

**MICROPLANKTON CHANGES THROUGH THE EARLY SILURIAN  
IREVIKEN EXTINCTION EVENT ON GOTLAND, SWEDEN**

Thesis submitted for the degree of  
Doctor of Philosophy  
at the University of Leicester

by

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September 2002

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“A little wobble can get worse  
until the whole system collapses.  
But those same little wobbles are essential to a living system.  
They mean the system is healthy and responsive.”

John Arnold, on Jurassic Park

*Jurassic Park* by Michael Crichton (p247)

## ABSTRACT

This thesis documents and analyses the extinction and origination patterns of acritarchs and prasinophyte algae at the Llandovery/Wenlock boundary in the Lower Silurian on the island of Gotland, Sweden. Closely spaced samples were collected from two sections: Lusklint 1 and Lickershamn 2, spanning the upper part of the Lower Visby Beds and almost all of the Upper Visby Beds. Errors associated with the palynological processing technique have been assessed and a new photographic technique has been developed. Five new species are described.

At least eight extinctions affecting the conodont record have been reported at this level (named the Ireviken Extinction Event (Aldridge *et al.* 1993, Jeppsson 1997)). The Ireviken Event has been interpreted as an example of the change from a P to an S climate state (Jeppsson 1993).

The data show a significant turnover in the phytoplankton at this time, with most of the extinctions at the end of the event (86.3% in the top four metres of the Lusklint 1 section), after many of the conodont extinctions had already taken place. The originations are more numerous than the extinctions (54 species originate at Lusklint 1 as opposed to 44 that became extinct) and they are distributed through the whole of the Ireviken event. There is an uneven distribution across the event with more originations in the Lower Visby Beds forming a convex pattern.

The two sections analysed were compared using graphic correlation, but palynomorph range end data show considerable scatter. Peaks in the number of palynomorphs per gram of sediment suggest that the two sections completely overlap. Deposition of the thickest bentonite produced a marked drop in the number of palynomorphs per gram of sediment, but a marked rise in numbers in the following few centimetres, probably caused by a fertilization effect.  $\delta^{13}\text{C}$  values at Lusklint 1 remain stable in the Lower Visby Beds, but show a marked gradual rise in the Upper Visby Beds. The  $\delta^{18}\text{O}$  values for the same interval vary little.

The P and S model does not successfully explain all the changes recorded, but is the most comprehensive model available at this time. Additions to the model, incorporating planktonic dimethyl sulphide production and iron fertilization are presented.



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## ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge the help and support of Dick Aldridge. It was Dick who devised this project and he has proved to be an excellent supervisor. His knowledge of the Silurian is difficult to surpass and he has always found time for me even when he is snowed under with his duties as head of department. His efforts in the field were very much appreciated. The other person without whom this project would not have been possible is Lennart Jeppsson. His help and enthusiasm in the field were invaluable. We would have really struggled in Gotland if he had not given up much of his field season to drive us about, show us localities and arrange all the accommodation details.

The other major contributors were Stewart Molyneux, Ken Dorning, Gary Mullins and Alain Le Hérissé. Stewart was fantastic help particularly in the early days of my project. My total lack of any palynology experience meant that to begin with there was a steep learning curve, which Stewart guided me along with lots of encouragement. The insatiable enthusiasm and the breadth of acritarch knowledge of Ken has been a big help throughout the project. My regular trips up to Sheffield have always been very useful and I have always been impressed by how much time he has set aside to discuss things with me. Gary is probably the unsung hero of my project. He has been so useful to have around to get quick answers on those little questions even if occasionally his response is "I've never seen any acritarchs like that before either". The number of times I've been round his office to check details of obscure papers, I think he might be as pleased as I am that I've finished! It was really fantastic to get help from Alain in the early days of my project. His vast knowledge of Gotland acritarchs was one of the things that really helped me on the right track when the task ahead seemed a little overwhelming.

I would also like to thank Derek Siveter and Richard Corfield for kindly letting me use their stable isotope data, David Loydell for detailed discussions on the Silurian sea level curves, Rex Harland for discussions with him on dinoflagellates, Andrew Swift for his technical help and Rod Branson for his help on the SEM. Sarah Gabbott has always been there for a chat when things were not going quite to plan.

I owe a huge thanks to my friends in Leicester. Thanks to my housemates Rachel and Simon for putting up with me writing up. Thanks to my office mates (Hannah, Matt, Andrew and Pat) for regular distractions especially on a Friday evening. Thanks especially to Pat who has taken the brunt of things and always been loads of fun. A special mention must be made for

the circuits team: Pat, Heike, Rich, and Gav who gave me a good excuse not to work on a Tuesday evening and have a laugh. Thanks to the other distracters: Dave, James T., James H., George, Mark Moocow, Annabel, Natalie, Craig B. and Craig C.. I'd also like to thank my Durham friends especially Bec, who are always there to remind me how much fun we had when we were undergrads and occasionally bring me back down to earth.

Finally, I am indebted to my family. To my Mum and Dad who have always been there to support and encourage me and to my brothers Andy and Mark who are always good fun.

## INTRODUCTION

## RESEARCH AIMS AND OBJECTIVES

*Aims*

THE aims of this study are to increase knowledge of the palynomorph changes over the Ireviken Event, expand our understanding of the environmental changes that occurred at this time and to test causative models.

*Objectives*

- 1). To collect high-density samples from the island of Gotland, Sweden across the Ireviken Event, which spans the Llandovery–Wenlock boundary. To process these samples for the recovery of palynomorphs and to document the ranges of microfossil taxa through the Event.
- 2). To compare the palynomorph record statistically to that of the conodonts through the Ireviken Event.
- 3). To compare the palynomorph record to that of stable carbon isotope ( $\sigma^{13}\text{C}$ ) and stable oxygen ( $\sigma^{18}\text{O}$ ) records.
- 4). To test the P & S ocean/atmosphere model of Jeppsson (1990) in explaining palaeoenvironmental change.

## THESIS STRUCTURE

*Chapter 1.*

Introduction. This chapter, written in the style of the journal *Palaeontology*, includes general information on the geology of Gotland, a brief history of research, the stratigraphy and list of localities.

*Chapter 2.*

Techniques. This chapter begins with a description of the sampling technique, goes on to describe in detail the processing technique used and outlines previous research. The adequacy of different processing and logging techniques is assessed and a modified processing technique is discussed. The logging and the photographic techniques are described. This

chapter is written in the style of the *Journal of Micropalaeontology*, where much of a preliminary version has already been published (Gelsthorpe 2002).

### *Chapter 3.*

The classification of palynomorphs and systematic palaeontology. A brief résumé of important and recent developments in palynomorph classification is presented. An annotated list of prasinophyte algae and acritarchs recovered is provided and the systematic palaeontology of selected taxa is presented. This chapter is written in the style of the journal *Palaeontology*.

### *Chapter 4.*

Results. This chapter, written in the style of the journal *Palaeontology*, reviews the available palynomorph, conodont and stable carbon and oxygen isotope record data for the Ireviken Event.

### *Chapter 5.*

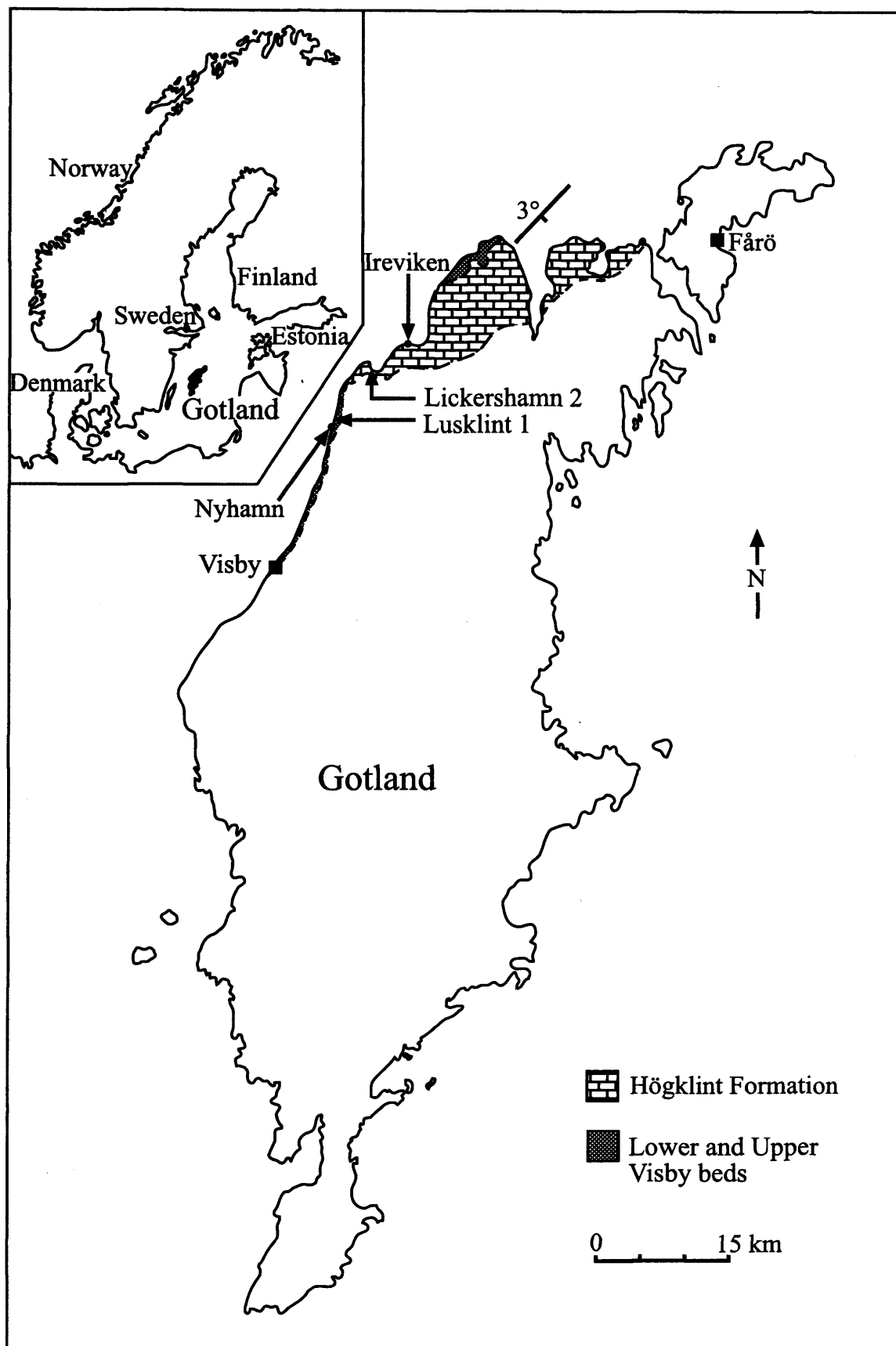
Discussion and conclusion. This chapter, written in the style of the journal *Palaeontology*, reviews the implications of the palynomorph record found on Gotland. The possible explanations of the patterns seen are discussed and more plausible scenarios are analysed in greater detail. A modified P and S model is presented. The focus of future studies is outlined.

## GEOLOGICAL SETTING

The Lower Silurian rocks of Gotland form an extensive outcrop on the island, with the Lower and Upper Visby beds and the Höglint Formation (the Llandovery/Wenlock boundary beds) in the north-west (Text-fig. 1.1). All the beds/formations dip at around 3° to the southeast.



## CHRONOSTRATIGRAPHY

The Llandovery and Wenlock series are the first and second series of the Silurian System (Text-fig. 1.2). The standard Silurian series are comprehensively reviewed in Holland and Bassett (1989). A K–Ar biotite sample from Ireviken 3 in Gotland has given an estimated age of  $430.5 \pm 6$  Ma for the Llandovery/Wenlock boundary (Dorning and Harvey 1999).



TEXT-FIG. 1.1 The outcrop of the Visby Beds and the Höglint Formation in Gotland (after Lé Hérisse 1989)



Series	Stage	Gotland stratigraphy	P and S states
Wenlock	Homerian	Mulde Fm  Halla Fm	Vattenfallet Secundo Episode
		Slite Group	
	Sheinwoodian	Tofta Fm 	
		Höglint Formation	
Llandovery	Telychian	Upper Visby Beds	Ireviken Event
		Lower Visby Beds	
	Aeronian	Below sea level  (Visby core shows Lower Visby Beds down to 142.5m below sealevel, where the boundary with Ordovician is present)	Snipklint Primo Episode
	Rhudd-anian		

TEXT-FIG. 1.2 Chronostratigraphy and lithostratigraphy stratigraphy of Gotland, after Holland and Bassett (1989). Oceanic P and S states after Jeppsson (1990, 1993, 1997). Formation and time intervals not to scale.

## BIOSTRATIGRAPHY

The Lower and Upper Visby beds have generally been considered to be late Llandovery to early Wenlock in age (Jaanusson *et al.* 1979), but the precise level of the Llandovery/Wenlock boundary in Gotland has never been directly correlated with the stratotype at Hughley Brook, Shropshire, England. The most accurate biostratigraphical correlation to date has been made by Jeppsson and Männik (1993) who, correlating with the Estonian Viki core and then to Gotland, placed the base of the Wenlock somewhere below conodont Datum 2 which is defined by the extinction of the conodont *Ozarkodina polinclinata*. Loydell *et al.* (1998) attempted a similar correlation using the Estonian Ohesaare core, but the conodont to graptolite correlation in the Llandovery/Wenlock boundary beds was recorded as being uncertain.

## LITHOSTRATIGRAPHY

A description of the lithologies of the late Llandovery and early Wenlock beds of Gotland is given below (after Hede 1960, Laufeld 1974).

The Lower Visby Beds are dominated by soft, blue-grey marls with common light greenish-grey limestone nodules. The nodules become more numerous upwards and increasingly coalesce into limestone bands, as the Lower Visby beds pass into the Upper Visby Beds. Three prominent bentonites are identified, with the largest (the upper bentonite, the base of which is used as a reference level) 55mm thick.

The change from the Lower to Upper Visby Beds is marked by the appearance of a dense layer of *Phaulactis* solitary corals at the base of the Upper Visby Beds. Upwards through the section, light grey bioclastic limestone becomes the dominant lithology in near continuous beds. An inconspicuous clay layer (a few millimetres thick), 1.9m below the base of the Höglint Formation, is used as a reference level.

The rapid transition into the massive bioclastic limestones of the Höglint Formation is marked by the first appearance of a light pink crinoid limestone; these beds are punctuated by occasional patch reefs (up to 35m thick Riding 1981), which severely compress the beds below. Along the outcrop there is little variation in overall lithology within the Lower and Upper Visby beds.

The geology of the north–west of Gotland is covered by the 1:50 000 Aa 183 Visby and Lummelunda sheet, 1940.

