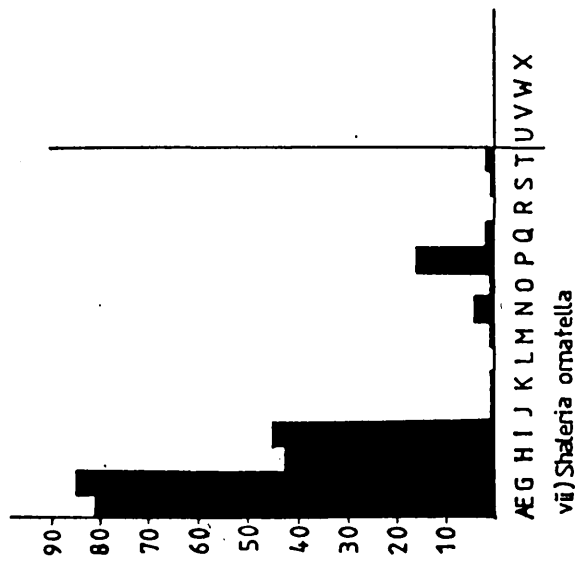


FIG.8 contd.

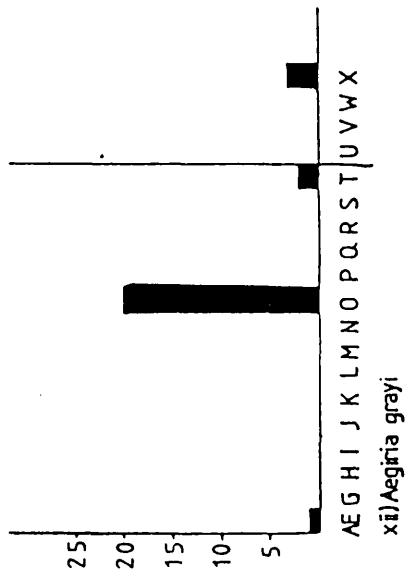
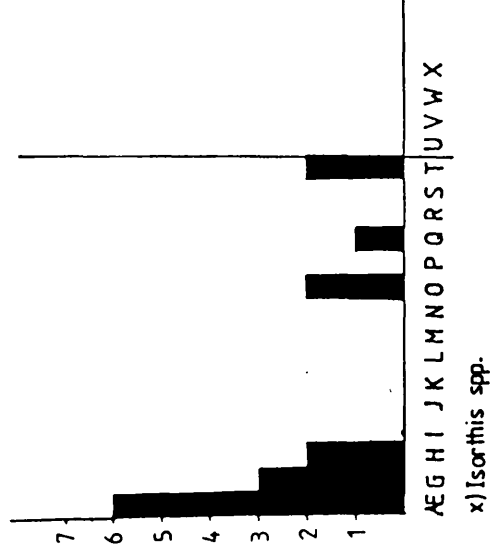
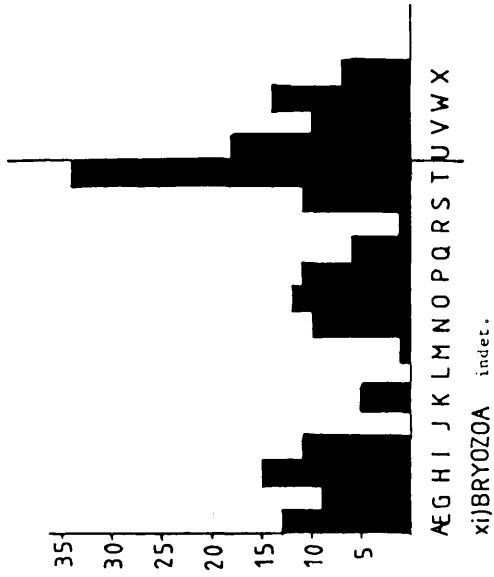
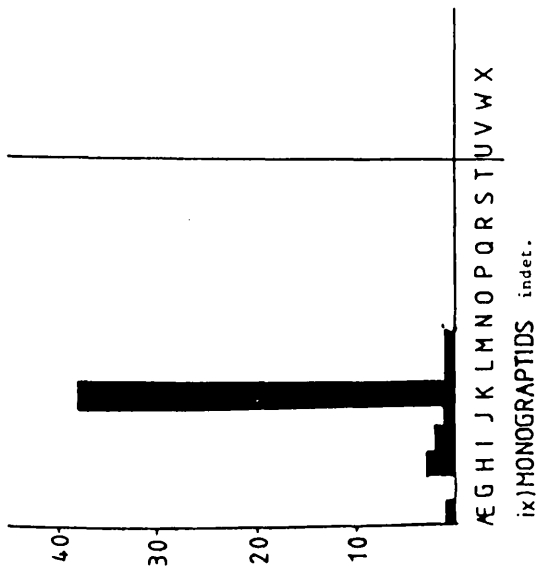


FIG. 8 contd.



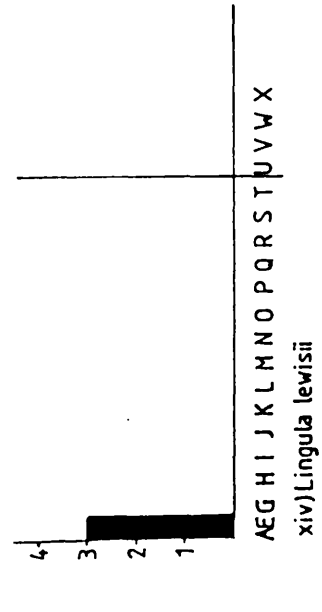
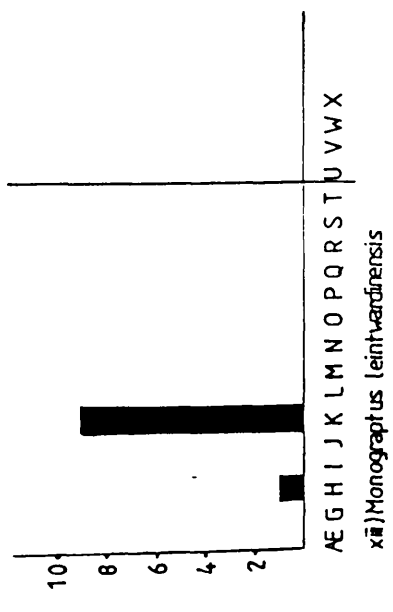
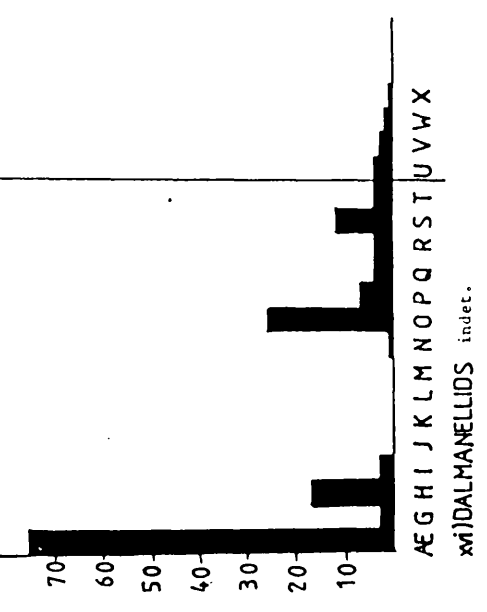
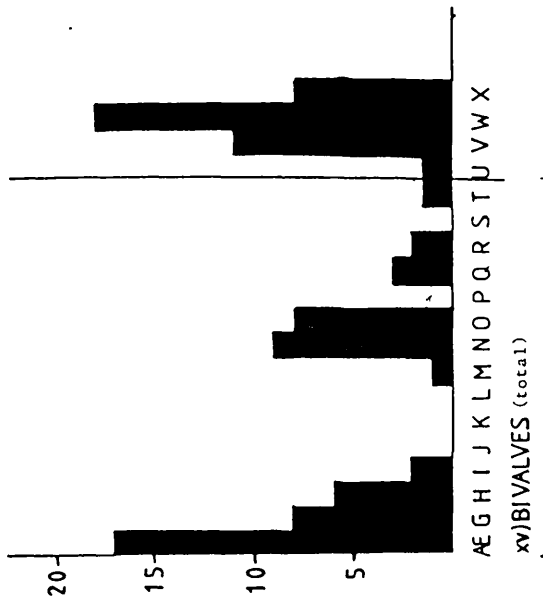


FIG.8 contd.

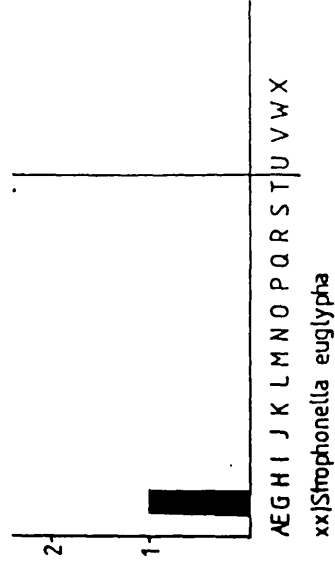
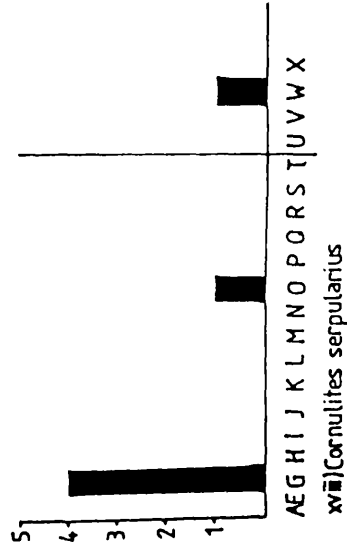
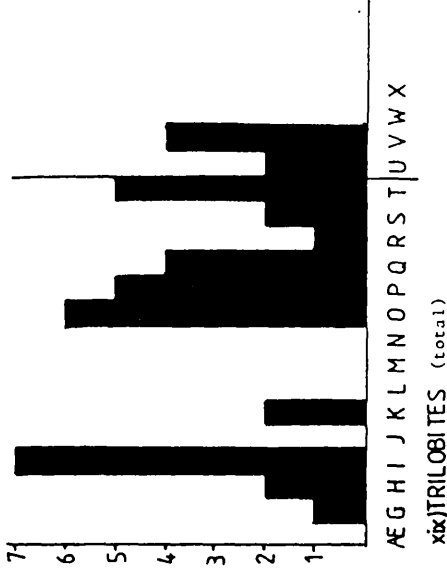
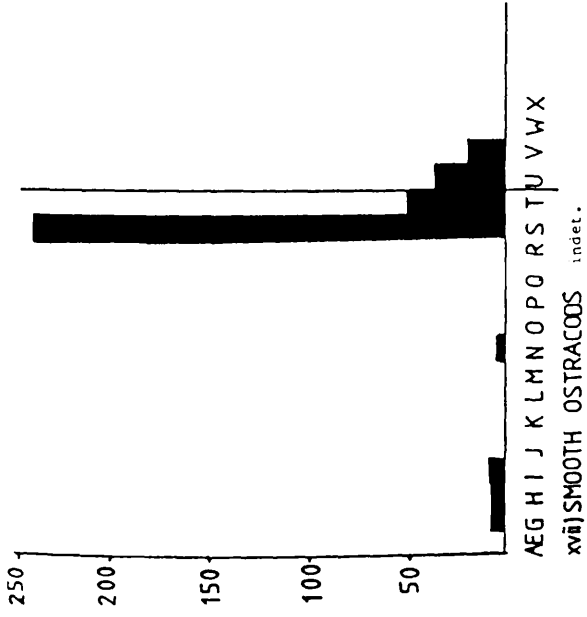


FIG. 8 contd.