## PREVIOUS RESEARCH ON GOTLAND AND THE IREVIKEN EVENT

### *Stratigraphy*

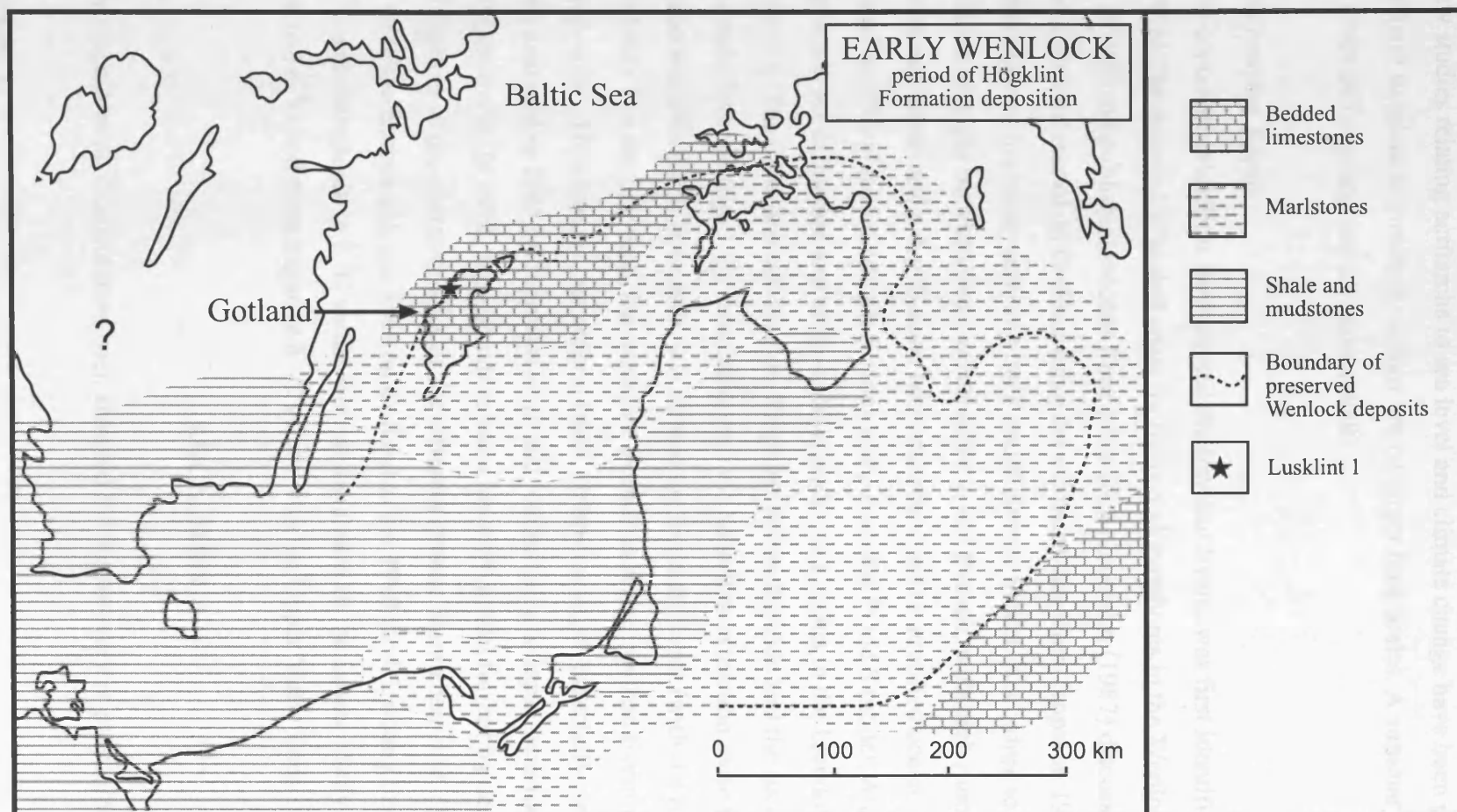
The first modern, comprehensive study of the stratigraphy of Gotland was completed by Hede (1960). After extensive restudy of the Lower and Upper Visby beds and the Högklint Formation, Manten (1971) expanded on Hede's work. The main features of Gotland geology were again reviewed in Laufeld and Bassett (1981), who suggested a pulsatory regression through the Silurian on a palaeoshoreline some distance to the north of Gotland. A palaeogeographic map for the early Wenlock (Text–fig. 1.3) was produced. Bassett *et al.* (1989) reviewed the tectonics, palaeogeography, palaeontology and stratigraphy of the region and correlated the strata with the type sections and other regions. A study of the development of Högklint Formation patch reefs was published in great detail by Watts and Riding (2000). The plate tectonics and structural geology of Baltica during the Palaeozoic was reviewed by Torsvik *et al.* (1990), who presented a plate reconstruction for the early Wenlock.

### *Palaeontology*

The pioneering work of Hede (1960) on the stratigraphy and palaeontology of Gotland provided a glimpse of the richness of the fossil record on the island.

The micropalaeontology of Gotland has been analysed by a number of authors. Significant publications include: Laufeld (1974) on chitinozoans, Martinsson (1962, 1967) on ostracods and numerous publications by Jeppsson (e.g. 1993, 1998) on conodonts. A study of the acritarchs through the entire Silurian succession of Gotland was published by Le Hérisse (1989), with species descriptions and ranges from the (Llandovery age) Lower Visby beds to the (Ludlow age) Sundre Formation. Le Hérisse showed that there are many originations and extinctions through the Lower and Upper Visby beds and the lowermost Högklint Formation, though he only presented the acritarch occurrences from five samples at this level.

The first major study into the late Llandovery and early Wenlock was based on the Vattenfallet section, just outside Visby, around 20km south of Luskint 1 (Jannusson *et al.* 1979). A team of 32 specialists analysed the occurrences of various fossil groups: The authors



TEXT-FIG. 1.3. Palaeogeography of the Baltic during the period of deposition of the Högklint Formation during the early Wenlock (after Laufeld and Bassett 1981).

included Cramer *et al.* (1979), who produced a range table of acritarchs through the Upper Visby Beds and the Högkint Formation.

Few studies relating acritarchs to sea level and climate change have been published. They are difficult to relate to this study as they are on larger time scales. A summary of recent studies is given in Tongiorgi and Di Milia (1999).

### *The Ireviken Event*

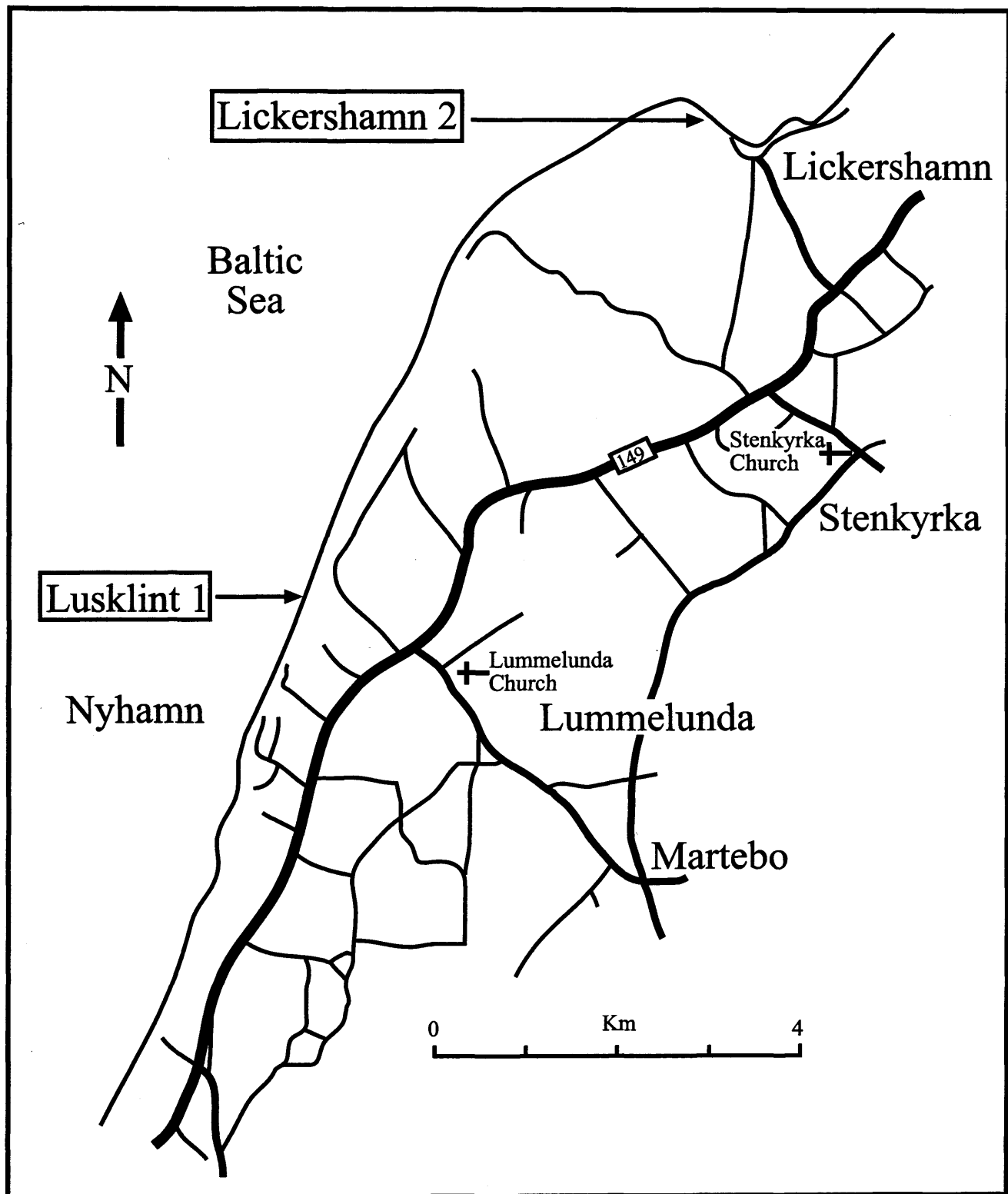
The conodont extinction, now termed the Ireviken Event, was first identified by Aldridge (1976). He recorded a 'global crisis for the conodontophores in the Wenlock' from collections in Britain and published records from other areas. Jeppsson (1987) discussed the lithological and conodont record on Gotland using the evidence that later (Jeppsson 1990) formed the foundation of his paper outlining the P and S climate model. According to the model, the Silurian changes between two climate states: a wet P-state, with high runoff and a well circulated ocean and a dry S-state, with low runoff and a stratified ocean. Using the global faunal and floral record and predictions made from the P and S model, Aldridge *et al.* (1993) identified six extinction and origination episodes and events in the Llandovery and earliest Wenlock. The transition between the Snipklint Primo Episode and the succeeding Vattenfallet Secundo Episode (fig. 1.2), associated with the conodont extinction close to the Llandovery/Wenlock boundary, was named the Ireviken Event (with the reference section on Gotland). For the first time, the conodont extinction at the Ireviken Event was described as 'step-wise'. The changes that several fossil groups undergo (especially the conodonts) were then analysed in 1995 by Jeppsson *et al.* and 'community collapse' was identified at the Ireviken event. In 1998, Jeppsson developed his 1990 model further by describing the differences in the characteristics of the different events. Samtleben *et al.* (1996) were the first to tie in the isotope changes seen on Gotland to the 1990 model, noting that more negative  $\delta^{18}\text{O}$  and more positive  $\delta^{13}\text{C}$  values were associated with the Lower Visby Beds and more positive  $\delta^{18}\text{O}$  and more negative  $\delta^{13}\text{C}$  values with the Upper Visby Beds.

## LOCALITIES

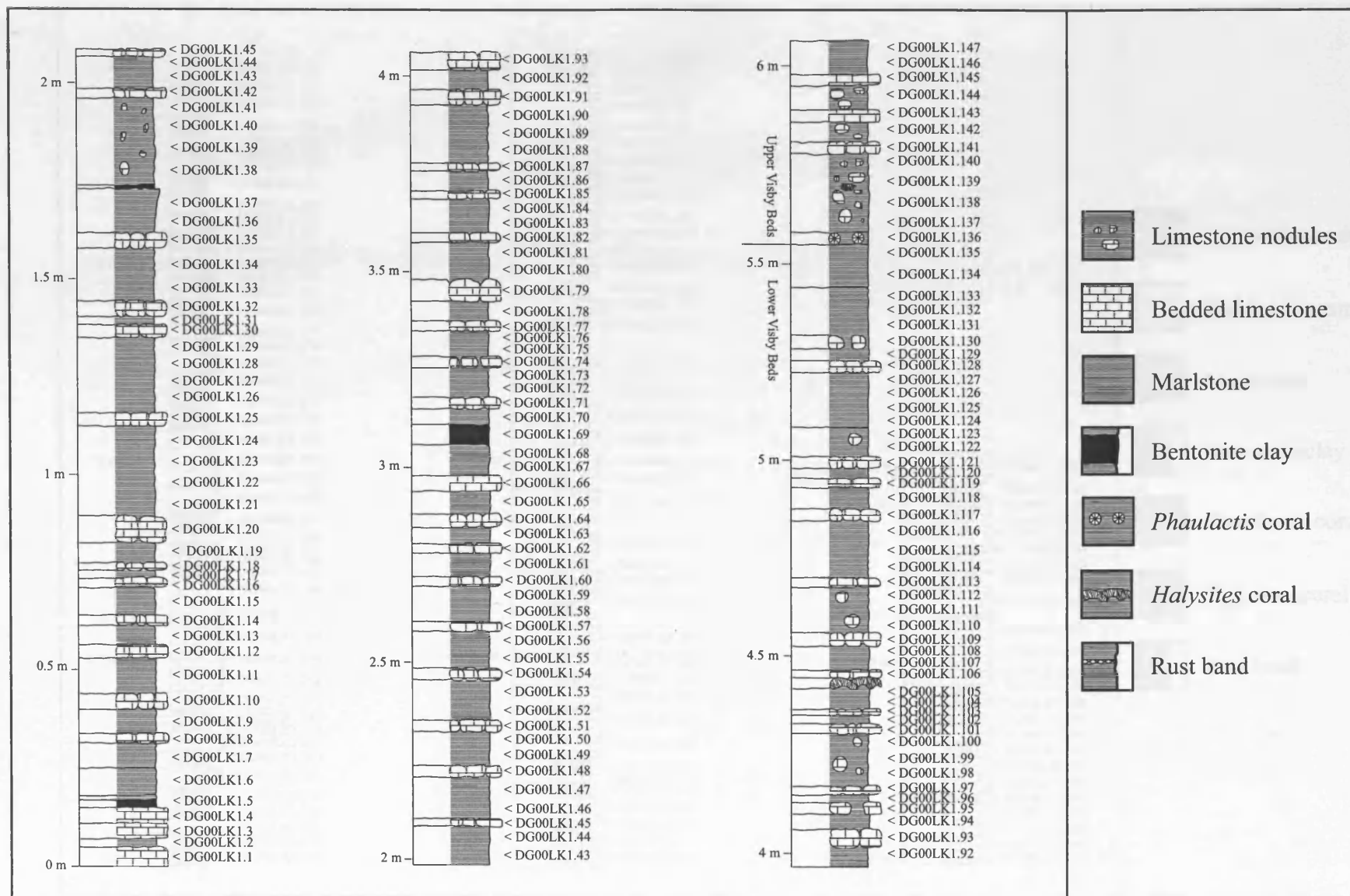
Two localities on Gotland have been sampled for the recovery of palynomorphs:

### *Lusklint 1.*

(CK 4675 0680); Text-figs. 1.1., 1.4., 1.5, 1.6., 1.7. A cliff section 2.08 km west-north-west of Lummelunda church. From the northwestern corner of the large raised beach quarry above