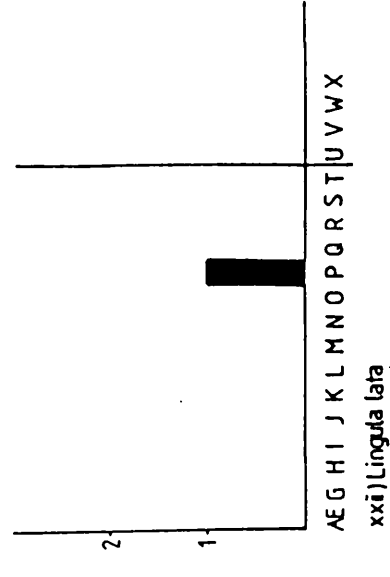
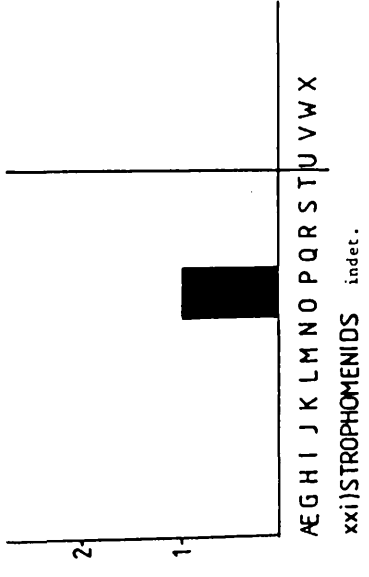
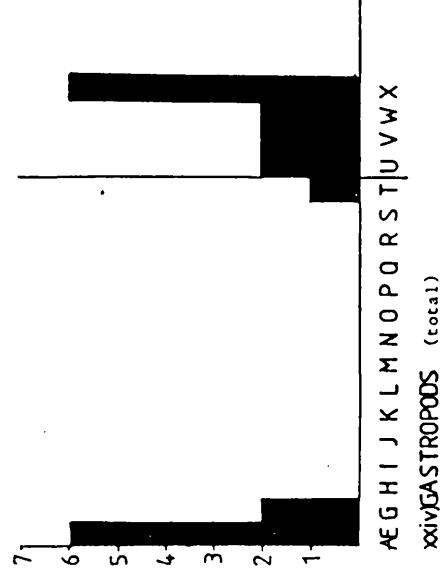
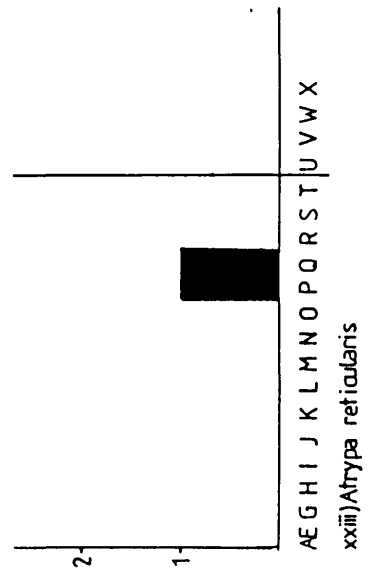


FIG. 8 contd.

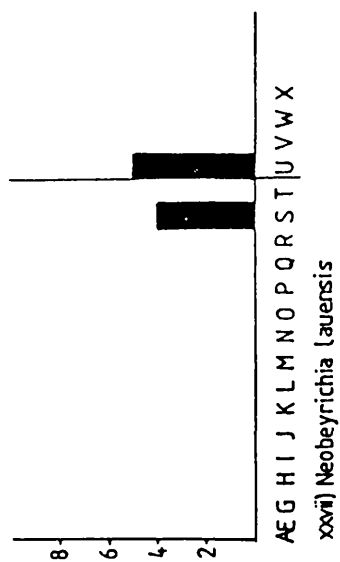
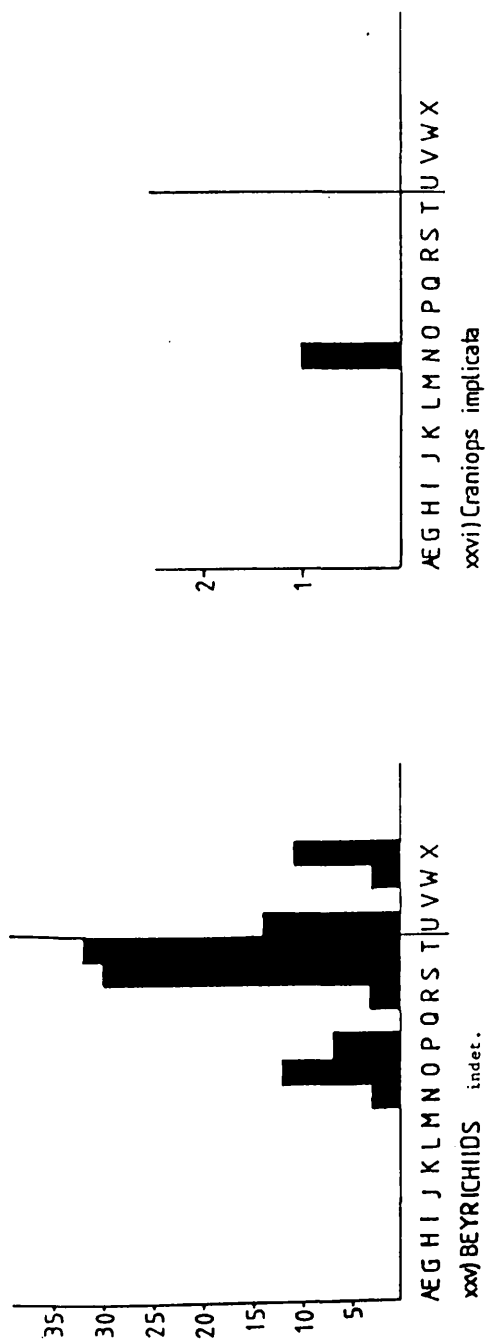


FIG. 8 contd.

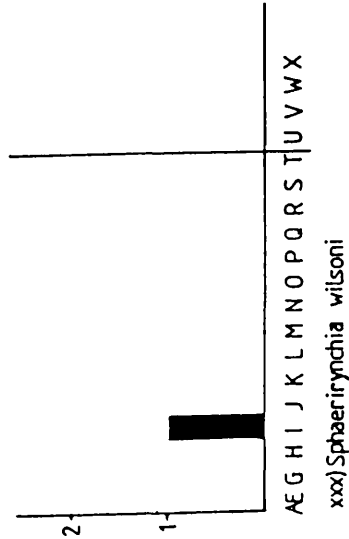
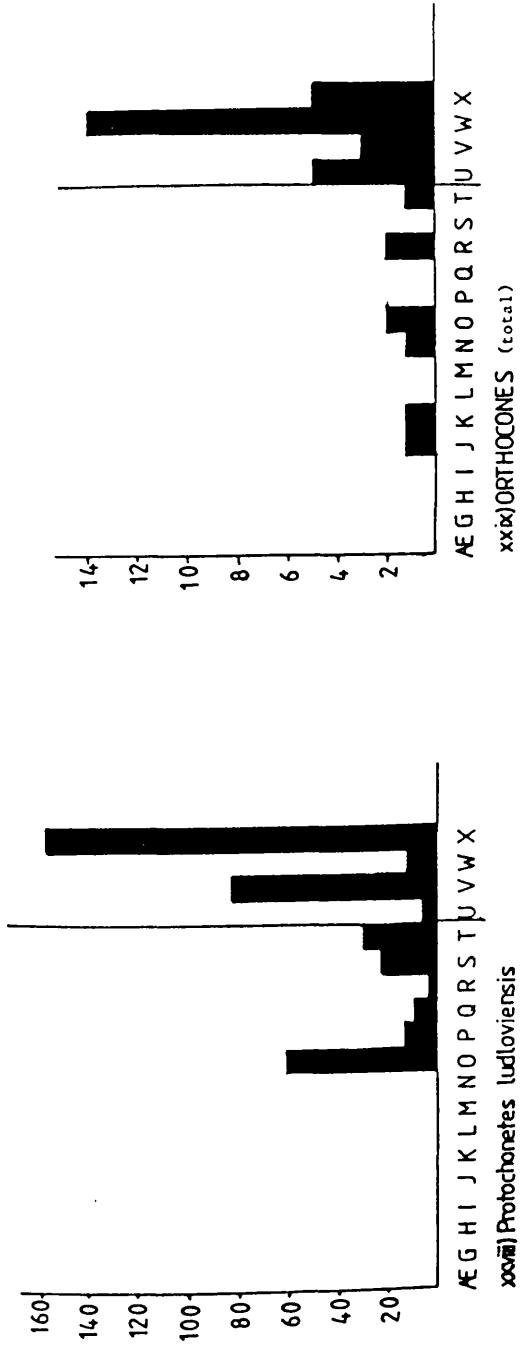


FIG.8 contd.

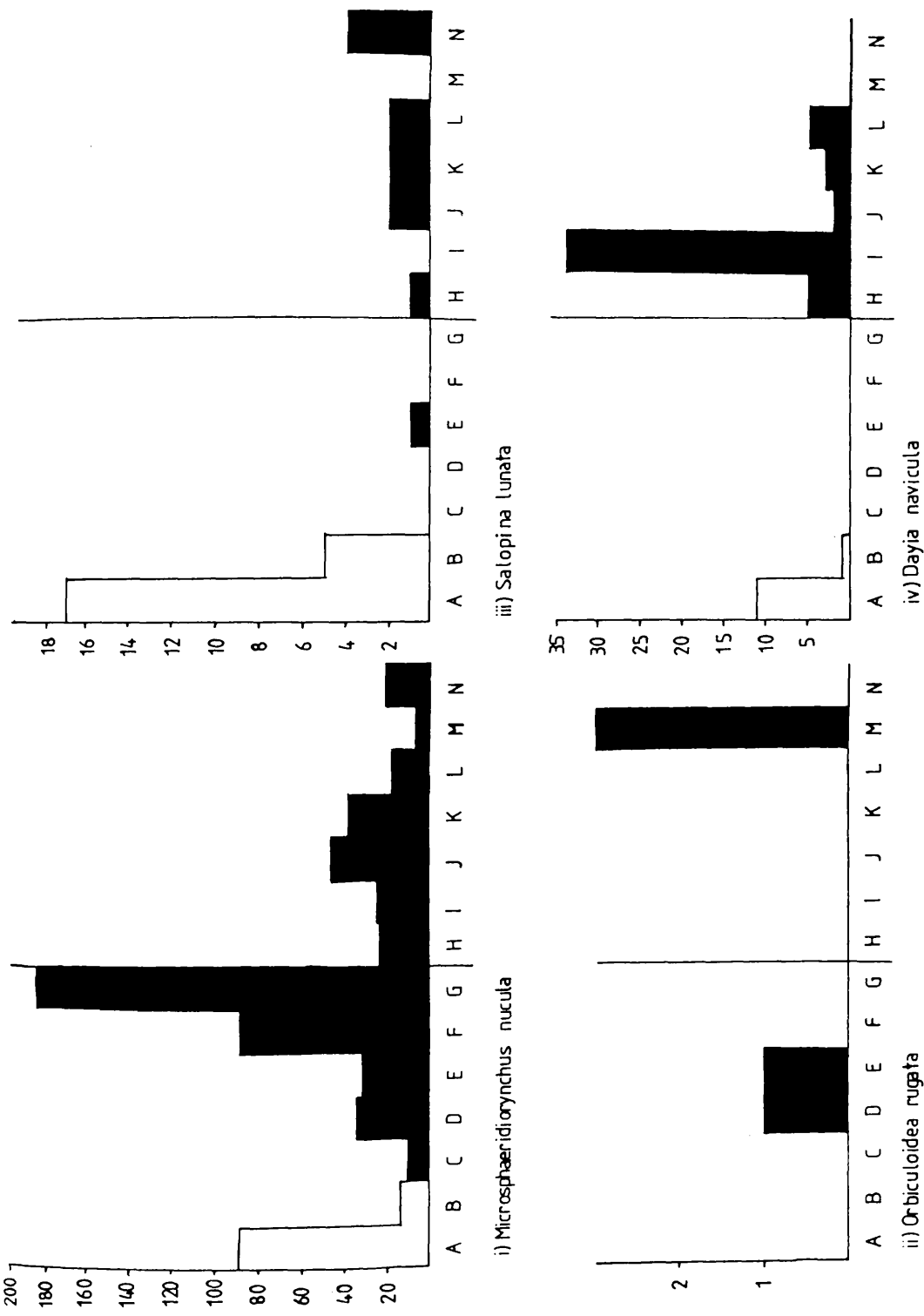


FIG.9 (i-xxvii). Frequency plots for Mortimer Forest 9X. Axes as Fig.1. A,B not continuous with C-K.