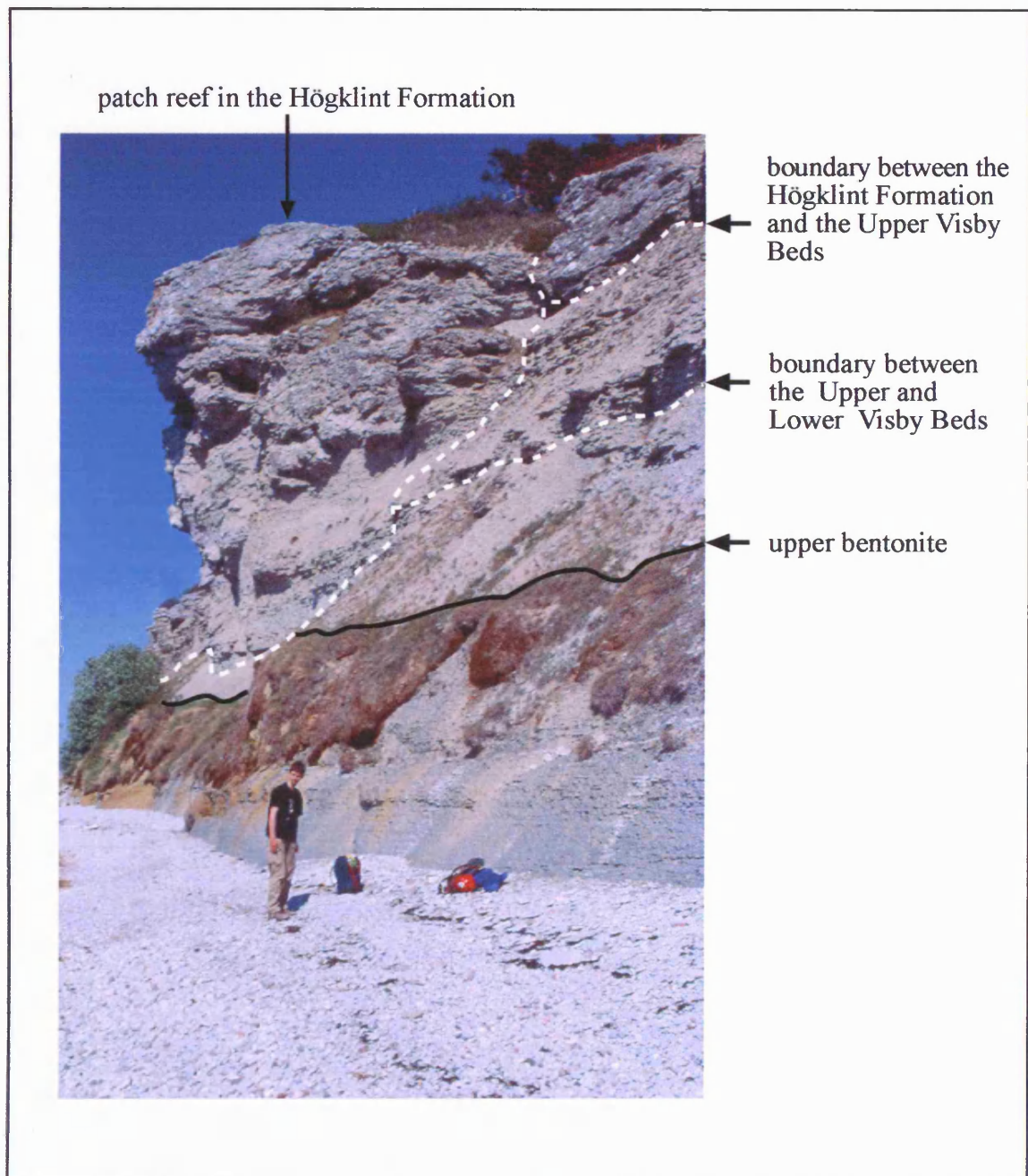
TEXT-FIG. 1.4. Sketch map showing the location of Lusklint 1 and Lickershamn 2.



TEXT-FIG. 1.5 Stratigraphic log of the lower part of the Lusklint 1 section. The positions of the samples are shown. Figures refer to the height in metres above the base of the section (reference level is the base of the lower bentonite 0.15m above the base of this section). The section is divided on the basis of bedding planes.

TEXT-FIG. 1.6. Stratigraphic log of the upper part of the Lusklint 1 section. The positions of the samples are shown. Figures refer to the height in metres above the base of the section (reference level is the base of the lower bentonite 0.15m above the base of this section). The section is divided on the basis of bedding planes.



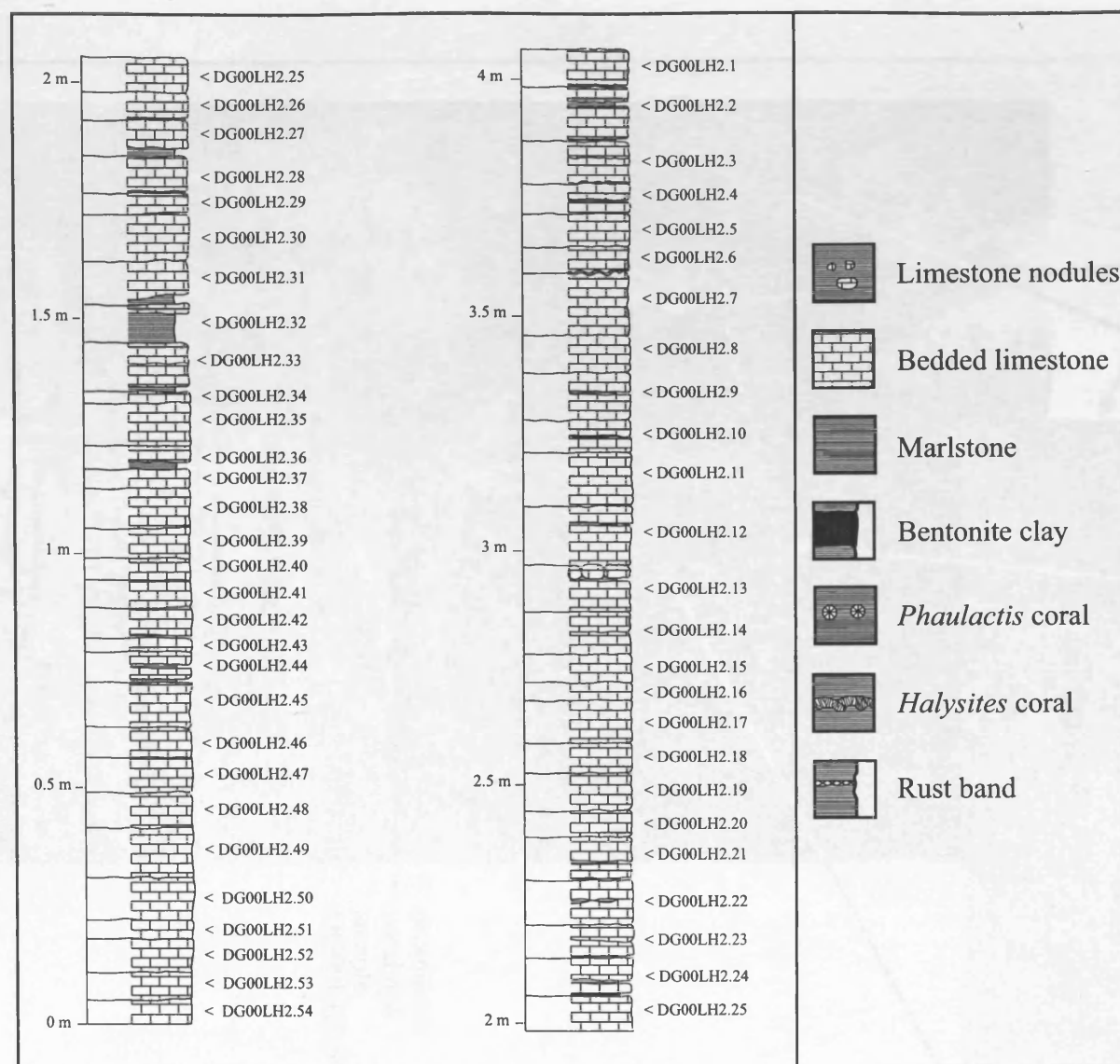


TEXT-FIG.1.7. Photograph showing the stratigraphy 150m north of Lusklint 1. (Photograph courtesy of R. J. Aldridge).

the cliff (600m south of Lusklint) the path is followed northwards into the pine forest. About 40m north of the quarry boundary the path branches (not marked on the map) and one branch descends to the shoreline. The locality begins where the travertine cover on the cliff has eroded away. The section sampled is about 150m north of where the path descends to the shore and 10m south of the old pine tree, situated two-thirds of the way down the slope. This section from the base to the top of the cliff displays the transition from the marlstone dominated Lower Visby beds to the limestone dominated Upper Visby beds. The section forms a subcrop and for this study the topsoil was removed to a depth of about 0.4m where the rock was exposed. Increasing thickness of the topsoil inhibits the collection of the higher parts of the Upper Visby beds and the Högklint Formation at this locality. The reference level is the base of the Lusklint bentonite (the lowest of the three) at 8.28 m above sea level.

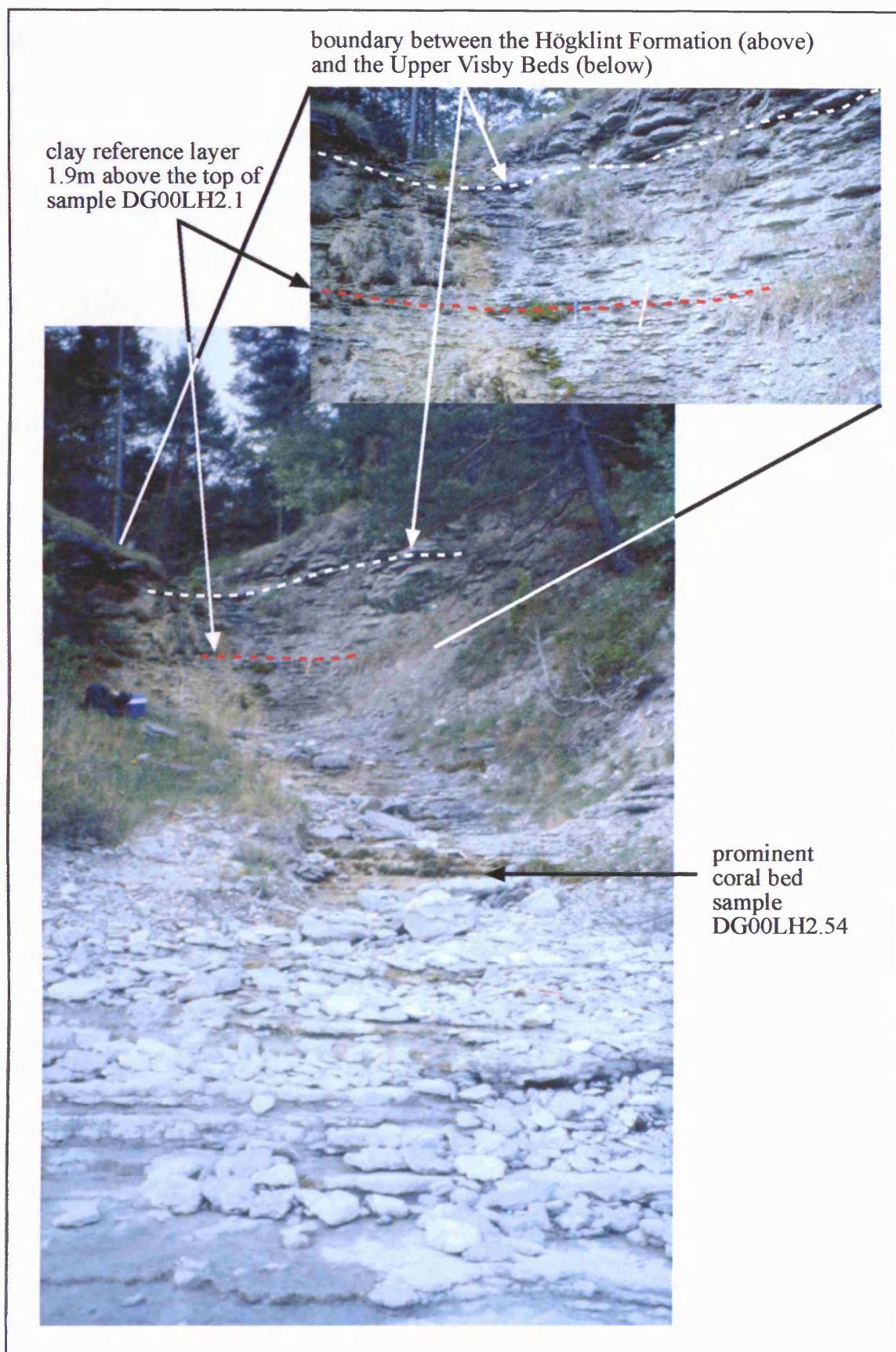
*Lickershamn 2.*

(CK 5199 1239); Text-figs. 1.1, 1.4., 1.8., 1.9. A stream section cutting into the cliff, 4080 m north-west of Stenkyrka church. The section is 100m west of the small bridge at the coast, about 260m northwest of the northwestern-most house at Lickershamn. This section displays the sharp change between the limestone-marlstone alternations of the Upper Visby beds and the massive limestone of the Högklint Formation. The reference level is at the base of an inconspicuous weathered clay layer 1.9 m below the base of the Högklint Formation.



TEXT-FIG. 1.8. Stratigraphic log of the Lickershamn 2 section. The positions of the samples are shown. Figures refer to the height in metres above the bottom of the sampled section (the section base is 5.97m below the clay reference layer).





TEXT-FIG.1.9. Photo showing the stratigraphy at Lickershamn 2.

## Techniques

### Sampling technique

At both Lusklint 1 and Lickersham 2 sampling strategy was dependant on lithology and bed thicknesses. Where marls were exposed the beds could be easily split, this was not the case for the limestone units for which sample thickness was mostly determined by bed thickness. At Lusklint 1, samples were collected on average every five centimetres and at Lickersham 2 roughly every ten centimetres, as this section was dominated by thicker limestone units. About one hundred grams of sediment was collected at each sample horizon and great care was taken to avoid contamination from other samples and organic debris.

### Testing of palynological processing techniques

## INTRODUCTION

The foundation to any palynological research is processing technique. The method must be reliable, consistent and accurate, so that biostratigraphical or palaeoecological data are meaningful. Although the processing method is often specifically tailored to the sample being analysed and the equipment available, it is important to maintain some constant factors and to quantify the losses experienced. Consistency of processing technique is the most important factor, so that samples can be compared.

Several publications outline techniques used in extracting palynomorphs from rock. These reviews include Funkhouser & Evitt (1959), Gray (1965), Barss & Williams (1973), Forster & Flenley (1989), Litwin & Traverse (1989), and Wood *et al.* (1996). Colbath (1985) is the only author who used Silurian material to compare some of the extraction techniques available.

This chapter focuses on the errors that may be introduced during the extraction of palynomorphs from rock. The palynomorph assemblages from the lower Wenlock of Gotland (Sweden) provide a large number of species and relatively high numbers of palynomorphs per gram of sediment, with a very low thermal alteration and only occasional pyrite growth. These factors mean the material is ideally suited to the testing of processing procedures.

The small size of palynomorphs and the techniques used for their removal from the mineral fraction mean that specimens are likely to be lost or gained (as contamination) during the processing of the samples. Specimens may be lost when the organic residue is separated from the mineral fraction using centrifuge separation with sodium polytungstate or other heavy liquid. Pyrite present in the fossils will increase the mass of the specimens, and the mineral

residue may clump around specimens (individuals with numerous processes may act as debris traps). Specimens may be lost through the sieve when washing the sample (regular tests can monitor any loss). A 7  $\mu\text{m}$  sieve was used because processing at 5  $\mu\text{m}$  is not time-effective. General human errors will also provide a source of loss, as some acritarchs may remain on the surface of equipment through inadequate recovery. Errors may also arise in the recording of data. A sample may gain specimens if it incorporates acritarchs that remain on the surface of equipment from the processing of previous samples.

Pyrite is present in the samples collected from Gotland. The pyrite grains slightly distort the specimens and may disguise some of their diagnostic features, such as plugged processes. This is not usually a problem, however, as the specimens are not totally enveloped in pyrite and can be identified accurately (Pl. 1, figs 1 and 2). The main problem created by pyrite is encountered during the separation process. Separation by heavy liquid depends upon the different densities of the acritarchs and the mineral portion of the sample. Any specimens with an increased mass due to the presence of pyrite (specific gravity 4.95–5.35) are, therefore, more likely to be forced into the lower part of the centrifuge tubes along with the mineral fraction. Even after treatment with nitric acid some specimens (especially those with large cavities such as *Schismatosphaeridium* (Pl. 1, fig. 2)) still contain pyrite grains. This may be due to the grains being protected from the nitric acid by the acritarch vesicle, or possibly insufficient time in the acid, or insufficient acid concentration. The presence of these specimens in the slides shows that a number were not pulled down with the mineral fraction; this may be due to their large relative size compared to their weight. Problems may result from any variations of pyrite content from sample to sample, with more specimens possibly lost in pyrite rich horizons.