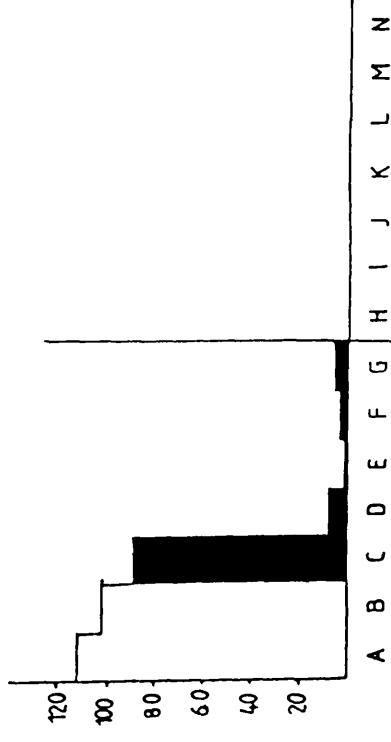
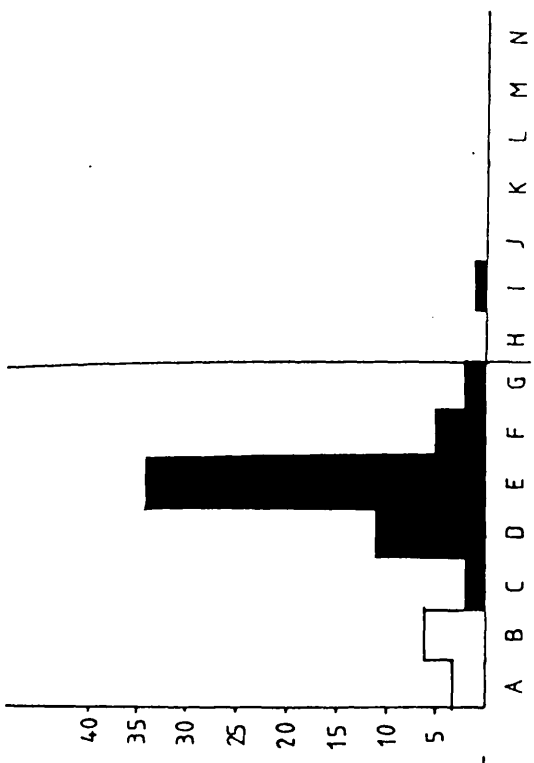
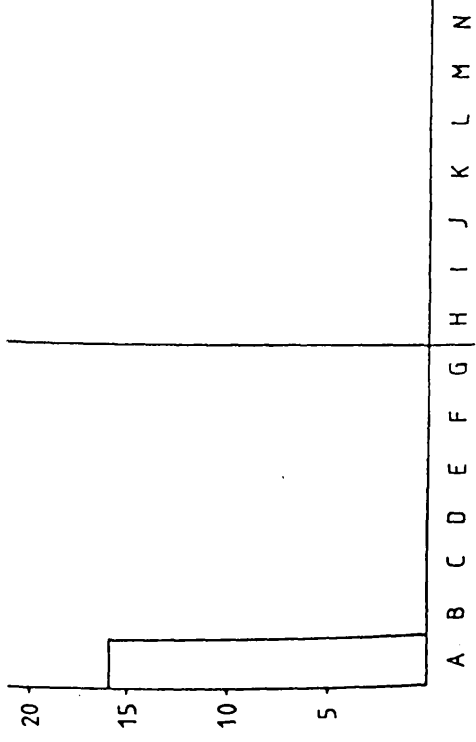
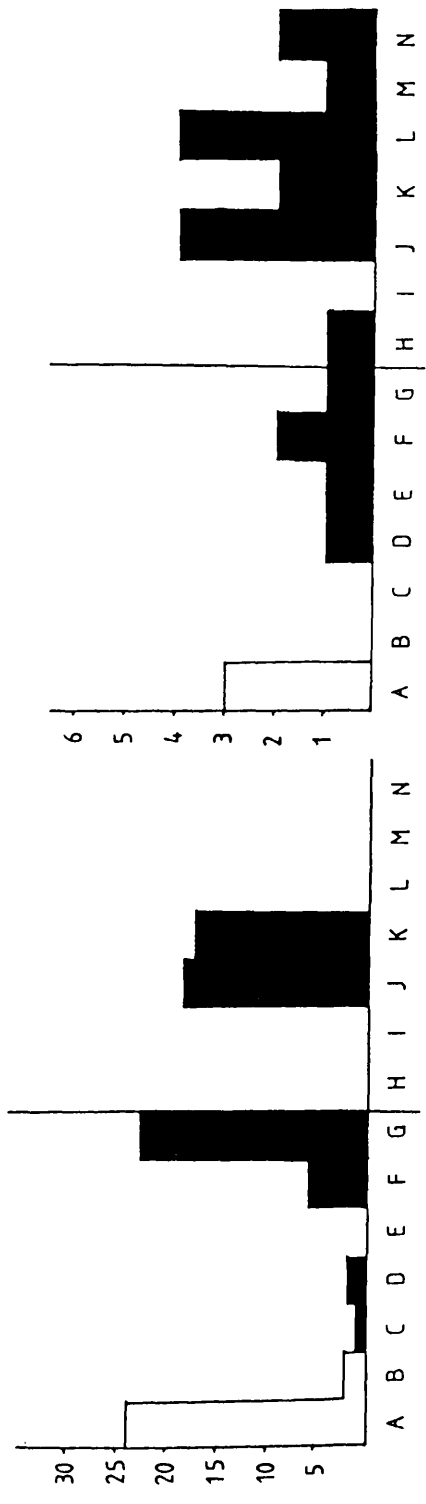
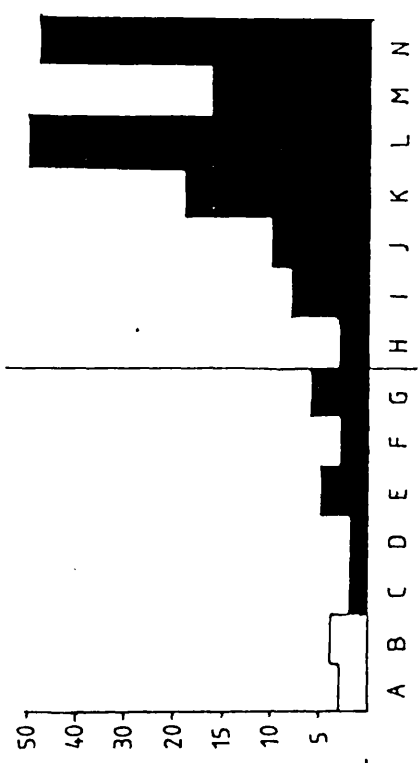


FIG. 9 contd.



ix) *Aegiria grayi*

xi) GASTROPODS (total)



x) MONOCRAPTIDS indet.

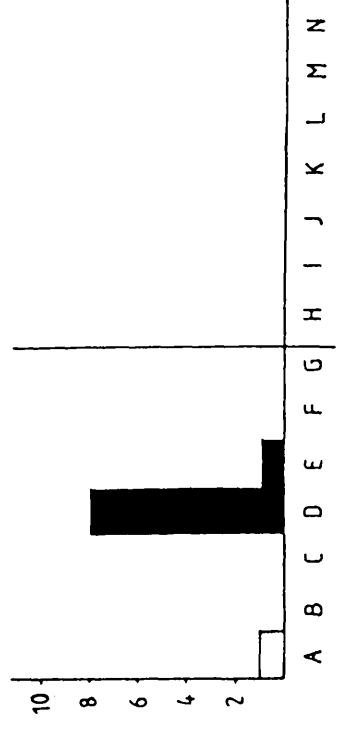


FIG.9 contd.



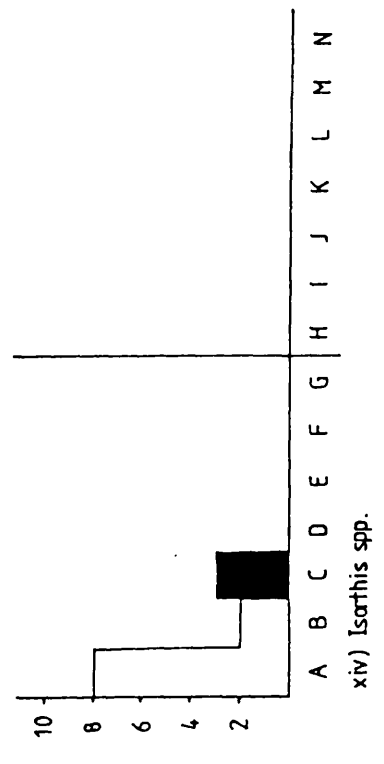
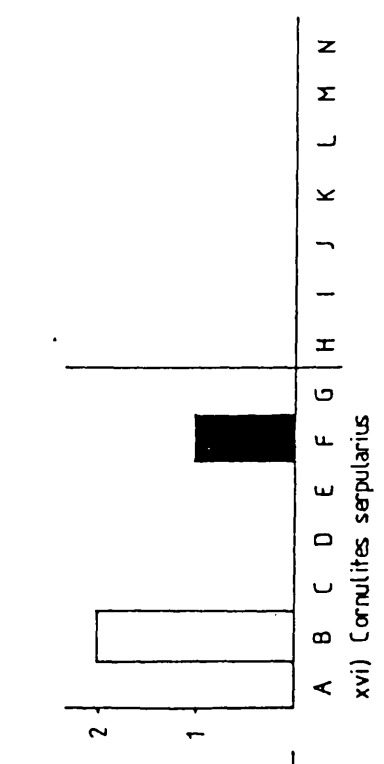
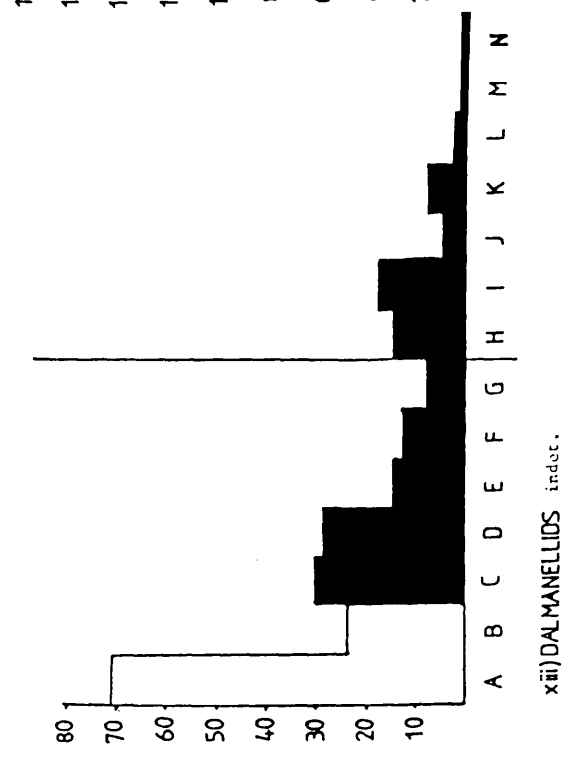
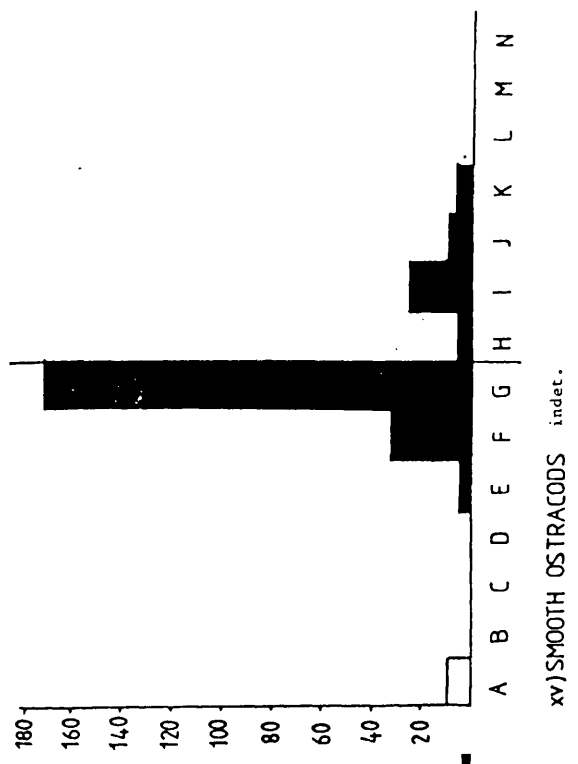
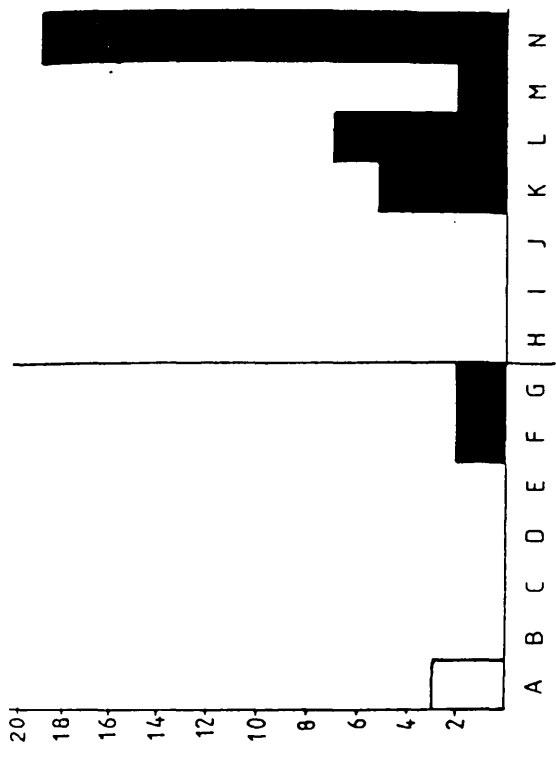


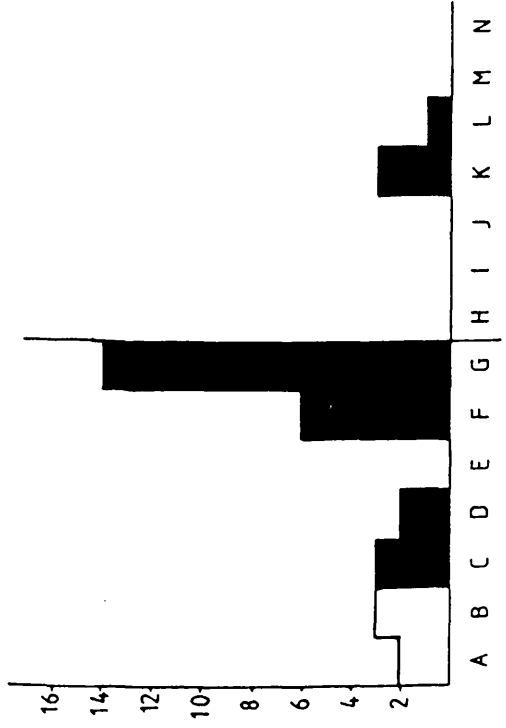
FIG. 9 contd.