The purpose of the processing technique is to provide samples where variations of species abundance and diversity, and numbers of palynomorphs per gram of sediment can be recorded. The processing should reflect these requirements and should aim to give the most accurate representations of the true values. It is important that the processing technique should be such as to minimise any artificial errors or biases in these observations.

## PROCESSING TECHNIQUE

- Wash and scrub the sample to remove lichen, fungi and other recent contaminants.
- Dry the sample in an oven to remove all moisture.
- Crush the sample to pea-sized fragments, using a sterile metal fly-press crusher.
- Weigh sample for processing (40 g) and put in to a polypropylene container with a screw top lid.
- Add HCl (32%) to remove the carbonate minerals, then decant three times to remove Ca and Mg.
- Add HF (40%) to the sample to remove the silicate mineral.
- Once the mineral portion of the sample has broken down, the acids are diluted with water until the sample bottle is full. When the mineral and fossil material has settled to the bottom of the bottle pour off the dilute acid, whilst ensuring no sample is lost. Repeatedly dilute the acid and pour off until the sample is neutralized. This needs to be carried out after each acid stage.
- Separate the sample by centrifuge at 2400 rpm for 14 minutes to remove the water.
- Pour the water off the sample.
- Mix the sample in a 50 ml centrifuge tube with 7% nitric acid to the 30 ml mark and leave for 10 minutes at room temperature to remove the pyrite.
- Concentrate the sample by centrifuging at 2400 rpm for 14 minutes.
- Pour the nitric acid off the sample.
- Mix the sample with sodium polytungstate (S.G. 2.0) to the 30 ml mark on the centrifuge tubes and separate off the organic residue by centrifuging for 14 minutes at 2400 rpm.
- Remove the organic residue from the sample by pipetting or pouring off the topmost sodium polytungstate into a 7  $\mu$ m Nylon square mesh sieve.
- Wash the residue with 1.5 litres of deionised water and pipette into a 5 ml container. Then, from the thoroughly mixed residue remove three portions of 0.05 ml and place onto 22 x 22 mm cover-slips, adding a few drops of cellosize to disperse the palynomorphs.
- Pass the remaining residue through a 53  $\mu$ m sieve to remove the chitinozoans and large acritarchs, and then a 7  $\mu$ m sieve, and mount the 53  $\mu$ m and 7  $\mu$ m residues separately, adding a few drops of cellosize.

- At room temperature slowly evaporate the water from the cover slips to avoid particle clumping.
- Mount the cover-slips onto glass slides using Petropoxy 154. A drop of Petropoxy is placed on the dry cover-slip, which is then overturned, slowly lowered onto the glass slide and heated to 120°C until the Petropoxy has set.
- Thoroughly wash the equipment before and after each use.

## TESTING THE PROCESSING TECHNIQUES

Before the samples can be analysed for numbers of palynomorphs per gram of sediment and species diversity, it is important that the possible sources of error in the processing technique are minimised and quantified. To this end a series of tests was carried out on three samples, DG00LK1.258, 257 and 255.

- To test for the effectiveness in removing acritarchs from the mineral residue at each separation by heavy liquid, and for any species biases in these separations, the sample DG00LK1.258 was separated by centrifuging at 2400 rpm for 14 minutes in sodium polytungstate. The residue was pipetted off and the resulting acritarchs sieved, mounted and logged. This provided a record of the numbers of palynomorphs recovered per gram of sediment after the first separation and the number and type of species that were seen at this stage. To quantify the number of acritarchs not recovered during the first separation, the dense residue at the bottom of the centrifuge tube was again mixed with sodium polytungstate and re-separated. The material removed from the second separation was logged in the same way as the first. This was repeated a further four times.
- To test the impact of the use of nitric acid for the removal of pyrite on the final assemblage composition, the sample DG001.257 was prepared using nitric acid before it was separated by centrifuging. The resulting slides were then logged for numbers of palynomorphs per gram of sediment and number of individuals of each species present. As a control, a further portion of the DG00LK1.257 was then processed using the same technique, but without nitric acid preparation and logged in the same manner. The results for the two samples were compared to quantify the effectiveness of the nitric acid treatment.
- To test the risk of loss of material through the 7 µm sieve, the fraction of sample DG00LK1.255 (along with samples 258 and 257) less than 7 µm was mounted and



analysed. This was carried out by saving the washings from the 7  $\mu\text{m}$  sieve and leaving them to settle in a sample bottle so that the water and sodium polytungstate could be poured off. The remaining material was then mounted onto cover-slips. This enabled the acritarchs penetrating the sieve mesh to be counted and analysed for preferential removal of particular species.

- To test the reliability of the volume method in estimating the number of acritarchs per gram of sediment an alternative method, the *Lycopodium* spores method was analysed. The number of acritarchs per gram of sediment in sample 255 was first calculated by counting the number of acritarchs in 10% of the volume of the total residue of the sample and then calculated up to give the number of acritarchs present in the whole sample, this was then divided by the weight of the sample to give the number of acritarchs per gram of sediment. Secondly a repeat of the same sample was undertaken, but this time a *Lycopodium* spore tablet was added. The *Lycopodium* spore tablets contain a known number of spores. If the number of spores encountered is noted whilst the sample is being logged, it can be used to calculate the number of acritarchs per gram of sediment, using the proportion of acritarchs to spores.
- To test how often recent contaminants occur in a sample and the likelihood of mistakenly identifying them as acritarchs, three slides were prepared using only deionised water. The occurrence, size and morphology of contaminants was noted.

## RESULTS OF REPEAT SEPARATION

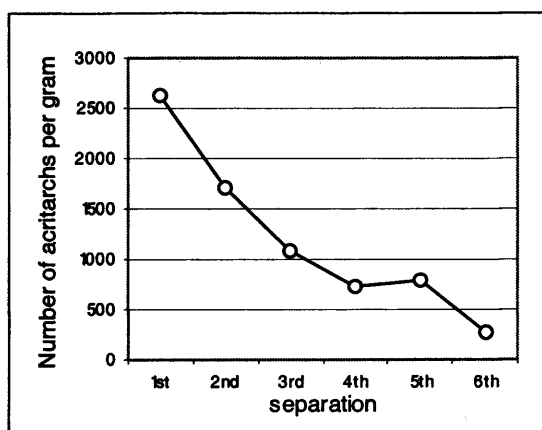
To obtain meaningful results the following questions must be answered: does the apparent diversity of a sample change between repeat separations? Is there a consistent gradual increase in the numbers of acritarchs per gram of sediment calculated, or are there an optimum number of separations after which the change in number of acritarchs per gram of sediment calculated becomes negligible? At first, sample DG00LK1.258 was separated three times, but the results proved inconclusive. To test that a consistent and representative sample was present when three separations had been carried out, it was decided to repeat the test, but mounting the recovered residues for six separations.

The number of acritarchs per gram of sediment was calculated by reducing the volume of the organic residue from a sample of known weight (usually 40 grams) to 5 ml. From this 5 ml three representative 0.05 ml portions were removed after thorough mixing. These 0.05 ml portions were mounted onto glass slides using the methods outlined above and the number of

acritarchs in each was recorded and the average calculated. This average figure, which represents the number of acritarchs in 1% of the sample, was then multiplied by 100 and divided by the weight of the sample to give the number of acritarchs per gram of sediment.

The first separation of sample DG00LK1.258 yielded 2620 acritarchs per gram of sediment, the second 1708, the third 1081, the fourth 733, the fifth 801 and the sixth 264 (fig. 2.1). For separations 1 to 4 there was a drop of around 35% in each separation, the fifth separation has slightly more than the fourth, but the drop resumes in the sixth.

These data suggest that mixing of the mineral residue to release the acritarchs from the mineral is extremely important. After one separation the calculated number of acritarchs per gram is a considerable underestimate of the population in that sample. The cumulative addition of the residues from repeated separations reduces this error. The mixing between separations should re-suspend as much of the mineral matter as possible back into the sodium polytungstate, even though it can be difficult to disperse the lumps of sample.

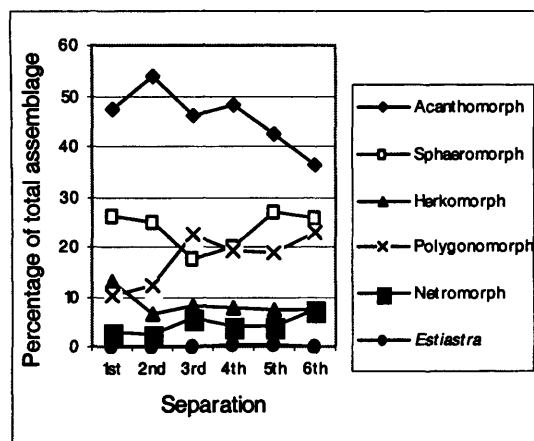


**Text-fig. 2.1,** Total number of palynomorphs per gram of sediment recorded in each separation procedure when carried out 1-6 times, sample DG00LK1.285.

The assemblage seen in sample DG00LK1.258 is dominated by *Micrhystridium stellatum* at an average across the six separations of 24.2%, with 11.38% *Veryhachium trispinosum*, *Leoisphaeridia* (small (<29  $\mu\text{m}$ ) thin walled) at 8.6% and *Diexallophasis gotlandica* at 7.38%.

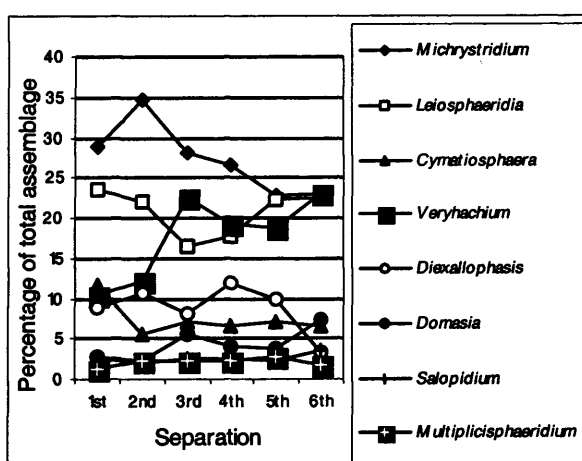
The relative proportion of each acritarch subgroup (subgroups of Downie *et al.* 1963) changes by only a small amount between the first separation and the sixth (fig. 2.2). The variation is greatest in the acanthomorph group, which at its highest makes up 53.9% of the assemblage, in the second separation, falling to a low of 36.3% in the sixth. The sphaeromorph acritarchs

begin and end the test at around 25% of the whole assemblage, but drop to 17.4% and 20.1% at the third and fourth separations respectively. The polygonomorph acritarchs appear to reach a plateau at around 22% of the whole assemblage in the 3<sup>rd</sup> to 6<sup>th</sup> separation, after a rise from 10.4% in the first separation to 12.1% in the second. The herkomorph prasinophytes vary little after their drop from 13.2% to 6.4% from the first to the second separation, and the netromorphs maintain a gradual rise from 2.8% of the assemblage in the first separation to 7.4% in the sixth. The rarer '*Estiastra* subgroup' shows almost no variation.



**Text-fig. 2.2,** Percentage abundance of each acritarch subgroup recorded in each of the six separations, sample DG00LK1.285.

The relative frequencies of genera (fig. 2.3) have also been plotted, ignoring those taxa which fall below 2% of the total assemblage. The < 2% data plot as noise and patterns are difficult to distinguish.



**Text-fig. 2.3,** Percentage abundance of each acritarch genus recorded in each of the six separations, sample DG00LK1.285.

The relative frequencies of *Micrhystridium*, *Leiosphaeridia* and *Veryhachium* show very similar plots to those seen for the acanthomorphs, the sphaeromorphs and the polygonomorphs respectively. This is not surprising as they are the dominant genera in these subgroups. However, *Diexallophasis* appears to maintain a near constant percentage abundance until it falls from 9.8% in the fifth separation to 3.4% in the sixth. *Cymatiosphaera* maintains a level of around 7% of the assemblage, after a fall from 11.6% recorded in the first separation. *Domasia*, *Salopidium*, and *Multiplicisphaeridium* vary little from separation to separation, with *Domasia* only rising from 2.8% to 3.4% and *Salopidium* and *Multiplicisphaeridium* maintaining a percentage of around 2.6%.

Very few species present in the population are not represented in the first three fractions (six very rare species recorded in this test). The main drawback of the heavy liquid separation procedure is that all the acritarchs in the sample are not removed by the third separation. A more accurate representation of numbers of acritarchs per gram of sediment would be achieved if the separations 1-6 were put together, but this increase in accuracy does not justify the extra time needed to complete six separations. The rarer species found when the sample was separated six times rather than three are also probably not significant enough to justify the extra time involved.

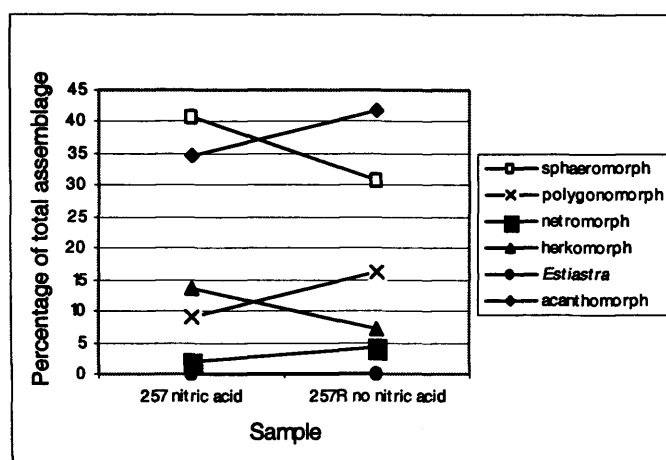
The recovery of acritarchs does not seem to be affected by any clumping of mineral matter around spinose genera, as the acanthomorph subgroup (fig. 2.2) actually shows a decrease in percentage removal as more separations are carried out and not an increase, which might be expected if they were mostly held in the mineral fraction during the initial separations.

## RESULTS FROM NITRIC ACID TESTING

Sample DG00LK1.257 was treated with 7% nitric acid for ten minutes. Only 7% nitric acid was used to prevent the sample from being unnecessarily over-oxidized. A repeat sample of DG00LK1.257 was processed in an identical way, but without the nitric acid treatment. It is essential the sample is thoroughly mixed with the nitric acid as lumps of mineral clustered around any palynomorphs may protect the pyrite from attack. Samples not mixed properly may expose fewer pyrite grains to digestion and yield fewer palynomorphs. It is estimated that treatment with 7% nitric acid removed 30-40% of the observed pyrite.

The sample treated with nitric acid yielded 4442 acritarchs per gram of sediment and the repeat sample (that had not undergone treatment with nitric acid) yielded 5325 acritarchs per gram of sediment. The yield of acritarchs in the sample treated with nitric acid is lower. The difference may be due to the nitric acid destroying or fragmenting the palynomorphs that contain pyrite while the pyrite is being digested. If the acritarch contains a split allowing the nitric acid to flow inside the vesicle, the reaction of the nitric acid with the pyrite may be violent enough to break up the vesicle. When calculating numbers of acritarchs per gram of sediment, specimens were only counted if more than half of the individual is preserved. Incomplete specimens, broken up by the reaction between nitric acid and pyrite, would therefore not increase the number of palynomorphs per gram of sediment calculated and could possibly decrease it if the broken specimens form fragments that are all less than half the original size.

If treatment with nitric acid has no effect, the acritarch subgroups should have a near identical percentage abundance in both the treated and un-treated samples. This is not the case, with the sphaeromorphs reducing in frequency from 40.9% to 30.8% and the herkomorphs reducing from 13.7% to 7.0% between the sample treated with nitric acid and the sample not treated with nitric acid (fig. 2.4). In contrast, the percentage abundance of acanthomorphs increases from 34.5% to 41.8% between the sample treated with nitric acid and the sample not treated with nitric acid, the polygonomorphs increase from 9.1% to 16.1% and the netromorphs from 2.1% to 4.4%. These differences may be due to natural variability, or to the destruction of some individuals in some subgroups by nitric acid. It is important to emphasise that the increase in the percentage abundance of acanthomorphs, polygonomorphs and netromorphs in the sample not treated with nitric acid may just be a reflection of the relative decrease in the number of sphaeromorphs and herkomorphs extracted.