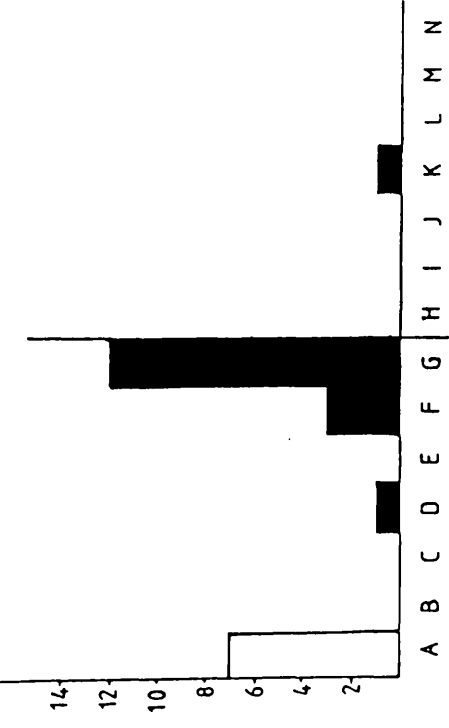
xix) ORTHOCONES (total)



xx) BEYRICHIIDS indet.



xvii) TRILOBITES (total)



xviii) *Neobeyrichia lauensis*

FIG. 9 contd.

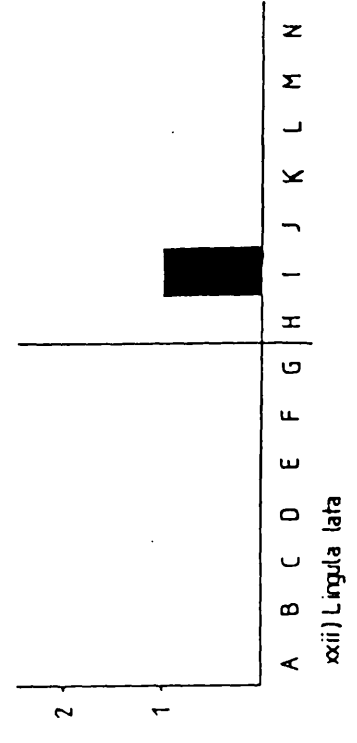
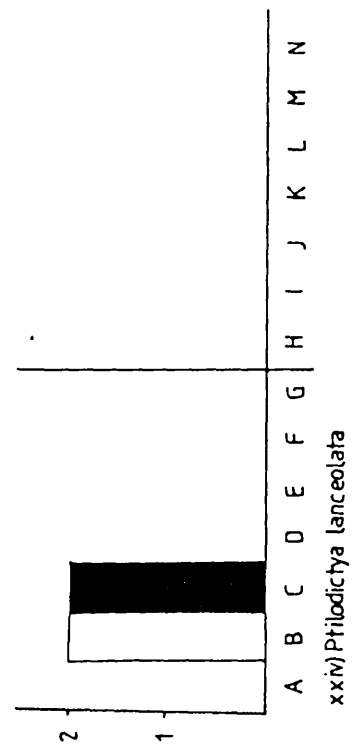
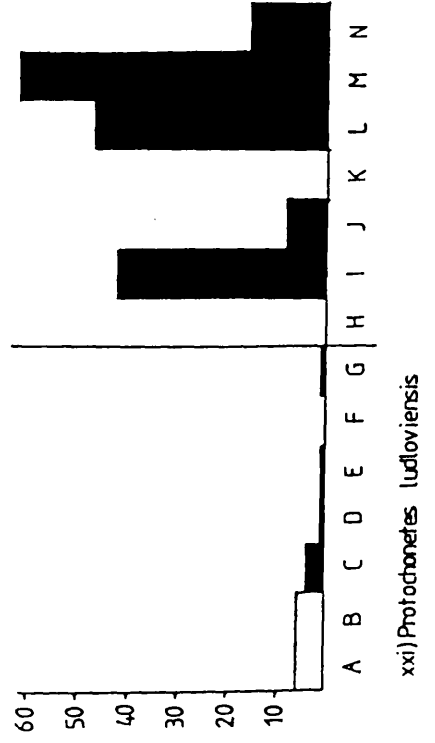
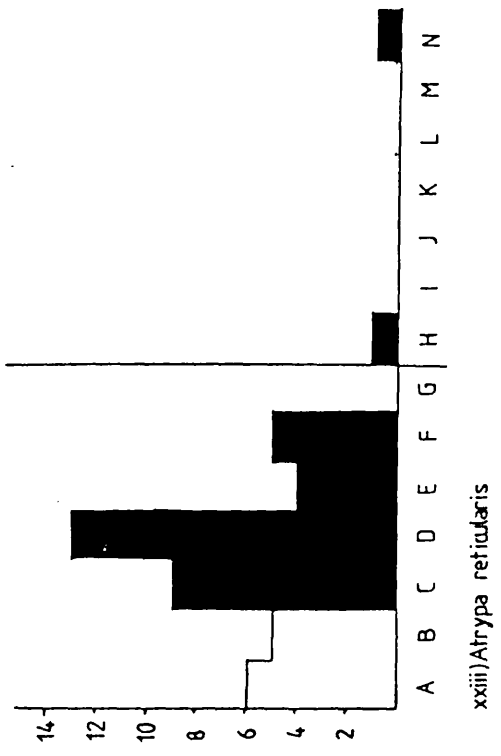


FIG. 9 contd.

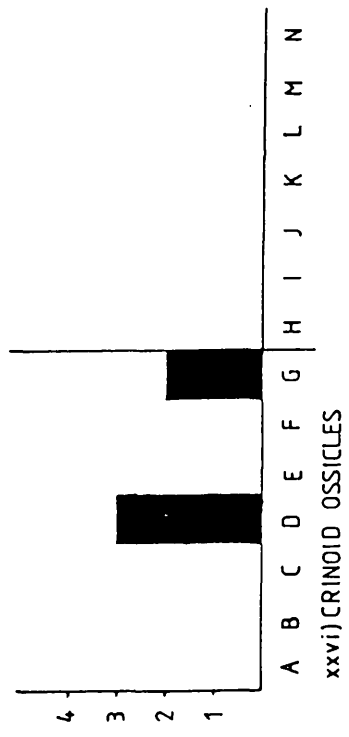
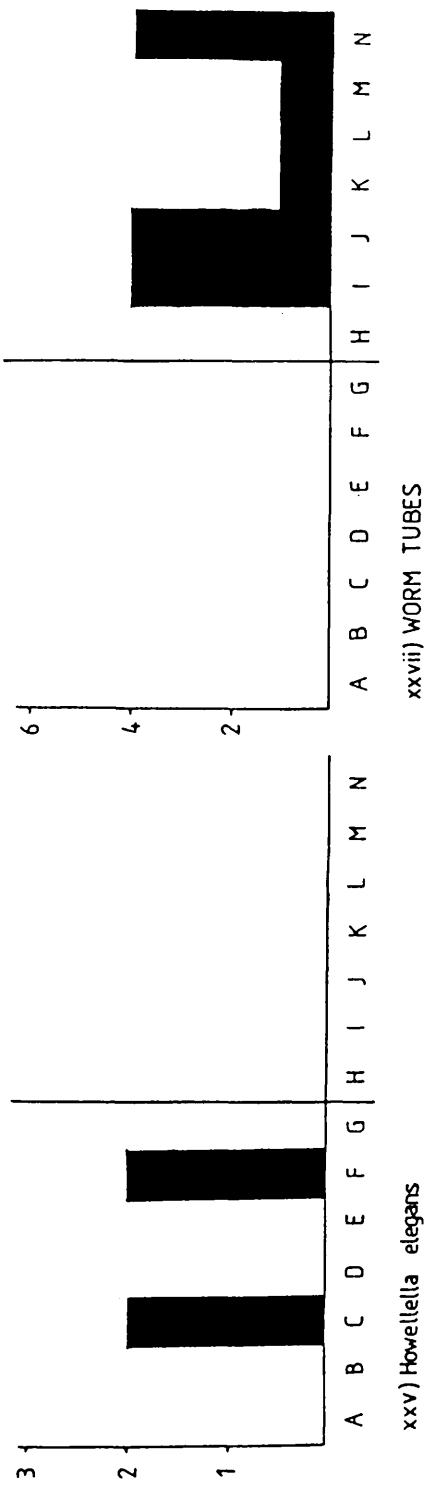


FIG. 9 contd.