**Text-fig. 2.4,** Percentage abundance of each acritarch subgroup recorded in sample DG00LK1.257 when the sample was treated with nitric acid and when nitric acid was not used during processing.

To investigate preferential pyrite growth in specific morphologies, the percentage of individuals containing pyrite in each subgroup was recorded after three separations of sample DG00LK1.258. The sphaeromorphs and the acanthomorphs contained the most pyrite, with 32.9% and 32.2% of the specimens showing its presence, 19.3% of the herkomorphs, 14.4% of the polygonomorphs and 1.2% of the '*Estiastra* subgroup' contained pyrite grains.

## RESULTS OF 7 $\mu$ m SIEVE TEST

The < 7  $\mu$ m fractions from samples DG00LK1.258, 257 and 255 were logged after three separations. Sample DG00LK1.258 yielded 30 acritarchs (0.7 < 7  $\mu$ m acritarchs per gram of sediment), of which 29 were *Leiosphaeridia* spp., with one *Veryhachium wenlockium*. DG00LK1.257 yielded 33 acritarchs (0.8 < 7  $\mu$ m acritarchs per gram of sediment), of which 24 were *Leiosphaeridia* spp., the remainder consisting of *Domasia trispinosa*, *Veryhachium trispinosum*, *Diexallophasis gotlandica*, *Micrhystridium stellatum* and *Cymatiosphaera* aff. *ledburica*. DG00LK1.255 yielded 23 acritarchs (0.6 < 7  $\mu$ m acritarchs per gram of sediment), of which 12 were *Leiosphaeridia* spp., 5 were *Veryhachium wenlockium*, 3 were *Micrhystridium stellatum*, 2 were *Domasia trispinosa* and one was *Micrhystridium irevikensis*.

No species were identified that had not been recorded in the > 7  $\mu$ m fraction, indicating that the lost data have little influence on the final diversity results, and the loss in numbers of acritarchs is minimal. The acritarchs recorded are species that tend to be small and their size

range would be likely to include specimens smaller than 7  $\mu\text{m}$ . DG00LK1.257 included specimens of *Diexallophasis gotlandica* and *Cymatiosphaera* aff. *ledburica* which are larger than 7  $\mu\text{m}$ ; this is probably a result of contamination from the > 7  $\mu\text{m}$  fraction, or even from another sample.

## RESULTS FROM *LYCOPodium* SPORE NUMBERS PER GRAM OF SEDIMENT TEST

The number of acritarchs per gram calculated using the volume method was 11243 and the number of acritarchs per gram calculated using the *Lycopodium* spore method was 22160. Nearly double value of calculated number of acritarchs per gram of sediment in the *Lycopodium* spore sample indicates the methods are not comparable. This is probably partially due to the low amount of *Lycopodium* spores counted. If more tablets had been added the numbers per gram would have been more accurate. It is impossible to say which of the two methods is nearest the true value as no control is available.

## RESULTS FROM THE MODERN CONTAMINANTS IN DEIONISED WATER TEST

The deionised water slides contain very sparse debris (Pl. 1, figs 3–5). It is usually in the form of amorphous organic fragments (Pl. 1, fig. 4), which are clearly distinguishable from the Silurian palynomorphs recovered in this project. The main problems may occur if any of these fragments obscure specimens. Plate 1, figs 3 and 5 show debris that superficially resembles *Baltisphaeridium* type Silurian acritarchs. On closer inspection, these specimens show no real spherical vesicle and they are several times larger than most Silurian acritarchs.

## DISCUSSION

The results from the repeat separation test show that the relative frequency of genera in the assemblages stabilises by the third separation. The variation seen in the fourth, fifth and sixth separations is probably due to low numbers remaining after the first three separations. A number of acritarchs do seem to remain after the third separation, but this does not appear to have an effect on the number of species recorded from a sample. The total number of acritarchs per gram of sediment is affected by factors such as sedimentation rate, preservation potential and current activity, as well as phytoplankton abundance. The difficulty in obtaining any extra meaningful interpretations from the sample that was separated six times, suggests it is not time effective to spend overly long periods obtaining and recording data. It can be

concluded that carrying out three separations provides a sufficiently representative assemblage and further separations do not significantly add to the accuracy and value of results.

Treatment with nitric acid caused a decrease in the number of acritarchs recovered per gram of sediment. The results show that herkomorph and sphaeromorph acritarchs are recovered more successfully when the sample is treated with nitric acid. The data suggest that acanthomorph and polygonomorph acritarchs are recovered more successfully if the sample is not treated with nitric acid, but this may well fall within the statistical limits of natural variation. The acanthomorph acritarchs show a fairly high occurrence of pyrite growth, suggesting that nitric acid reacting with the pyrite may have a detrimental effect on the occurrence of this subgroup. The polygonomorph acritarchs, which have a low occurrence of pyrite growth, show a decreased yield when treated with nitric acid.

From this test it can be concluded that treatment with nitric acid probably had little detrimental influence on the acritarchs recorded in sample DG00LK1.257. This may be due to the relatively low amount of pyrite present. The real influence of pyrite presence and nitric acid treatment on the recovery of palynomorphs should ideally be tested on many samples of various types and should involve precise quantification of the pyrite present. It is suggested that to reduce problems associated with pyrite, nitric acid treatment should be routinely adopted in sample processing. This will make the species diversity and numbers of acritarchs per gram of sediment of pyrite rich and pyrite poor samples more comparable. The degree of possible destruction of acritarchs during the growth of pyrite grains larger than the specimens cannot be calculated and must be considered as a factor when analysing pyrite rich horizons.

The  $< 7 \mu\text{m}$  sieve test data indicate that the loss of acritarchs during washing of the sample through a  $7 \mu\text{m}$  sieve is minimal and can be considered as a minor factor, that can be monitored by regular testing.

In the absence of a control, it is very difficult to compare the *Lycopodium* spore method and the volume method in calculating the most accurate number of acritarchs per gram of sediment.



The use of *Lycopodium* spores has the advantage of greater speed in processing and logging. Fewer slides have to be prepared and any volume can be used for mounting on a cover slip (avoiding having to reduce the residue down to 5ml). Only one slide needs to be logged, as opposed to three slides in the volume method and then the diversity logged separately. The inaccuracy of the volume method (variations in the number of acritarchs removed in the numbers per gram fractions) is avoided.

However the values generated by the counting of *Lycopodium* spores have numerous inconsistencies, which render them inferior. The number of *Lycopodium* spores in a single tablet is innately inaccurate. The introduction of the spores to the sample adds an extra variable to the processing technique. This may change the dynamics of the sample during processes such as the settling of material through the water in the sample bottle and the digestion in acid. If samples are particularly sparse in palynomorphs large numbers of *Lycopodium* spores would need to be counted for each acritarch encountered. Finally *Lycopodium* spores are less widely used during counting, introducing unnecessary inconsistencies when comparing data with those of other workers. If time permitted, further tests would be carried out with repeat sampling for greater numbers of tablets, to test where the threshold of consistency for numbers per gram is achieved. Then a more realistic comparison to the volume method could be made.

The volume method is by no means perfect, but it is thought that the variables encountered during the *Lycopodium* spore numbers per gram method are greater than those encountered during the volume method. Consistency of processing technique is the most important factor.

## CONCLUSIONS

Two important points that emerged from Colbath's (1985) investigations still remain: consistency of technique and the trade-off between the accuracy of results and the time incurred in obtaining them. 100% repeatability of results is unlikely to be achieved; repeat sampling of modern biological communities gives a certain percentage of random variation (Watkins *et al.* 1990, Muylaert *et al.* 2000). Population variability and errors associated with repeat sampling, such as differential preservation and uneven distribution of palynomorphs within the rock sample mean that repeatability is never perfect. Variations in apparent diversity may result from the recording of species represented by very few individuals, which may be seen in one sample, but not the next. Consistency in the processing technique reduces

errors as much as possible and the accuracy of estimates of the number of palynomorphs per gram of sediment and of the number of species present are very important. It is very unlikely every acritarch can be extracted from a rock sample. Even if every acritarch could be extracted, the time incurred in recording all the individuals could not be justified for the increase in the accuracy of the results. Three separations, nitric acid treatment and well monitored sieving, provide a justifiable compromise between the time spent processing and the precision of the results. A similar conclusion may apply to other palynological assemblages.

This study has suggested that the losses incurred at various stages in the processing technique are significant, but can be reduced and quantified. Although palynological samples from different localities and time periods will yield different numbers of palynomorphs per gram of sediment and different species, tests should be carried out as appropriate to quantify the loss of data.

### **Logging technique**

Firstly, 250 specimens were counted from a representative portion of the sample. A rarefaction curve of number of species against number of specimens was then plotted. If a plateau had not been reached at this stage, the count continued until this was achieved. At this point, the percent abundance of each species was calculated. The species were then ranked in order of frequency. Starting with the most common species, the cumulative percent abundance was calculated until approximately 45% of the total assemblage was reached. This enabled the most common taxa to be identified. The remainder of the sample continued to be logged, but the common species were no longer recorded, until a count of 1000 specimens (including the predicted values) was reached.

### **Photographic technique**

Palynomorphs recovered from samples collected in stable cratonic areas have often undergone little thermal alteration (TAI 1.5 (Traverse, 1988)). This is of benefit to the taxonomist as fragile diagnostic characters are often well preserved. Unfortunately, when the specimens are photographed under a light microscope they often contrast poorly with their backgrounds.

The palynomorphs recovered from the lower Silurian of Gotland typify these problems; they show excellent preservation of fine detail, but have a very low contrast to the background under light microscopy. To increase this contrast a new technique has been developed whereby a portion of the residue is heated to increase the thermal alteration. This enables the specimens to be more easily identified on photographs, whilst not overheating and damaging the palynomorphs. Staining with safranin or other dyes can give variable results, with some specimens absorbing the stain whilst others remain unaffected.

Samples were processed using standard palynological processing techniques (Gelsthorpe 2002), logged and the number of palynomorphs per gram of sediment recorded. Part of the remaining residue was then mixed with two drops of cellosize to disperse the specimens (high concentrations of cellosize readily burns, obscuring the specimens). This mixture was then evenly spread over the required number of coverslips and left to evaporate at room temperature. Once evaporated, the cover slips were heated to 200°C on a hotplate for 30 minutes. To achieve this temperature it was usually necessary to cover the cover slips to insulate them from room temperature (a household baking tray was found to be adequate). Once the cover slips had cooled they were mounted and labelled in the normal way. Examples of specimens of the same taxa heated and unheated, are illustrated in Plate 1, figs 6–9.

It could be argued that once the samples have been artificially heated they are so altered that it is inappropriate to compare them to unheated samples or samples from other localities. This may be the case, but as long as the samples are prepared and logged in the normal way prior to heating (as is suggested here), these problems are avoided. Scanning electron micrographs showing highly detailed high contrast photographs are commonly used in palynological publications, but a method of high quality light microscope photography is still necessary. Light microscopes are routinely used for logging samples and some diagnostic features such as wall thickness and plugged processes can only be identified under transmitted light.

Many of the palynomorphs illustrated herein have not undergone the treatment outlined above, as they are so rare that specimens have not been relocated on treated residues. Those that have undergone heating are identified by the initials 'ckd' in the sample name.

*Acritarch and Prasinophyte algal classification*

The informal group Acritarcha Evitt (1963) comprises organic walled, unicellular microfossils of 'unknown and probably varied biological affinities' (Evitt 1963). Many acritarchs are probably algal (Downie 1973, Martin 1993, Colbath and Grenfell 1995, Servais *et al.* 1996). There is a large variation in size and morphology between genera. Silurian acritarchs range in size from *Michrystridium stellatum* Deflandre, 1945 at 10µm across, to *Pulvinosphaeridium pulvinellum* Eisenack, 1954 at 170µm (Plate 2, figs 1–2). Most acritarchs and prasinophyte algae have a spherical to subspherical vesicle (Plate 2, fig. 3) with or without ornament on the surface (Plate 2, fig. 4), some possess membranes perpendicular to the surface (some of the prasinophyte algae) (Plate 2, fig. 5) and some possess simple or branched processes (Plate 2, figs 6–7). Vesicle shape varies from spherical, to fusiform, to triangular (Plate 2, figs 3, 8–9). The wide variation in acritarch and prasinophyte algal morphology and size is a constant problem when trying to identify interspecific and intraspecific characters.

It has been suggested by Pirozynski (1976) that Palaeozoic acritarchs may be related to spores of oomycete fungi. The possibility of a fungal origin has been given little attention in the literature, but Colbath and Grenfell (1995) suggested the present morphological and chemical evidence implies that acritarchs are not fungal. Dorning (1981a) suggested that because of the association of some of the large acritarch genera (*Hogklintia*, *Estiastra* and *Pulvinosphaeridium*) with carbonate reef complexes, these particular taxa may be benthic thallose macroalgae. This was disputed by Colbath and Grenfell (1995) as these forms bear little resemblance to modern macroalgae. The discovery of triaromatic dinosteroids in Precambrian to Cenozoic rocks by Moldowan *et al.* (1996) suggests that some acritarchs probably belong to the same clade as dinoflagellates. A specific set of sterol chemicals (including dinosteroids) are associated almost exclusively with dinoflagellates. The good correlation between the presence of dinosteroids and the relatively high abundance of dinoflagellates and acritarchs in the fossil record forms the basis of the theory that they share a common origin (Moldowan *et al.* 1996, fig. 2c).

Prasinophyta algae are classified as green algae (modified by Colbath and Grenfell 1995 from Tappan 1980), for which there is a much greater biological understanding than for the acritarchs. Many prasinophytes have a distinct flange or flanges, which is equatorial or

together forms a hexagonal pattern. Prasinophyta have many morphological similarities to the genus *Leiosphaeridia* Eisenack, 1958a (a genus which is probably polyphyletic), some forms of which may be included in the prasinophytes. Without further work, *Leiosphaeridia* affinities are disputable (Colbath and Grenfell 1995).

Acritarchs and prasinophyte algae are treated under the International Code of Botanical Nomenclature (Deflandre 1936, Downie *et al.* 1961, 1963). Herein, acritarch genera are listed in alphabetical order in accordance with generally accepted principles, so that inferences introduced by artificial classifications (e.g. Downie *et al.* 1963, 1973) are avoided.

Given the present level of understanding of acritarch classification, Colbath and Grenfell (1995, pp. 307) have suggested the Linnaean system is inappropriate. In an attempt to stabilize the informal subgroupings of acritarchs they have put forward three acritarch clades (*Baltisphaeridium* Eisenack, 1958b, *Peteinosphaeridium* Staplin *et al.*, 1965, and *Cymbosphaeridium* Lister, 1970), which are defined on features such as wall and process structure and excystment mechanism. Colbath and Grenfell (1995, pp. 310) concluded that acritarchs which excyst utilizing a cryptopylome resemble dinocysts, but that they are sufficiently different to be grouped separately, as that they do not possess a paracingulum or paratabulation.