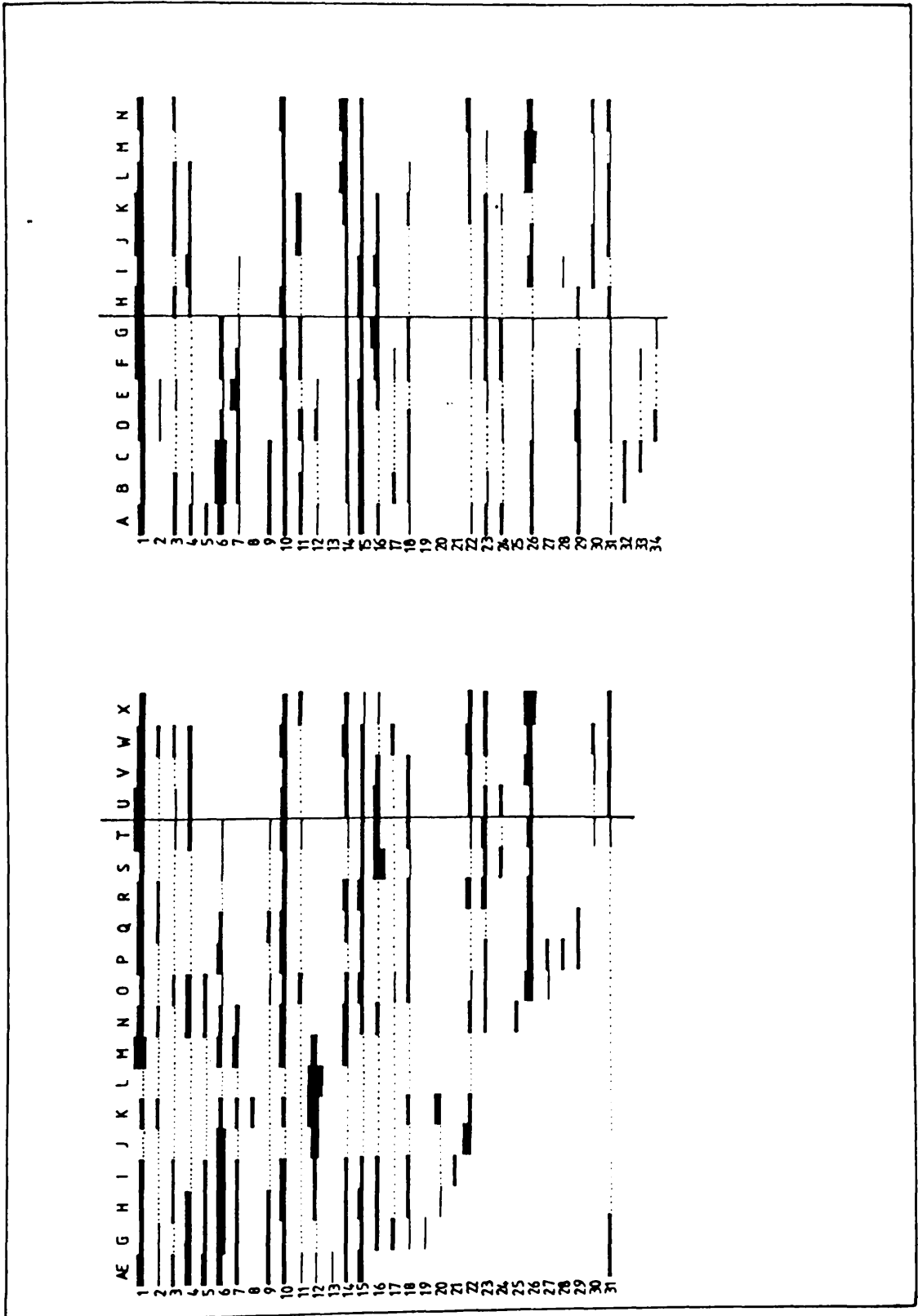


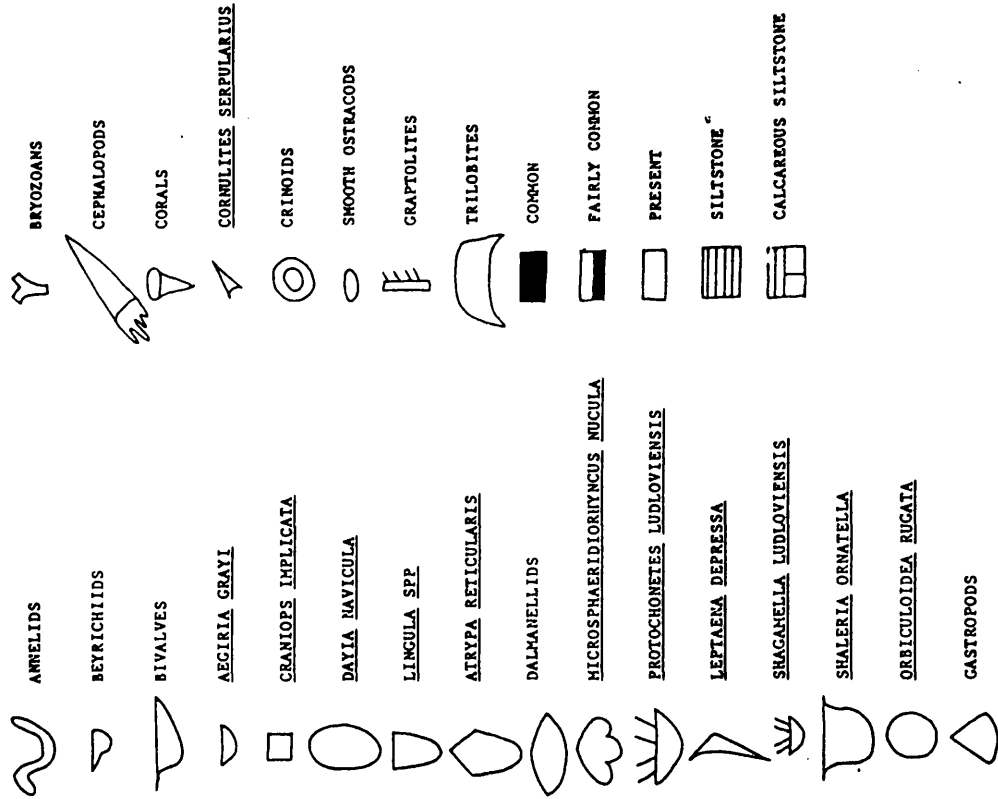
FIG.10. Range charts for Mortimer Forest collections, sections 62 (AE-X) and 9X (A-N). Leintwardine-Whitcliffe boundary marked. Key on separate sheet.

## FIGURE 10 - KEY

1. M.nucula
2. O.rugata
3. S.lunata
4. D.navicula
5. Sludloviensis
6. S.ornatella
7. L.depressa
8. S.longissimus
9. Isorthis spp.
10. Bryozoa
11. A.grayi
12. Monograptid
13. L.lewisii
14. Bivalves total
15. Dalmanellids total
16. Smooth ostracods
17. C.serpularius
18. Trilobites total
19. S.euglypha
20. M.leintwardinensis
21. S.wilsoni
22. Orthocones indet.
23. Beyrichiids indet.
24. N.lauensis
25. C.implicita
26. P.ludloviensis
27. Strophomenids
28. L.lata
29. A.reticularis
30. Worm tubes
31. Gastropods total
32. P.lanceolata
33. H.elegans
34. Crinoid ossicles



KEY FOR FIGURE 11



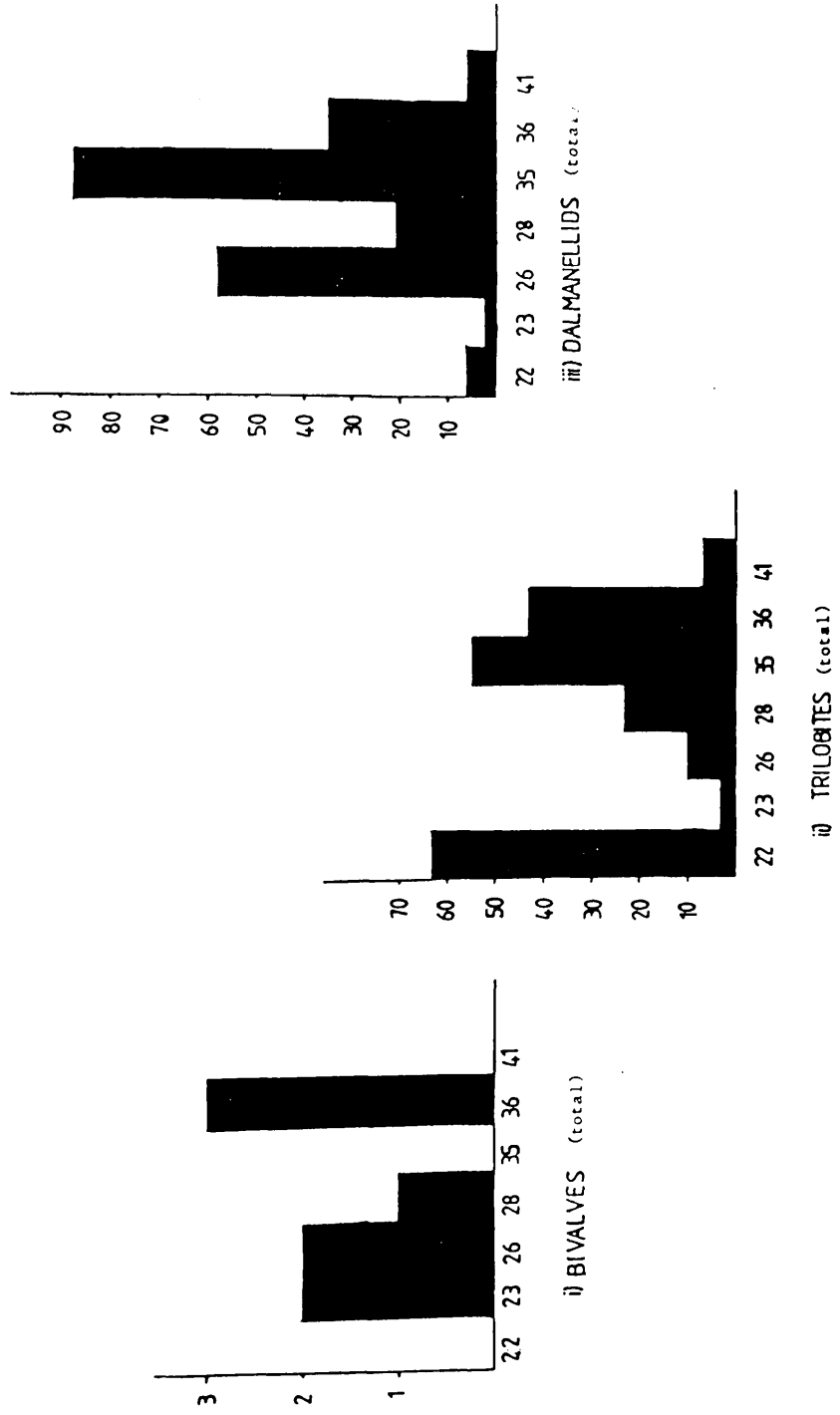
The information has been compiled from collections and published sources as follows: Holland 1959 (Knighton); Straw 1937 and collections (Builth); Lawson 1973 and collections (Aymestrey); Holland, Lawson and Wamsley 1963, Antia 1981 and collections (Ludlow). The Inner Shelf comprises Lawson 1955 (May Hill), Wamsley 1959 (Usk), Squirrel and Tucker 1960 (Woolhope), Phipps and Reeve 1967 (the Malverns). Generally, published lists record fossils as being Present, Fairly Common, or Common. Occasionally records include Rare and Abundant also. Actual numbers or percentages for genera and species are rarely, if ever, given. Therefore, although percentages are known for the Ludlow collections, fossils have been grouped as Present (<10%), Fairly Common (10-30%) and Common (>30%). This generalisation however, masks any slight changes that may occur in faunal abundances and may vary according to different authors. Abundances and diversity on the diagram will also depend on the number of references available for that locality. It is therefore somewhat subjective, and intended only to provide a general view of faunal changes across the area.

FIGURE 11. DISTRIBUTION OF THE MOST COMMON FOSSILS ACROSS AN AREA OF THE WELSH BORDERLANDS IN THE UPPER LEINTWARDINE AND LOWER WHITCLIFFE FORMATIONS.



<p>LOCALITY FORMATION</p>	<p>LOWER WHITCLIFFE</p>	<p>UPPER LEINTWARDINE</p>
<p>KNIGHTON</p>		
<p>BUILTH</p>		
<p>AMESTREY</p>		
<p>LUDLOW</p>		
<p>INNER SHELF</p>		

FIG12 (i - xxix). Frequency plots for Gotland fauna. Vertical axes = frequency. Horizontal axes = localities.



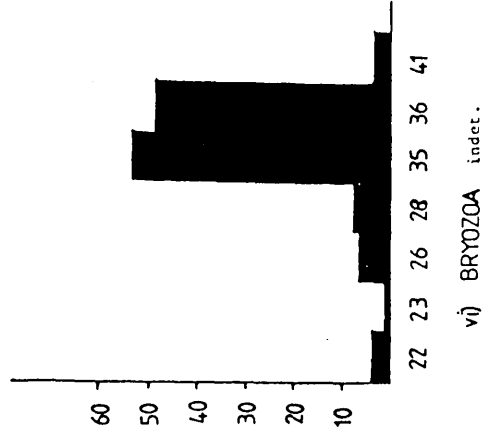
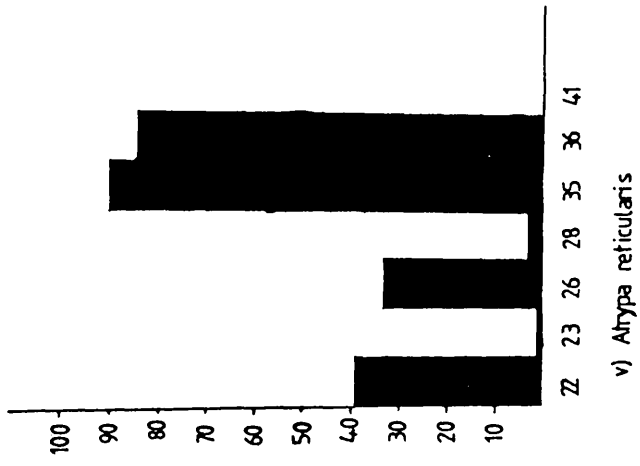
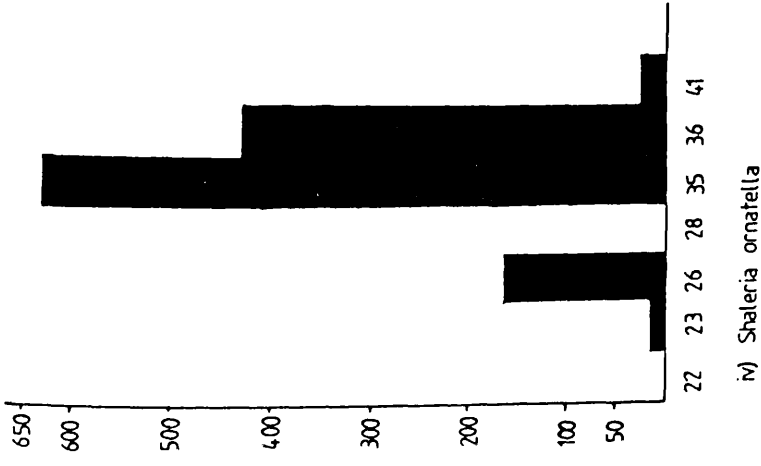


FIG. 12 contd.

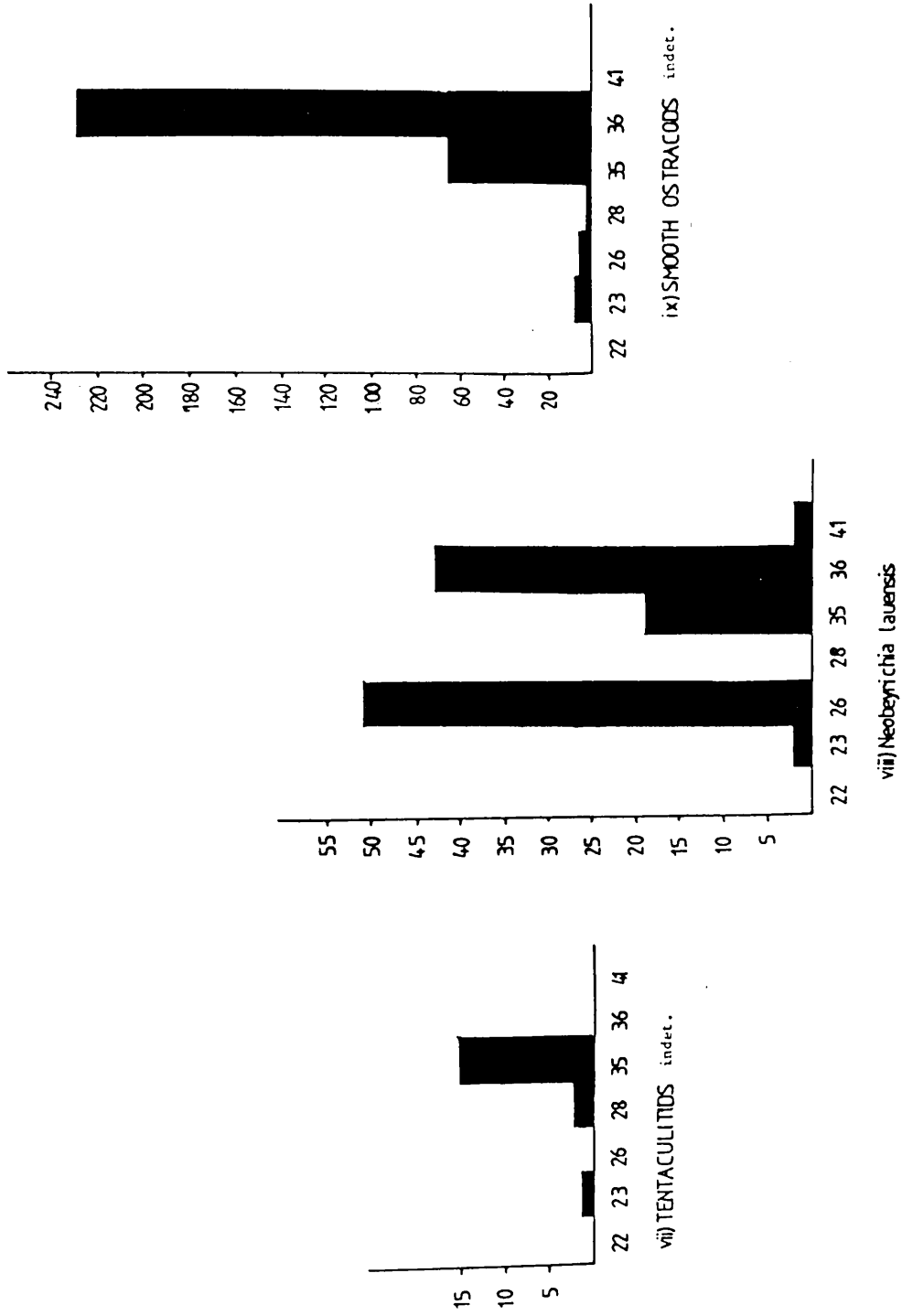


FIG. 12 cont'd.

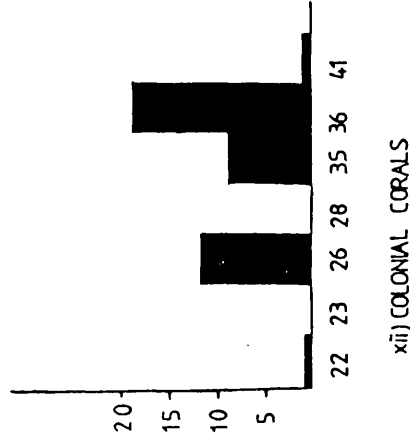
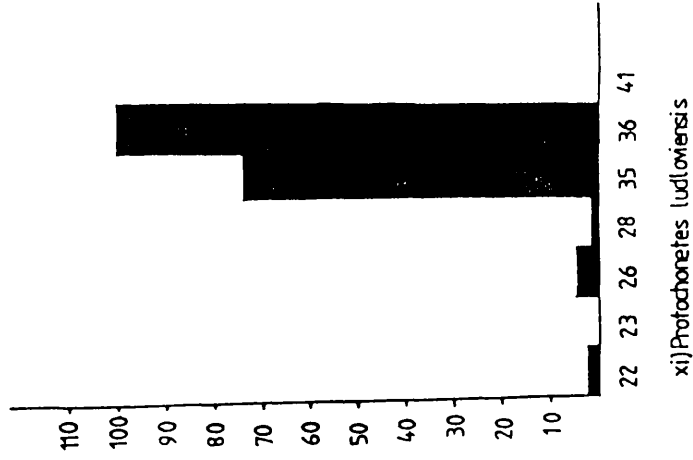
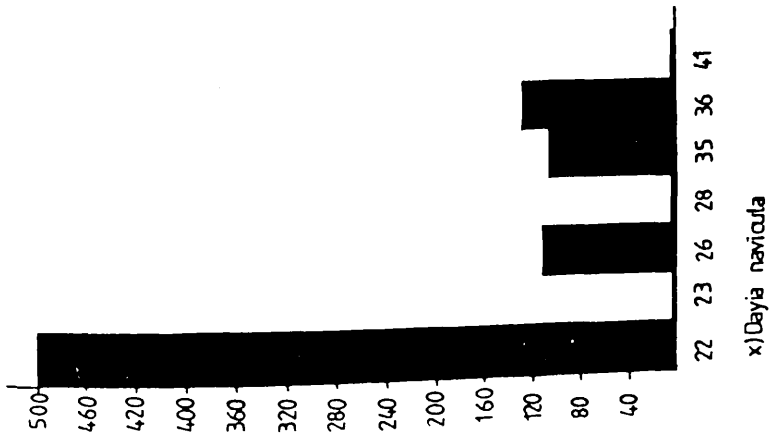


FIG. 12 contd.

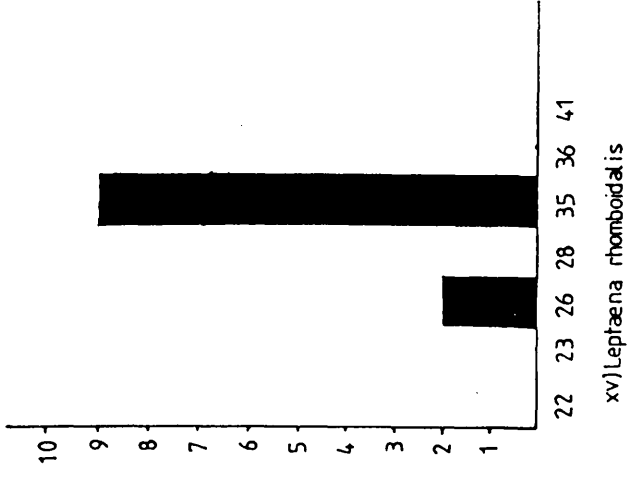
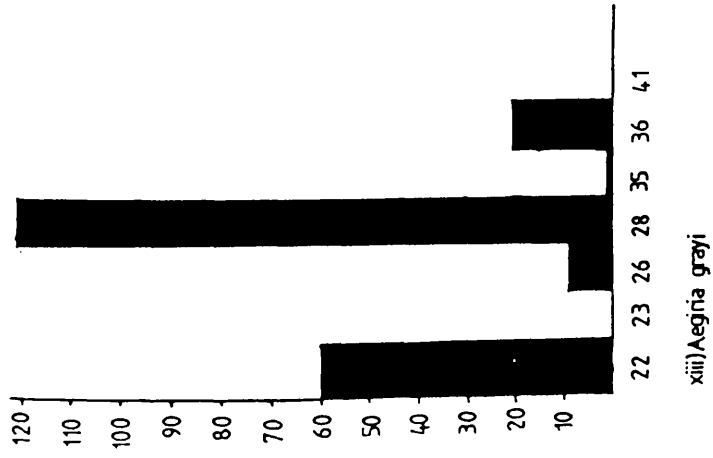


FIG. 12 contd.

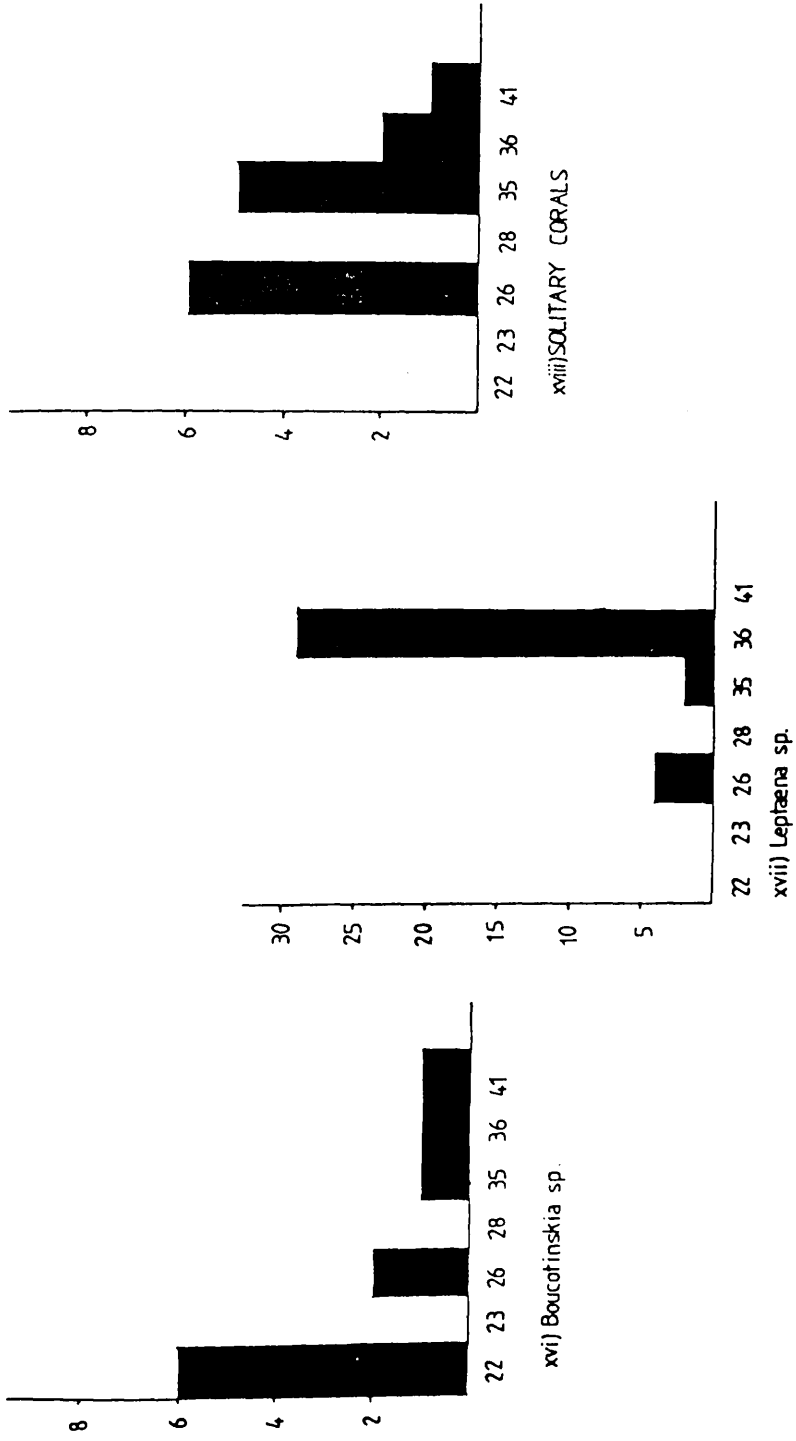


FIG. 12 contd.