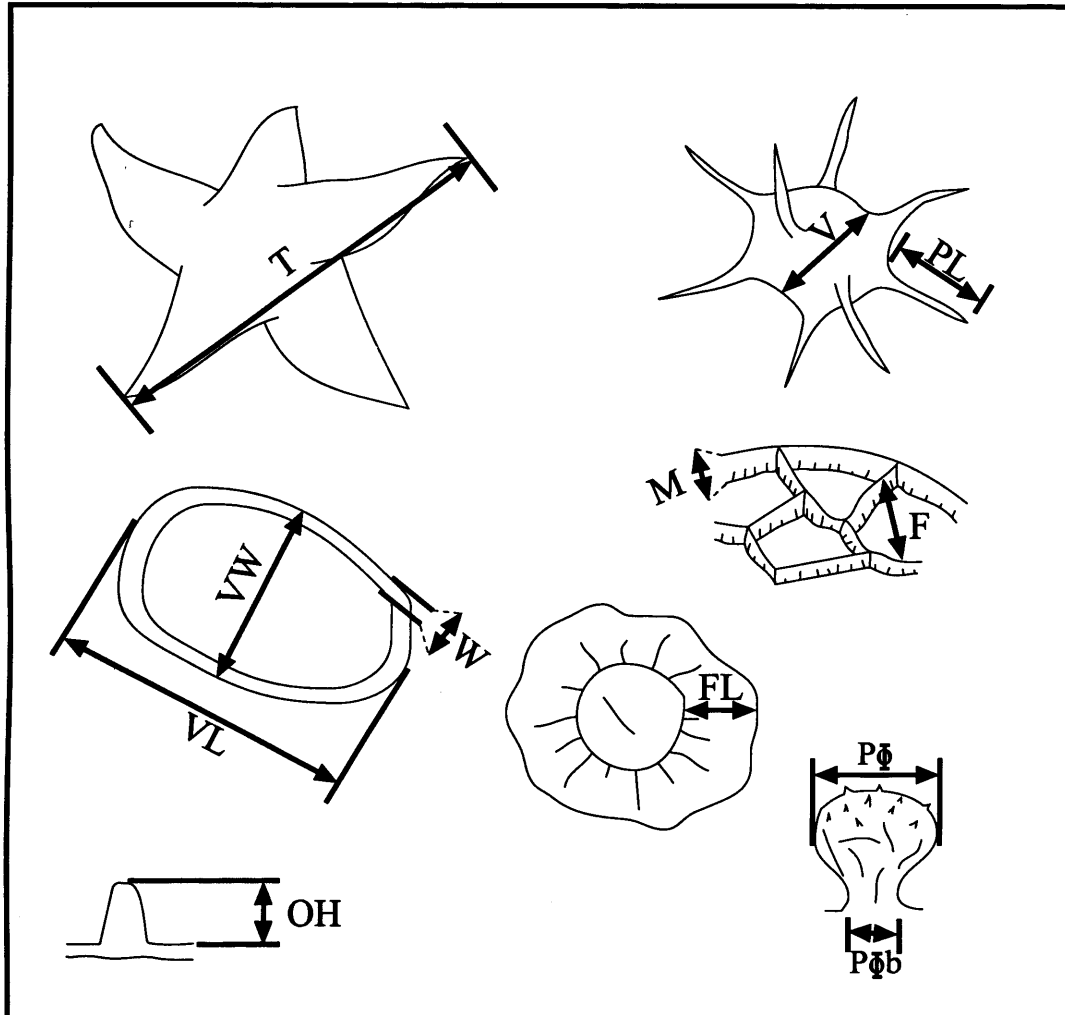
## SYSTEMATIC PALAEOONTOLOGY

### *Terminology*

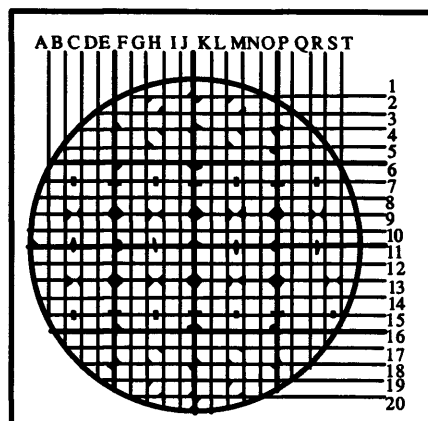
Details of the measurements referred to below are given in Text-fig. 3.1. Further glossaries of terms can be found in Lister (1970, pp. 24–26) and Williams *et al.* (1978). The excystment openings observed in Palaeozoic acritarchs have been described and illustrated by Colbath and Grenfell (1995, p. 306, pl. 18).

### *Plate explanations*

Samples are labelled as follows: eg. DG00LK1.100npg1 (DG, the initials of the author; 00, samples were collected in the year 2000; LK1, locality Luskint 1, or alternatively LH2, locality Lickersham 2; 100, the sample number; npg1, sample containing 10% of the residue and suitable for calculating the number of palynomorphs per gram of sediment). The location of individual specimens on a slide is given as an England Finder reference. The location of specimens photographed using the scanning electron microscope is recorded using the grid system shown in Text-fig. 3.2.



TEXT-FIG. 3.1. Examples of the positions of the measurements referred to in Chapter 3 (systematics).  $T$  = total length/diameter;  $VL$  = vesicle length;  $VW$  = vesicle width;  $V$  = vesicle diameter;  $PL$  = process length;  $P\Phi b$  = basal process diameter;  $P\Phi$  = process diameter;  $PN$  = process number;  $M$  = membrane height;  $F$  = field width;  $FL$  = flange width;  $W$  = wall thickness;  $OH$  = ornament height. (After Mullins 1996).



TEXT-FIG. 3.2. Diagram showing the grid and grid reference code used in locating palynomorphs under the SEM.

### *Synonymy lists*

Details of the authors who originally proposed the synonymies that are not explained herein can be found in Fensome *et al.* (1990). The annotations used in the synonymy list are those of Matthews (1973).

### *Repository*

Specimens illustrated herein are deposited in the British Geological Survey, Keyworth, Nottingham, UK.

### *Systematic descriptions*

A list of every species recorded in this study is provided below (illustrations can be found in plates 3–19). A full systematic palaeontology is provided for all new species.

### *Annotated species list*

#### **PRASINOPHYCEAE Christensen, 1962**

*Cymatiosphaera heloderma* Cramer and Díez, 1972b. Pl. 3, figs 10–11.

Description of Cramer and Díez (1972, p. 158, pl. 32, fig. 22, pl. 34, fig. 46) used.

*Cymatiosphaera* aff. *ledburica* Dorning, 1981. Pl. 3, figs 1–2, 12–13.

Description of Dorning (1981, p. 185, pl. 2, figs. 13–14) used. The specimens illustrated here conform with the written description given by Dorning (1981), but examination of the holotype has revealed a raised circular structure on the vesicle in the centre of each field. The specimens illustrated here are not designated a new species, because in most respects they are identical to the *C. ledburica* holotype.

*Cymatiosphaera octoplana* Downie, 1959. Pl. 3, figs 3–5, 9.

Description of Downie (1959, p. 63, pl. 11, figs 4–7, 8–11) used. This species was emended by Mullins (2001) to include *C. prismatica* Deunff, 1954 and thus encompasses specimens such as that illustrated in Pl. 3 fig. 6.

*Cymatiosphaera* sp. B of Le Hérisse, 1989. Pl. 3, figs 7–8.

Description of Le Hérisse (1989, pp. 77–78, pl. 1, figs 21–24) used. It is considered that too few specimens have been recorded in this study to erect a species name.

*Dictyotidium alveolatum* (Kiryanov, 1978) Le Hérisse, 1989. Pl. 4, figs 1–2.

Description of Le Hérisse (1989, p. 107, pl. 3, figs 1–2, 4–5) used.

*Dictyotidium dictyotum* (Eisenack, 1938) Eisenack, 1955. Pl. 4, figs 4–5.

Description of Eisenack (1938, p. 27–28, pl. 3, figs 8a–c) used. Eisenack (1955, p.179) noted that the original holotype has been lost, but did not designate a neotype. Mullins (2001, p.41) suggested that the specimen illustrated by Le Hérisse (1989, pl. 3, fig. 12) should be designated as the neotype.

*Dictyotidium faviforme* Schultz, 1967. Pl. 4, figs 7–8.

Description of Schultz (1967, p. 183, pl. 1, fig. 16) used.

*Dictyotidium perlucidum* Le Hérisse, 1989. Pl. 4, fig. 6.

Description of Le Hérisse (1989, p. 110, pl. 3, figs 10,11) used.

*Dictyotidium stenodictyum* Eisenack, 1965. Pl. 4, fig. 10.

Description of Eisenack (1965, pp. 264–265, pl. 2, figs. 2–3) used.

*Duvernaysphaera aranaides* (Cramer, 1964) Cramer and Díez, 1972b. Pl. 3, figs 14–15.

Description of Cramer (1964, pp. 329–330, pl. 14, fig. 7, as *Helios*) used.

*Pterospermella foveolata* Dorning, 1981. Pl. 5, figs 1–3.

Description of Dorning (1981, p. 197, pl. 3, fig. 18) used. No comparison between *P. foveolata* and *P. martinii* has been made in the literature. It is considered herein that they are very similar, but *P. foveolata* has a granulate vesicle (as mentioned by Dorning, 1981, p. 197) and *P. martinii* has a smooth vesicle (the holotype needs further investigation to confirm this).



*Pterospermella martinii* Cramer, 1966a. Pl. 5, figs 4–6.

Description of Cramer (1966a, p. 250, pl. 1, fig. 9, text-fig. 4, no. 4) used.

*Pterospermella marysae* Le Hérissé, 1989. Pl. 5, figs 7–8.

Description of Le Hérissé (1989, p. 79, pl. 5, figs. 1–5) used.

*Pterospermella saturniforme* sp. nov. Pl. 19, figs 8–9, Text-fig. 3.2 G–H.

New species, see full description below.

*Quadraditum fantasticum* Cramer, 1964b. Pl. 4, figs 11–12.

Description of Cramer (1964b, p. 334, pl. 14, figs. 3–4) used.

*Tasmanites* Newton, 1875. Pl. 4, fig. 15.

Diagnosis of Newton (1875, p. 341) used.

### **ACRITARCHA Evitt, 1963**

*Ammonidium microcladum* (Downie, 1963) Lister, 1970. Pl. 4, figs 13–14.

Description of Downie (1963, p. 645, pl. 91, fig. 6, text-fig. 3g, as *Baltisphaeridium*) used.

*Buedingiisphaeridium? globulosum* sp. nov. Pl. 19, figs 10–11, Text-fig. 3.2 I–J.

New species, see full description below.

*Buedingiisphaeridium? aff. globulosum* sp. nov. Pl. 19, fig. 11.

A taxon similar to *B? globulosum* sp. nov., but with more numerous processes and a slightly larger vesicle (45µm).

*Deunffia brevifurcata* Hill, 1974. Pl. 5, fig. 9.

Description of Hill (1974, p. 16, pl. 1, figs 5–9) used.

*Deunffia monospinosa* Downie, 1960. Pl. 5, fig. 12.

Description of Downie (1960, p. 198, pl. 1, fig. 8) used.

*Deunffia ramusculosa* Downie, 1960. Pl. 6, figs 1–2.

Description of Downie (1960, p. 199, pl. 1, fig. 2) used.

*Diexallophasis denticulata wolynica* Kiryanov, 1978. Pl. 6, fig. 5.

Description of Le Hérissé (1989, p. 128, pl. 12, figs 1–2 as *Evittia*) used.

*Diexallophasis gotlandica* Cramer, 1970. Pl. 6, figs 3–4.

Description of Cramer (1970, pp. 138–140, pl. 10, fig. 151 and pl. 20, fig. 302, text-fig 43b) used. The description of *D. ontariensis* Cramer by Cramer (1970, p. 140, pl. 10, figs 152–153, 157–158, text-fig. 43c) is extremely similar to that of *D. gotlandica*; the two species are probably the same and have not been differentiated in this study.

*Diexallophasis granulatispinosa* (Downie, 1963) Hill, 1974. Pl. 6, figs 6–7.

Description of Downie (1963, pp. 640–641, pl. 91, fig. 1,7, as *Baltisphaeridium*) used.

*Diexallophasis remota* (Deunff, 1955) Playford, 1977. Pl. 5, figs 10–11.

Description of Playford (1977, p. 19–21) used.

*Dilatisphaera laevigata* Lister, 1970. Pl. 6, figs 8–10.

Description of Lister (1970, p. 66, pl. 6, figs 10–12, text-figs 18h, 20d) used.

*Dilatisphaera williereae* (Martin, 1966) Lister, 1970. Pl. 7, figs 1–2.

Description of Martin (1966, p. 389–390, pl. 1. fig. 23, text-figs 33–34) used.

*Dilatisphaera quadratica* sp. nov. Pl. 19, figs 1–3, Text-fig. 3.2 A–B.

New species, see full description below.

*Domasia amphora* (Martin, 1969) emend. Hill, 1974. Pl. 7, fig. 3.

Description of Le Hérissé (1989, p. 99, pl. 8, figs 11–13) used.

*Domasia bispinosa* Downie, 1960. Pl. 7, figs 4.

Description of Downie (1960, p. 200, pl. 1, fig. 3) used.

*Domasia quadrispinosa* Hill, 1974. Pl. 7, figs 5–6.

Description of Hill (1974, p. 18, pl. 1, figs 12–15) used.

*Domasia trispinosa* (Downie, 1960) Hill, 1974. Pl. 7, figs 7–8.

Description of Downie (1960, p. 199–200, pl. 1, fig. 7) used

*Eisenackidium ranaemanum* Le Hérissé, 1989. Pl. 7, fig. 9.

Description of Le Hérissé (1989, p. 120, pl. 9, figs 9–13) used.

*Elektoriskos aurora* Loeblich, 1970. Pl. 7, figs 11–12.

Description of Loeblich (1970, p. 717–718, fig. 12 A–D) used.

*Eupoikilofusa filifera* (Downie, 1959) Dorning, 1981 emend. Pl. 7, fig. 13.

Description of Mullins (2001, p. 80, pl. 8, fig. 1; pl. 17, fig. 8) used. The specimen illustrated by Mullins has the same morphology as the specimen Le Hérissé assigned to *E. strifiera typica* (an invalid name, see Fensome *et al.* p. 216); see discussion by Mullins (2001).

*Eupoikilofusa striatifera* Cramer, 1964a. Pl. 8, figs 12–13.

Description of Cramer (1964, p. 35–36, pl. 2, figs 9, 13) used.

*Elektoriskos longispinosum* sp. nov. Pl. 19, figs 6–7, Text-fig. 3.2 C–D.

New species, see full description below.

*Gorgonisphaeridium succinum* Lister, 1970. Pl. 8, figs 1–2.

Description of Lister (1970 p. 75, pl. 8, figs 1–4) used.

*Gracilisphaeridium encantador* (Cramer, 1970) *ex* Eisenack *et al.*, 1973. Pl. 8, figs 3–5.

Description of Cramer (1970, pp. 189–190, pl. 19, figs 196–299, as *Baltisphaeridium*) used.

*Helosphaeridium citrinipeltatum* (Cramer and Díez, 1972) Dorning, 1981. Pl. 8, figs 8–9.

Description of Cramer and Díez (1972b, pp. 166–169, pl. 35, figs 58–59, as *Lophosphaeridium*) used.

*Helosphaeridium clavispinulosum* Lister, 1970. Pl. 8, figs 6–7.

Description of Lister (1970, p. 76, pl. 8, figs 8, 12, 16) used.

*Helosphaeridium pseudodictyum* Lister, 1970. Pl. 8, figs 10–11.

Description of Lister (1970, pp. 76–77, pl. 8, figs 9–11, 13–14, 17) used.

*Hoegklingia corallina* (Eisenack, 1959) Dorning, 1981. Pl. 9, fig. 1.

Description of Eisenack (1959, p. 201, pl. 16, figs 15–16, as *Baltisphaeridium corallinum*) used.

*Hoegklintia digitata* (Eisenack, 1938) Dorning, 1981. Pl. 9, figs 2–3.

Description of Eisenack (1938 pp. 20–22, pl. 4, figs 3–5, as *Hystriosphæridium*) used.

*Hoegklintia visbyensis* (Eisenack, 1959) Dorning, 1981. Pl. 9, fig. 4.

Description of Eisenack (1959, pp. 200–201, pl. 16, figs 12–14, as *Baltisphaeridium*) used.

*Leiofusa parvitatilis* Loeblich, 1970. Pl. 9, figs 5–6.

Description of Le Hérisse (1989, p. 151, pl. 16, fig. 1) used.

*Leiofusa* cf. *banderillae* Cramer, 1964b. Pl. 9, figs 7–8.

The specimens illustrated here are similar to the holotype, but show a more elongate (yet still inflated) vesicle than the rounded vesicle illustrated by Cramer (1964b, p. 36, figs 4–5, 12). A similar form to that found in this study was illustrated by Le Hérisse (1989, pl. 16 fig. 2).

*Leiosphaeridia* (Eisenack, 1958b) Downie and Sarjeant, 1963 emend. Turner, 1984. Pl. 10, figs 1–4.

Description of Turner (1984, p. 116) used. In this study the genus was split into four categories: large (>29µm) with thick walls, large (>29µm) with thin walls, small (≤29µm) with thick walls, and small (≤29µm) with thin walls. These arbitrary splits are not intended to imply that these morphological categories accord with species diagnoses.

*Leprotolypa gordonense* Cramer, 1963. Pl. 10, fig. 5.

Description of Le Hérisse (1989, p. 154, pl. 18, fig. 16) used.

*Micrhystridium eatonense* Downie, 1959. Pl. 10, figs 6–7.

Description of Downie (1959, p. 62, pl. 11, fig. 15) used.

*Micrhystridium irevikensis* Le Hérisse, 1989. Pl. 10, figs 8–9.

Description of Le Hérisse (1989, p. 157, pl. 18, figs 3–5) used.

*Micrhystridium stellatum* Deflandre, 1945. Pl. 10, fig. 10.

Description of Deflandre (1945, p. 27, pl. 3, figs 16–19) used.

*Micrhystridium* sp. A. Pl. 19, figs 4–5, Text–fig. 3.2 E–F.

New species, see full description below.

*Moyeria uticaensis* Thusu, 1973. Pl.7, fig. 10.

Description of Thusu (1973, p. 142, pl. 2, figs 18–22) used.

*Multiplicisphaeridium arbusculum* Dorning, 1981. Pl. 10, figs 11–12.

Description of Dorning (1981, p. 194–195, pl. 1, fig. 7) used.

*Multiplicisphaeridium cladum* (Downie, 1963) Eisenack, 1969. Pl. 10, figs 13–14.

Description of Downie (1963, pp. 643–644, pl. 92, fig. 5, Text–fig. 3a, as *Baltisphaeridium*) used.

*Multiplicisphaeridium fisheri* (Cramer, 1968) Lister, 1970. Pl. 11, fig. 1.

Description of Cramer (1968a, p. 65, pl. 1, fig. 1, as *Baltisphaeridium*) used.

*Multiplicisphaeridium forquiferum* (Cramer and Díez, 1972) Eisenack *et al.*, 1973. Pl. 10, figs 15–16.

Description of Cramer and Díez (1972b, p. 151, pl. 32, fig. 20, as *Baltisphaeridium*) used.

*Multiplicisphaeridium forquillum* (Cramer and Díez, 1972b) Eisenack *et al.*, 1973. Pl. 11, figs 4–5.

Description of Cramer and Díez (1972b, p. 152, pl. 32, fig. 15, as *Baltisphaeridium*) used.

*Multiplicisphaeridium minguisi* Le Hérisse, 1989. Pl. 11, figs 2–3.

Description of Le Hérisse (1989, p. 161–162, pl. 19, figs 6–8, 16) used.

*Multiplicisphaeridium monki* Le Hérisse, 1989. Pl. 11, fig. 6.

Description of Le Hérisse (1989, p. 162, pl. 19, figs 9–11) used.

*Multiplicisphaeridium neaghae* Cramer, 1970 *ex* Eisenack *et al.*, 1973. Pl. 11, fig. 7.

Description of Cramer (1970, pp. 134, p. 9, figs 139–142, 391) used.

*Multiplicisphaeridium osgoodense* (Cramer and Díez, 1972) Eisenack *et al.*, 1973. Pl. 11, fig. 8.

Description of Cramer and Díez (1972, p. 153, pl. 33, fig. 26, as *Baltisphaeridium*) used.

*Multiplicisphaeridium rochesterense* (Cramer and Díez, 1972) Eisenack *et al.*, 1973. Pl. 11, fig. 9.

Description of Cramer and Díez (1972b, p. 157, pl. 34, fig. 45, pl. 35, fig. 60, as *Baltisphaeridium*) used.

*Multiplicisphaeridium variabile* (Lister, 1970) Dorning, 1981. Pl. 12, figs 1–2.

Description of Lister (1970, pp. 87–88, pl. 11, figs 4–7, 9–10, as *Multiplicisphaeridium arbusculiferum* var. *variabile*) used.

*Multiplicisphaeridium* cf. *variabile* (Lister, 1970) Dorning, 1981. Pl. 12, fig. 3.

This taxon, which is similar to *M. variabile*, has fewer branched processes (often up to half are simple) and a more consistent, although still variable, branching pattern.

*Onondagella asymmetrica* (Deunff, 1954 *ex* Deunff, 1961) Cramer 1966b, emend. Playford, 1977. Pl. 12, fig. 4.

Description of Le Hérisse (1989, p. 168, pl. 20, figs 3–4.) used.

*Oppilatala ferrosa* (Cramer, 1970) Le Hérisse, 1989. Pl. 12, figs 5–6.

Description of Le Hérisse (1989, p. 171, pl. 23, figs 10–13, Text-fig. 14.8) used.

*Oppilatala grahni* Le Hérisse, 1989. Pl. 13, fig. 1.

Description of Le Hérisse (1989 p. 172, pl. 23, figs 1–4, Text-fig. 14.6) used.

*Oppilatala insolita insolita* Cramer and Díez, 1972. Pl. 13, figs 3–4.

Description of Le Hérisse (1989, p. 172–174, pl. 22, figs 7–8, Text-fig. 14.2) used.

*Oppilatala insolita compacta* Le Hérisse, 1989. Pl. 12, figs 7–8.

Description of Le Hérisse (1989, p. 175–176, pl. 22, figs 9–12, Text-fig. 14.3) used.

*Oppilatala juvenis* Le Hérisse, 1989. Pl. 13, fig. 2.

Description of Le Hérisse (1989, p. 176, pl. 23, figs 8–9, 15 Text-fig. 14.9) used.

*Oppilatala ramusculosa* (Deflandre, 1945) Dorning, 1981. Pl. 13, figs 5–6.

Description of Le Hérisse (1989, pp. 177–178, pl. 23, figs 5–7, Text-fig. 14.5) used.

*Oppilatala singularis* Le Hérissé, 1989. Pl. 13, fig. 7.

Description of Le Hérissé (1989, p. 178, pl. 24, figs 1–9, Text-fig. 14:11) used.

*Polygonium* sp. B of Le Hérissé, 1989. Pl. 14, fig. 1.

Description of Le Hérissé (1989, p. 183, pl. 21, figs 12–13) used.

*Pulvinosphaeridium pulvinellum* Eisenack, 1954. Pl. 14, fig. 2.

Description of Eisenack (1954, p. 210, pl. 1, fig. 10) used.

*Salopidium fragelliforme* Le Hérissé, 1989. Pl. 14, fig. 3.

Description of Le Hérissé (1989, pp. 189–190, pl. 24, figs 16–17) used.

*Salopidium granuliferum* (Downie, 1959) Dorning, 1981. Pl. 14, figs 4–5.

Description of Le Hérissé (1989, p. 188, pl. 24, figs 11–13) used.

*Salopidium* aff. *granuliferum* (Downie, 1959) Dorning, 1981. Pl. 14, figs 8–9.

Description of Le Hérissé (1989, under ‘Acritarches anormaux’ p. 218, pl. 30 figs 11–12) used. Some specimens have been observed with extremely expanded bases and reduced process tips.

*Salopidium wenlockense* (Downie, 1959) Dorning, 1981. Pl. 14, figs 6–7.

Description of Le Hérissé (1989, p. 189, pl. 24, fig. 14) used.

*Salopidium woolhopense* Dorning, 1981. Pl. 14, figs 10–11.

Description of Dorning (1981, p. 198–199, pl. 1, fig. 14) used.

*Schismatosphaeridium algerense* Cramer and Díez, 1976. Pl. 15, figs 1–2.

Description of Cramer and Díez (1976a, p. 93, although the holotype is illustrated in Cramer and Díez, 1972b, pl. 36, fig. 83) used.

*Schismatosphaeridium longhopense* Dorning, 1981. Pl. 15, figs 3–4.

Description of Dorning (1981, p. 199, pl. 3, figs 1–2) used.

*Schismatosphaeridium perforatum* Staplin *et al.*, 1965. Pl. 15, figs 7–8.

Description of Staplin *et al.* (1965, p. 179, pl. 18, figs. 4–6, 11–12) used.

*Schismatosphaeridium rugulosum* Dorning, 1981 emend. Mullins 2001, Pl. 15, figs 5–6.

Description of Mullins (2001, p. 113, pl. 14, fig. 7, 8) used. The specimens illustrated by Le Hérissé (1989, pl. 25 figs 5–6) as *S. guttulaferum* are now *S. rugulosum*, as *S. guttulaferum* is considered a junior synonym.

*Tunisphaeridium parvum* Deunff and Evitt, 1968. Pl. 15, fig. 9.

Description of Deunff and Evitt (1968, pp. 3–4, pl. 2, figs 15–18) used.

*Tunisphaeridium tentaculaferum* (Martin, 1967) Cramer, 1970. Pl. 15, figs 10–11.

Description of Martin (1967, p. 312, pl. 1, fig. 23, as *Baltisphaeridium*) used.

*Tylotopalla gaupa* (Cramer, 1964b) Eisenack *et al.*, 1973. Pl. 15, figs 13–14.

Description of Le Hérissé (1989, p. 196, pl. 26, figs 1–4) used.

*Tylotopalla robustispinosa* (Downie, 1959) Eisenack *et al.*, 1973 emend. Pl. 15, fig. 12.

Description of Downie (1959 p. 61, pl. 10, fig. 7, as *Baltisphaeridium*) used.

*Veryhachium checkleyense* Dorning, 1981. Pl. 16, fig. 1.

Description of Dorning (1981, p. 200, pl. 1, fig. 10) used.

*Veryhachium pertonense* Dorning, 1981. Pl. 16, figs 2–3.

Description of Dorning (1981, p. 201, pl. 1, fig. 4) used.

*Veryhachium rhomboidium* (Downie, 1959) Turner, 1984. Pl. 16, fig. 4.

Description of Turner (1984, p.145, pl. 11, figs 6, 9) used.

*Veryhachium trispinosum* (Eisenack, 1938) Stockmans and Willièrè, 1962a. Pl. 16, figs 5–6.

Description of Eisenack (1938, pp. 14–15, text–figs 2–3, as *Hystrichosphaeridium*) used.

*Veryhachium wenlockium* (Downie, 1959) Stockmans and Willièrè, 1962b. Pl. 16, figs 7–8.

Description of Downie (1959, p. 62, pl. 12, figs 9, 11, as *Veryhachium europaeum* forma *wenlockianum*) used.

*Visbysphaera brevifurcata* (Eisenack, 1954) Lister, 1970. Pl. 17, figs 1–2.

Description of Eisenack (1954, pp. 207–208, pl. 1, fig. 2, as *Hystrichosphaeridium*) used.



*Visbysphaera connexa connexa* Le Hérissé, 1989. Pl. 17, figs 3–4.

Description of Le Hérissé (1989, pp. 203–204, pl. 27. figs 7–11, text-fig. 18.2) used.

*Visbysphaera connexa crispa* Le Hérissé, 1989. Pl. 17, figs 5–6.

Description of Le Hérissé (1989, p. 204, pl. 27. figs 12–14, text-fig. 18.3) used.

*Visbysphaera connexa hirsuta* Le Hérissé, 1989. Pl. 17, figs 7–8.

Description of Le Hérissé (1989, p. 204–206, Pl. 27. figs 15–18, text-fig. 18.4) used.

*Visbysphaera erratica brevis* Le Hérissé, 1989. Pl. 17, figs. 10–11.

Description of Le Hérissé (1989, p. 206, pl. 28. figs 1–4, text-fig. 18.5) used.

*Visbysphaera gotlandica* Eisenack, 1954. Pl. 17, fig. 9.

Description of Le Hérissé (1989 p. 207–208, pl. 28, figs 6–8, text-fig. 18.6) used as it refers to the dominant form of the processes as being clubbed (rather than funnel-shaped or forked-shaped as Eisenack (1954) suggested).

*Visbysphaera meson* (Eisenack, 1955) Lister 1970. Pl. 17, figs 12–13.

Description of Eisenack (1954, p. 208, pl. 1, figs 3, 9, text-figs 3–4, as *Hystrichosphaeridium*) used.

*Visbysphaera microspinosa* (Eisenack, 1954) Lister, 1970. Pl. 18, figs 1–2.

Description of Eisenack (1954, pp. 209–210, pl. 1, fig. 8, as *Hystrichosphaeridium*) used.

*Visbysphaera oligofurcata* Eisenack, 1954. Pl. 18, figs 3–4.

Description of Eisenack (1954, p. 208, pl. 1., fig. 4) used.

*Visbysphaera pirifera pirifera* (Eisenack, 1954) Kiryanov, 1978. Pl. 18, figs 5–7.

Description of Eisenack (1954, p. 206, pl. 1, fig. 1, text-fig. 1, as *Hystrichosphaeridium*) used.

*Visbysphaera pirifera minor* Le Hérissé, 1989. Pl. 18, figs 8–9.

Description of Le Hérissé (1989, pp. 213–214, pl. 28. figs 12–15, text-fig. 19:10) used.

*Visbysphaera* cf. *gotlandica* (Downie, 1959) Dorning, 1981. Pl. 17, fig. 14.

Taxon with larger and more robust processes and larger vesicle than typical *V. gotlandica*.

*Abnormal Acritarchs*

Two unique specimens, (Plate 19, figs 13, 14), are very rare species probably related to *Multiplicisphaeridium cladum*. The specimen in fig. 13 possesses a process which has multiple primary branching, very different from the simple bifurcate process seen in the top right of the specimen and too complexly branched to be included within *M. cladum*. The specimen in fig. 14 shows the terminal branching diagnostic of *M. cladum*, but only on one process, possibly indicating an affinity to *Micrhystridium stellatum*. These specimens are not dealt with further as only one specimen has been found of each morphotype.

## Class PRASINOPHYTA, Christensen, 1962

## Genus PTEROSPERMELLA Eisenack, 1972

*Type species. Pterospermella aureolata* (Cookson and Eisenack 1958, p. 49, pl. 9, figs 10–12) Eisenack 1972, p. 597–598, Cretaceous (Cenomanian–Early Turonian).

*Diagnosis.* (translated by Mullins (2001) from Eisenack 1972, p. 597). “Microfossil in organic substance, in plan view central shell exists, in axial section most are long oval, rarely spherical and in the equatorial are circular, double-walled, with a smooth rimmed or serrated wing. This can be smooth or have radial folds.”

*Remarks.* Eisenack (1972) transferred the species formerly included in *Pterospermopsis* to *Pterospermella*, apart from the type species *Pterospermopsis danica* Wetzel (1952), which is considered to be a damaged chorate dinoflagellate cyst (Morgenroth 1968; Fensome *et al.* 1990, p.249; Colbath and Grenfell, 1995 p. 293).

*Pterospermella saturniforme* sp. nov.

Plate 19, figs 8–9, Text-fig. 3.2 G–H.

*Derivation of name.* From the Latin *Saturnus* (= Saturn) and *forma* (=shape), in reference to the equatorial membrane present in this taxon.

*Holotype.* DG00LK1.56npg1, N34, 4, Plate 19, fig 8, Text-fig. 3.1 g–h, Lower Visby Beds Luskint 1, Gotland.

*Diagnosis.* Single and thick-walled, with a spherical to subspherical, granular vesicle. Occasionally the granulation develops into very short processes. The equatorial flange is thin and flexible and smooth to granulate. The short length of the flange is of particular note. Specimens are usually flattened laterally so that the flange straddles the vesicle and is only observable at the two poles. Excystment opening not observed.

*Dimensions.* V, 31–33  $\mu\text{m}$ ; M, 3–4  $\mu\text{m}$  (4 specimens measured).