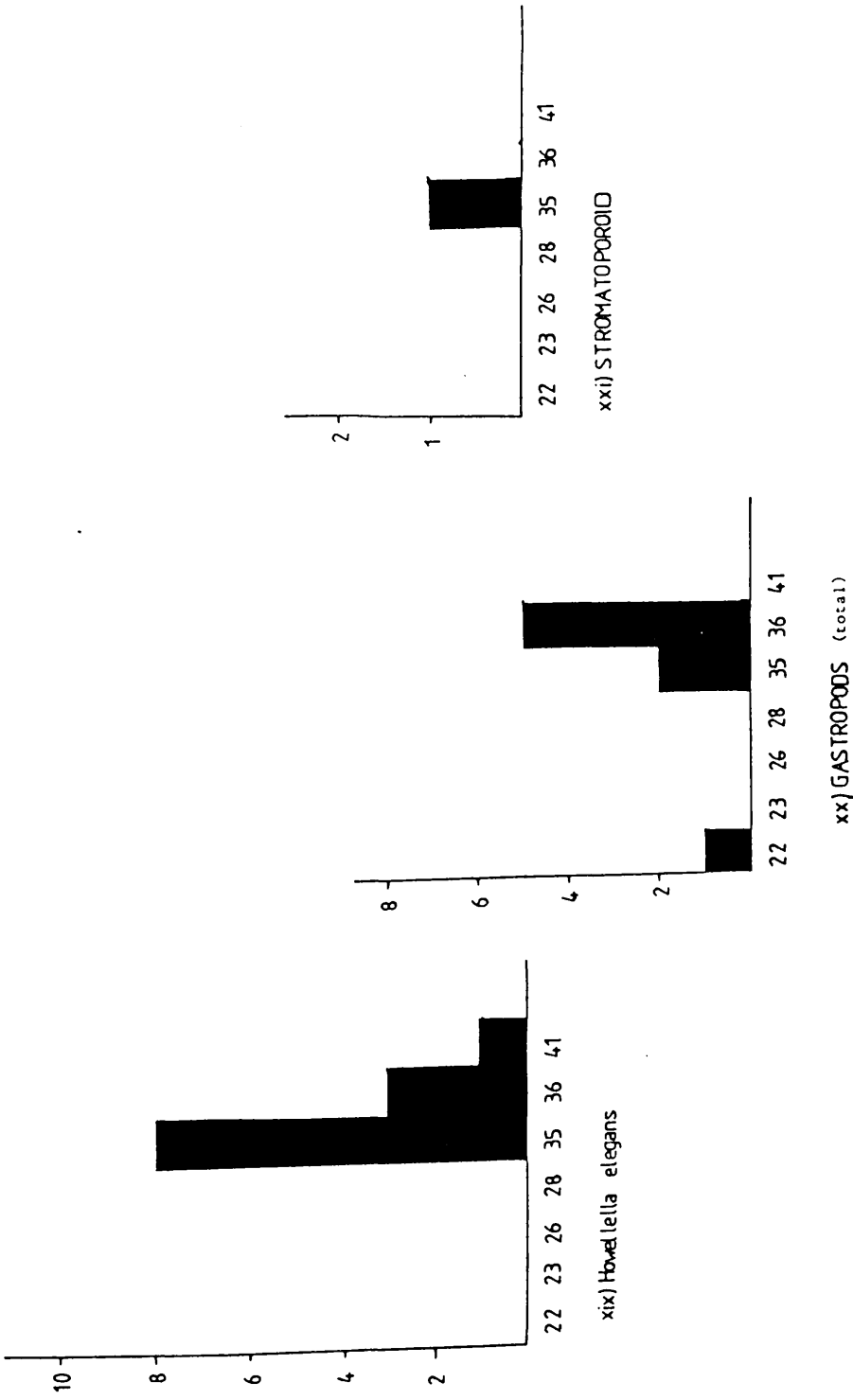


FIG. 12 contd.



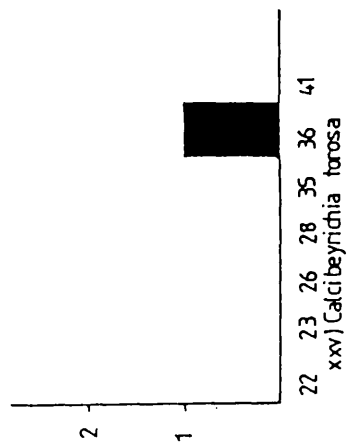
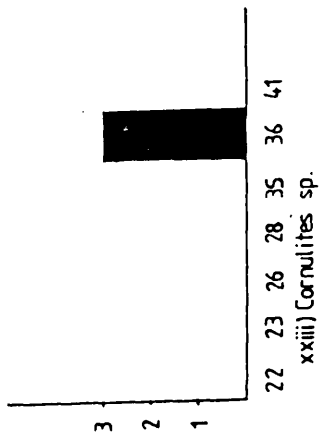
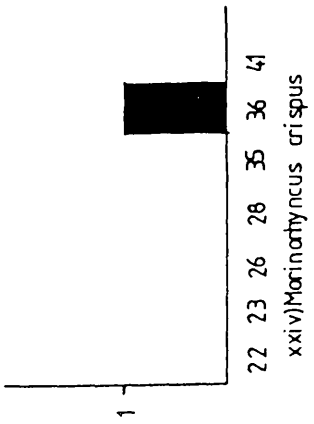
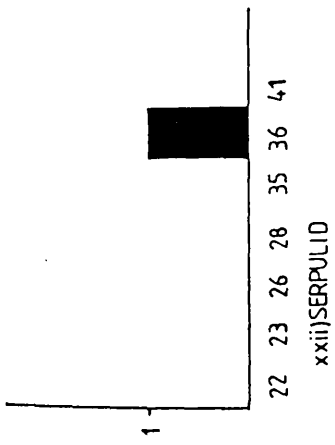


FIG. 12 contd.

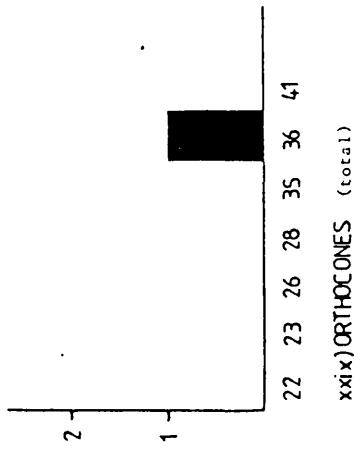
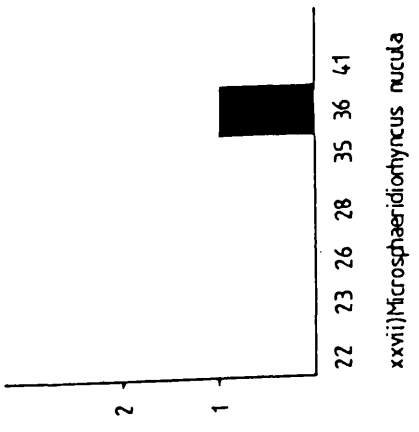
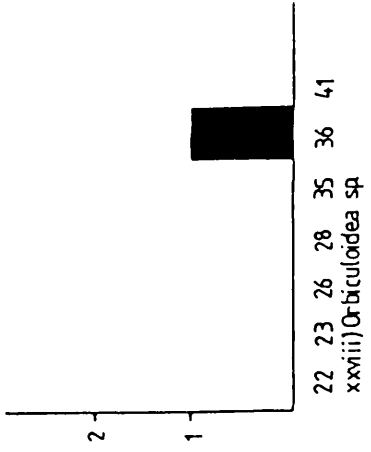
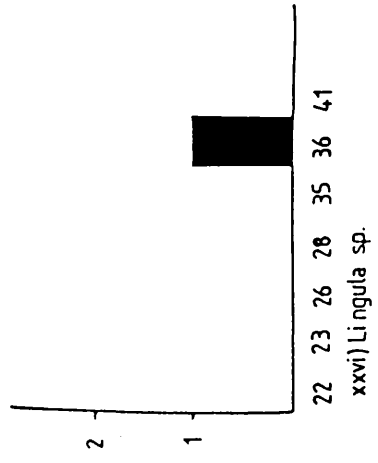


FIG. 12 contd.

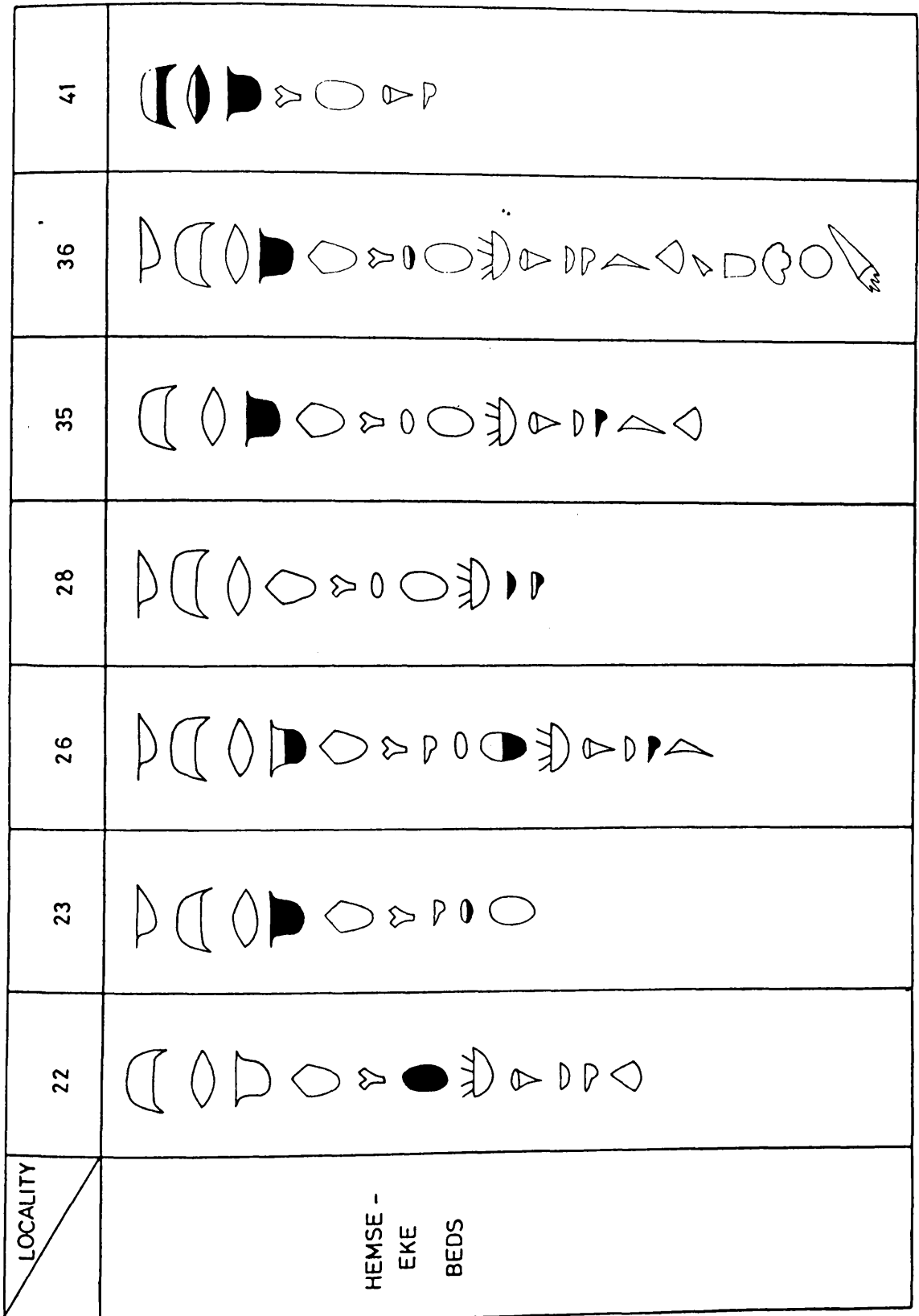


FIG.13. Faunal distribution diagram for Gotland collections.  
For discussion see text. Key as for Fig.11.

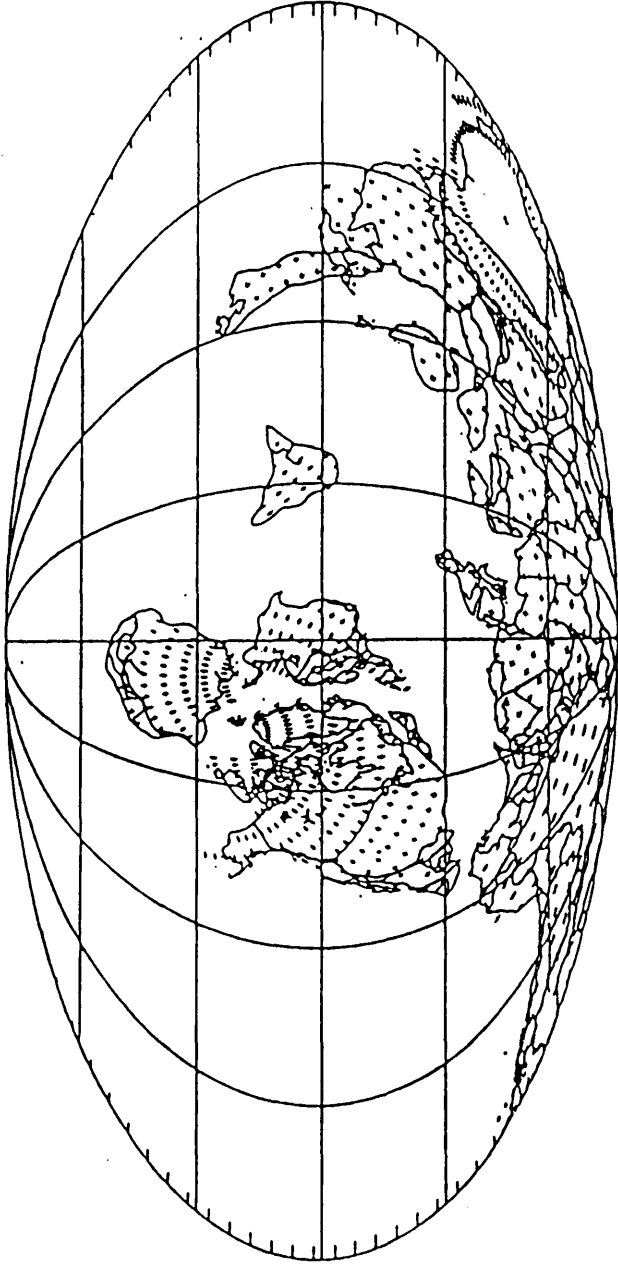


FIG.14. Palaeogeographic map for the late Silurian (from Scotese et al. 1985).

FAUNA	WELSH BORDERLANDS	GOTLAND DIVIDED BY 1.39	GOTLAND
BRACHIOPODS			
<u>S.ornatella</u>	126	931.13	1298
<u>M.nucula</u>	857	0.71	1
<u>D.navicula</u>	73	611.19	852
<u>A.reticularis</u>	34	179.34	250
<u>A.grayi</u>	94	152.08	212
<u>P.ludloviensis</u>	580	133.42	186
<u>L.depressa</u>	56	-	-
<u>L.rhomboidalis</u>	-	7.89	11
<u>Leptaena sp.</u>	-	25.12	35
<u>H.elegans</u>	4	8.61	12
<u>S.ludloviensis</u>	8	-	-
<u>O.rugata</u>	8	0.71	1
<u>L.lata</u>	2	-	-
<u>S.lunata</u>	31	-	-
<u>Boucotinskia spp.</u>	-	7.89	11
Dalmanellids total	227	154.95	216
Strophomenids	2	-	-
MOLLUSCS			
Bivalves total	228	5.74	8
<u>Cornulites spp.</u>	3	2.15	3
Gastropods total	32	5.74	8
Tentaculitids	-	12.91	18
OSTRACODS			
<u>N.lauensis</u>	26	83.93	117
Beyrichiids total	151	802.73	1119
Smooth ostracods	598	223.09	311
GRAPTOLITES			
Monograptids	9	-	-
TRILOBITES			
Trilobites total	58	146.34	204
cont.			

BRYOZOA			
Bryozoa total	302	91.11	127
CORALS			
Colonial corals	-	30.13	42
Solitary corals	-	10.04	14
CEPHALOPODS			
Orthocones total	69	0.71	1
ANNELIDS			
Worm tubes	23	-	-
TOTAL	3614	3627.66	5032

TABLE 1A. COMPARISON OF TOTAL FAUNAS FROM THE WELSH BORDERLANDS AND GOTLAND. ACTUAL FIGURES. GOTLAND FIGURES HAVE BEEN DIVIDED BY 1.39 TO ALLOW FOR GREATER ABUNDANCE OF FOSSILS.

FOSSIL	WELSH BORDERLANDS	GOTLAND
BRACHIOPODS		
<u>Shaleria ornatella</u>	3.49	25.20
<u>Microsphaeridiorhyncus nucula</u>	23.75	0.02
<u>Dayia navicula</u>	2.02	16.93
<u>Atrypa reticularis</u>	0.94	4.97
<u>Aegiria grayi</u>	2.60	4.21
<u>Protochonetes ludloviensis</u>	16.07	3.70
<u>Leptaena rhomboidalis</u>	0.00	0.22
<u>Leptaena depressa</u>	1.55	0.00
<u>Leptaena sp.</u>	0.00	0.70
<u>Howellella elegans</u>	0.11	0.24
<u>Boucotinskia spp.</u>	0.00	0.22
<u>Shagamella ludloviensis</u>	0.22	0.00
<u>Orbiculoidea rugata</u>	0.22	0.02
<u>Lingula lata</u>	0.06	0.00
<u>Salopina lunata</u>	0.36	0.00
Strophomenids total	0.06	0.00
Dalmanellids total	7.01	4.29
MOLLUSCS		
Bivalves total	6.32	0.16
<u>Cornulites spp.</u>	0.08	0.06
Gastropods total	0.89	0.16
Tentaculitid	0.00	0.36
OSTRACODS		
<u>Neobeyrichia lauensis</u>	0.72	2.33
Beyrichiids total	4.18	22.24
Smooth ostracods	16.57	6.18
GRAPTOLITES		
Monograptids total	0.25	0.00
TRILOBITES		
Trilobites total	1.61	4.05

cont.

BRYOZOA		
Bryozoa total	8.37	2.52
CORALS		
Colonial corals	0.00	0.83
Solitary corals	0.00	0.28
CEPHALOPODS		
Orthocones	1.92	0.02
ANNELIDS		
Worm tubes	0.64	0.36

TABLE 1B. COMPARISON OF TOTAL FAUNAS FROM THE WELSH BORDERLANDS  
AND GOTLAND. PERCENTAGES.



FAUNA	ACTUAL FIGURE	PERCENTAGE
<u>M.nucula</u> (J. de C.Sowerby)	857	23.71
Smooth ostracods	598	16.55
<u>P.ludloviensis</u> (Muir-Wood)	580	16.05
Bryozoa (total)	300	8.30
Bivalves (total)	228	6.31
Dalmanellids (total)	227	6.28
Beyrichiids (indet.)	151	4.18
<u>S.ornatella</u> (Davidson)	126	3.49
<u>A.grayi</u> (Davidson)	94	2.60
<u>D.navicula</u> (J. de C.Sowerby)	73	2.02
Cephalopods (indet.)	69	1.91
Trilobites (total)	58	1.60
<u>L.depressa</u> (J. de C.Sowerby)	56	1.55
<u>A.reticularis</u> (Linnaeus)	34	0.94
Gastropods (total)	32	0.89
<u>S.lunata</u> (J. de C.Sowerby)	31	0.86
<u>N.lauensis</u> (Kiesow)	26	0.72
Annelids (total)	23	0.64
Monograptids (indet.)	9	0.25
<u>Isorthis spp.</u>	8	0.22
<u>S.ludloviensis</u> (Boucot and Harper)	8	0.22
<u>O.rugata</u> (J. de C.Sowerby)	8	0.22
Crinoid ossicles	5	0.14
<u>H.elegans</u> (Muir-Wood)	4	0.11
<u>C.serpularius</u> (Schlotheim)	3	0.08
Strophomenids (indet.)	2	0.06
<u>L.lata</u> (J. de C.Sowerby)	2	0.06
<u>P.lanceolata</u> (Goldfuss)	2	0.06
TOTAL	3614	100.02

TABLE 2. WELSH BORDERLANDS, MORTIMER FOREST, LUDLOW. TOTAL FAUNA IN ORDER OF ABUNDANCE.

FOSSIL	ACTUAL FIGURE	%
<u>Shaleria ornatella</u> (Davidson)	1268	25.20
Beyrichiids indet.	1119	22.24
<u>Dayia navicula</u> (J. de C.Sowerby)	852	16.93
Smooth ostracods (total)	311	6.18
<u>Atrypa reticularis</u> (Linnaeus)	250	4.97
Dalmanellids (total)	216	4.29
<u>Aegiria grayi</u> (Davidson)	212	4.21
Trilobites (total)	204	4.05
<u>Protochonetes ludloviensis</u> (Muir-Wood)	186	3.70
Bryozoa (total)	127	2.52
<u>Neobeyrichia lauensis</u> (Kiesow)	117	2.33
Colonial corals	42	0.83
<u>Leptaena spp</u>	35	0.70
Tentaculitids	18	0.36
Solitary corals	14	0.28
<u>Howellella elegans</u> (Muir-Wood)	12	0.24
<u>Leptaena rhomboidalis</u> (Wahlenberg)	11	0.22
<u>Boucotinskia spp</u>	11	0.22
Bivalves (total)	8	0.16
Gastropods (total)	8	0.16
<u>Cornulites spp</u>	3	0.06
Stromatoporoid	1	0.02
Serpulid	1	0.02
<u>Morinorhyncus crispus</u> (Lindstrom)	1	0.02
<u>Calcibeyrichia torosa</u> (Jones)	1	0.02
<u>Lingula sp</u>	1	0.02
<u>Microsphaeridioryhncus nucula</u> (J. de C.Sowerby)	1	0.02
<u>Orbiculoidea sp</u>	1	0.02
Orthocone	1	0.02
TOTAL	5032	100.01

TABLE 3. GOTLAND FAUNA IN ORDER OF ABUNDANCE.

HOST	BRYOZOA ERECT	BRYOZOA ENCRUSTING	BRACHIOPODS	<u>Vermiforichnus</u>	<u>Serpulites</u>	<u>Cornulites</u>
BRACHIOPODS						
<u>L.depressa</u>	1	1		2		
<u>M.nucula</u>	1	1				
<u>O.rugata</u>		1				
<u>P.ludloviensis</u>	3			2	1	
<u>S.ornatella</u>	1					2
BIVALVES						
<u>F.amygdalina</u>	1	3	2	1		1
<u>P.tenuistriata</u>		1		1		
Bivalve indet.				1		2
Shell frag. indet.	1	6		4		2
CEPHALOPODS						
Orthoconic nautiloids		10	3	6	4	3
GASTROPODS						
<u>B.expansus</u>				1		
Gastropod indet.		1				
ANHELIDS						
Worm tubes	1	3				
TOTALS	9	27	5	18	5	10

TABLE 4. EPIZOA AND HOSTS, MORTIMER FOREST. FOR DISCUSSION SEE TEXT.

GROUP	DESCRIPTION	MEMBERS	COMMENTS
A	INFAUNAL	<u>L.lata</u> Annelids	Need soft sediment for burrowing, and slow sedimentation
B	SEMI-INFAUNAL SLIGHT TURBULENCE WITH SOME SEDIMENTATION	<u>C.interrupta</u> <u>G.cymbaeformis</u> <u>F.amygdalina</u> <u>P.retroflexa</u>	Need soft sediment for burrowing
C	EPIFAUNAL HIGH ENERGY (MAY BE SHALLOW)	Bryozoa Crinoids <u>H.elegans</u> <u>A.reticularis</u> <u>M.nucula</u>	Must be within photic zone with low sedimentation rate and no turbidity. Some soft sediment available
D	EPIFAUNAL LOW ENERGY	<u>S.lunata</u> <u>Isorthis spp.</u> <u>L.depressa</u> <u>P.ludloviensis</u> <u>P.tenuistriata</u> <u>D.navicula</u> <u>S.ornatella</u>	Need quiet environment with slow sedimentation and some hard substrate available
E	EPIFAUNAL HARD SITE ESSENTIAL	<u>O.rugata</u> <u>C.implicita</u>	Possibly tolerant of a wide range of conditions
F	NEKTONIC/BENTHIC MOBILE	Cephalopods Trilobites Gastropods Ostracods	Dependent on food, algae and plankton. May escape localised conditions

TABLE 5. PALAEOECOLOGICAL REQUIREMENTS FOR WELSH BORDERLANDS FAUNA. FOR DISCUSSION SEE TEXT.