*Remarks.* This species of *Pterospermella* differs from others in the genus as it has a relatively large vesicle and short equatorial flange. The flange is commonly one-tenth of the vesicle diameter. The vesicle diameter is much larger than that seen in *P. foveolata* (20–25  $\mu\text{m}$ ), the flange much more narrow than in *P. martini* (15–18  $\mu\text{m}$ ) and *P. marysae* (5–7  $\mu\text{m}$ ). It occurs very rarely and only four specimens have been identified.

*Occurrence.* Lower Visby Beds, upper Telychian Stage, Llandovery Series, Locality Luskint 1, Gotland. Known range: sample DG00LK1.4 to 56.

### Group ACRITARCHA Evitt, 1963

Genus BUEDINGIISPHAERIDIUM Schaarschmidt 1963 emend. Lister 1970  
emend. Sarjeant and Stancliffe 1994

*Type species.* By original designation, *Buedingiisphaeridium permicum* Schaarschmidt, 1963, p. 70, pl. 20, figs 4–6, text-fig. 26, from the Upper Permian (Zechstein), Germany.

*Diagnosis.* (Sarjeant and Stancliffe 1994, p. 24). “Vesicle spherical, of small to moderate size. Eilyma ornamented by numerous low verrucae or conical tubercles, closed at the tip, often thickened or solid, sometimes hollow, or partially so, and with cavities communicating with the vesicle interior. Height of verrucae or tubercles typically less than 2  $\mu\text{m}$ .”

*Remarks.* The diagnosis of Staplin *et al.* 1965 p. 179 is considered by Lister (1970) to be a translation of the original diagnosis of Schaarschmidt 1963. Staplin *et al.* did not state it was a direct translation and they did not formally state that it was an emendation. Sarjeant and Stancliffe (1994, p. 24), however, emended the genus following the proposals of Staplin *et al.* (1965, p.179). The comparison between *Buedingiisphaeridium* and *Lophosphaeridium* begun by Staplin *et al.* (1965, p.180) was briefly referred to in Sarjeant and Stancliffe (1994, p. 32) and Mullins (2001, p. 59). Both suggested that the two genera should remain separate until the morphology of the type species of *Lophosphaeridium* is more clearly understood.

*Buedingiisphaeridium? globulosum* sp. nov.

Plate 19, figs 10–11, Text-fig. 3.3 I–J

*Derivation of name.* From the Latin *globus* (= ball/globe) in reference to the distinctive globular processes.

*Holotype.* DG00LK1.24npg1. Plate 19, fig 10, Text-fig. 3.3 I, Lower Visby Beds, Llandovery Series, Luskint 1, Gotland.

*Diagnosis.* Subspherical, thick-walled vesicle; the bases of the processes are often indistinguishable from the vesicle. Processes (7–26) mostly regularly spaced, but occasionally clumped. The processes are very globular to semi-spherical and have no definite point to the process tips. The processes are very stunted, simple, hollow, and occasionally slightly narrower at the base. The vesicle has a granulate surface. Excystment mechanism was not observed.

*Dimensions.* VW, 16–30  $\mu\text{m}$ ; VL, 17–34  $\mu\text{m}$ ; PL, 2–3.5  $\mu\text{m}$ , PΦb, 2.5–6  $\mu\text{m}$  (6 specimens measured).

*Remarks.* This species does not conform closely to the diagnosis of *Buedingiisphaeridium*, as it does not possess ‘an ornament of solid tubercles’ (Lister 1970 p. 61). The characters of this species are not considered distinctive enough to erect a new genus and is therefore questionably assigned to *Buedingiisphaeridium*. *Buedingiisphaeridium* and *Psenotopus* Tappan and Loeblich, 1979 share a number of common characters, such as a spherical vesicle and small globular ornament. These characters are not considered close enough for this species to be assigned to *Psenotopus*.

**Occurrence.** Lower and Upper Visby beds, Telychian Stage, Llandovery Series and Sheinwoodian Stage, Wenlock Series, Locality Luskint 1, Gotland. Known range: sample DG00LK1.28 to 251.

### Genus DILATISPHAERA Lister, 1970

**Type species.** By original designation *Dilatisphaera laevigata* Lister, 1970, p. 66, pl. 6, figs 10–12, text–figs 18, 20d; Upper Elton Formation, Ludlow Series, Ludlow, Shropshire, UK.

**Diagnosis.** (Lister 1970, p. 65). “Vesicle hollow, double-walled, spherical to subspherical; processes few in number, single-walled, hollow, broad; proximally they are closed to the vesicle cavity, distally they are open. Excystment aperture apical, controlled by obvious suture.”

**Remarks.** *Dilatisphaera* has many features similar to those seen in dinoflagellates (Lister 1970); including apical excystment aperture, double-walled vesicle and open-ended processes. However, it was not included by Colbath and Grenfell (1995) in the *Cymbosphaeridium* clade, which was suggested as a possible candidate for Palaeozoic dinoflagellates (Colbath and Grenfell 1995, p. 310).

#### *Dilatisphaera quadratica* sp. nov.

Plate 19, figs 13, Text–fig. 3.3 A–B.

**Derivation of name.** From the Latin for square (*quadratum*), after the stunted processes which are often square shaped.

**Holotype.** DG00LK1.227npg1, U42, Plate 19, fig. 1, Text–fig. 3.3 A, Upper Visby Beds, Wenlock Series, Luskint 1, Gotland.

**Diagnosis.** Vesicle single-walled, spherical to subspherical; 3–5 regularly spaced processes, which are translucent and filmy. The unbranched processes are short, often square in shape, unornamented, and distally open. The vesicle is granulate grading to a dense covering of short, or very short, fine hairs or processes. Excystment mechanism was not observed.

**Dimensions.** V, 13–19  $\mu\text{m}$ ; PL, 6–13  $\mu\text{m}$ ; P $\Phi$ , 6–8  $\mu\text{m}$  (10 specimens measured).

**Remarks.** This species of *Dilatisphaera* is very similar to *D. williereae*, but *D. quadratica* has much shorter and often wider processes. The processes commonly have a 1:1 width:height ratio. The processes are often very difficult to discern, unless differential interference contrast is used. Lister described *D. laevigata* as having a smooth vesicle, but when re-examined the holotype clearly has a granulate vesicle. *D. quadratica* differs from *D. laevigata* in having a more prominent ornamentation on the vesicle and shorter processes.

**Occurrence.** Upper Visby Beds, Sheinwoodian Stage, Wenlock Series, localities Luskint 1 and Lickershamn 2, Gotland. Known range: samples DG00LK1.38 to 255 and DG00LH2.37 to 5.

### Genus ELEKTORISKOS Loeblich, 1970

**Type species.** By original designation, *Elektoriskos aurora* Loeblich, 1970, p. 717–718, figs 12 A–D; Malpewood Shale, middle Silurian, Genesee River, Rochester, New York.

**Diagnosis.** (Loeblich 1970, p. 717) “Circular to subcircular vesicle central body, wall apparently single layered, psilate, chagrenate to granulate with numerous slender, flexible but solid processes which do not communicate with the interior of the central body.”

**Remarks.** *Elektoriskos* is a distinctive genus with a combination of simple, thin, moderately long, wiry processes and a very thin, transparent vesicle. This genus differs from *Comasphaeridium* Staplin *et al.*, 1965 because the processes have a lower density and are not ‘crowded’ (as described by Staplin *et al.* 1965, p. 192) and from *Filisphaeridium* Staplin *et al.*, 1965 because the processes are much finer and not thickened.

*Elektoriskos longispinosa* sp. nov.

Plate 19, figs 6–7, Text–fig. 3.3 C–D.

**Derivation of name.** From the Latin for long and spine (*longus* and *spina*) referring to the extended processes length.

**Holotype.** DG00LK1.171npg1, O42, Plate 19, fig. 6, Text–fig. 3.3 D, Upper Visby Beds, Wenlock Series, Luskint 1, Gotland.

**Diagnosis.** Subspherical, thin-walled, transparent vesicle, with 5–8 regularly spaced processes, which are very fine and wiry. The processes are long, simple, solid, and slightly expanded at the base. The vesicle is smooth to granulate with a slightly wrinkled surface. Excystment mechanism not observed.

**Dimensions.** V, 19  $\mu\text{m}$ ; PL, 16–22  $\mu\text{m}$ ; P $\Phi$ b, 1–1.5  $\mu\text{m}$ ; P $\Phi$ , 0.5–0.75  $\mu\text{m}$  (2 specimens measured).

**Remarks.** *E. longispinosa* has very similar vesicle ornament and dimensions to *E. aurora*, but the former has far fewer and much longer processes. The process length is commonly equivalent to the vesicle diameter. *E. longispinosa* differs from other species of *Elektoriskos* in having slightly expanded process bases. *E. longispinosa* was not assigned to *Comasphaeridium* as the processes are not as densely crowded as described by Staplin *et al.* (1965).

**Occurrence.** Upper Visby Beds, Sheinwoodian Stage, Wenlock Series, Locality Luskint 1, Gotland. Known range: sample DG00LK1.167 to 171.

## Genus MICRHYSTRIDIUM Deflandre, 1937, emend. Sargeant and Stancliffe, 1994

1965 *Solisphaeridium* Staplin, Jansonius and Peacock

1974 *Exilisphaeridium* Wicander

**Type species.** By original designation *Micrhystridium inconspicuum* Deflandre 1935, p. 233, pl. 9, figs 11–12; Upper Cretaceous, France.

**Diagnosis.** (Sargeant and Stancliffe 1994, p. 12). “Acritarchs with a spherical, oval to rounded–subpolygonal vesicle whose outline in optical section is not significantly modified by the bases of the spines. Vesicle size small, generally less than 20  $\mu\text{m}$ ; larger species very rarely range above 27  $\mu\text{m}$  in diameter. Eilyma typically single-layered, rarely two-layered. Surface psilate to granulate or with other fine microstructure, but not divided into fields or plates. Arising from the vesicle, generally at right angles to the eilyma, are from 9 to 35

spines with closed tips, usually simple but rarely clavate. The spines may flare somewhat at their bases. Spines hollow to solid; if hollow their central cavity may or may not communicate with that of the vesicle. A few spines may exhibit distal bifurcations or have small holes in their mid section. The spine length can range from ca.  $1.5\mu\text{m}$  to greater than the vesicle diameter. Release of the vesicle contents occurs by formation of a linear slit or a crescentic to horseshoe-shaped opening (epityche) or by opening of a cryptosuture, causing loss of an irregularly shaped portion of one surface: regularly formed circular polygonal openings (pylomes) are not developed”.

*Remarks.* The diagnosis of *Micrhystridium* has been emended by many authors (see Sarjeant and Stancliffe 1994) and numerous genera have been considered synonyms (Eisenack *et al.* 1979, Sarjeant and Stancliffe 1994). Many of the genera listed by Sarjeant and Stancliffe (1994) do not truly conform to their emended diagnosis of *Micrhystridium* (see discussion in Mullins 2001, p. 93). Eisenack *et al.* (1979, p. 381) charted the history of the discussions on *Micrhystridium*.

*Micrhystridium* sp. A

Plate 19, figs 4–5, Text-fig. 3.3 E–F.

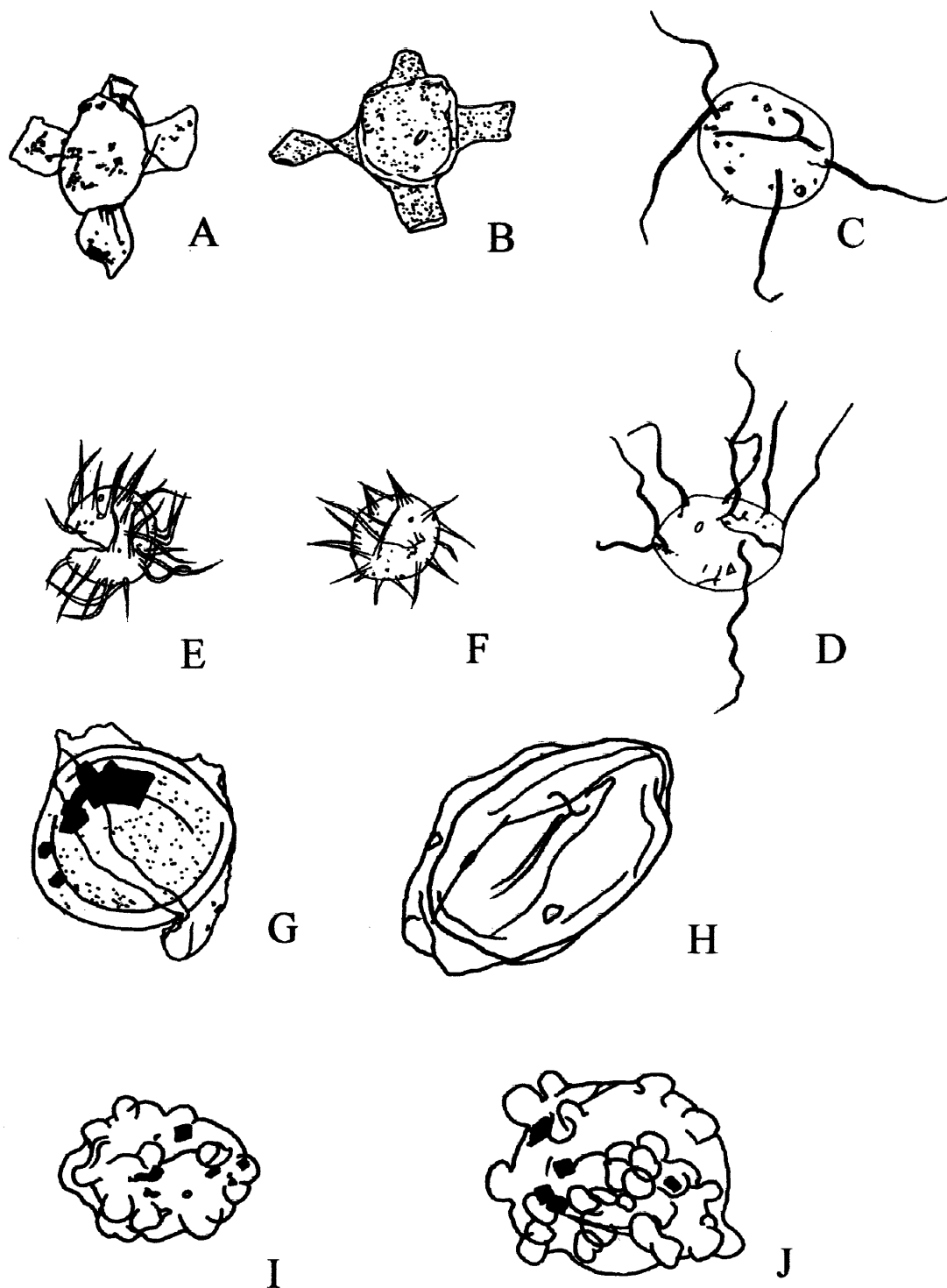
*Description.* Vesicle spherical, but commonly deformed into an elongate form. There are 9–25 regularly spaced processes, which are solid and translucent. The processes are long and thin, simple and evenly spaced. The vesicle is smooth to microgranulate. Excystment is by lateral split, only seen in a few specimens.

*Dimensions.* V, 10–18  $\mu\text{m}$ ; PL, 8–13  $\mu\text{m}$ ; PΦb, 0.5  $\mu\text{m}$  (10 specimens measured)

*Remarks.* *M. sp. A* is distinct from *M. stellatum* and *Salopidium granuliferum* because of the translucent processes, and has more robust and transparent processes than *Elektoriskos aurora*. *M. sp. A* is often very difficult to identify and can be easily confused with a small leiosphere, as the processes are hard to observe unless differential interference contrast is used.



***Occurrence.*** Lower and Upper Visby beds, Telychian Stage, Llandovery Series and Sheinwoodian Stage, Wenlock Series, Locality Lusklint 1 and Lickershamn 2, Gotland.  
**Known range:** samples DG00LK1.68 to 257 and DG00LH2.53 to 13.



TEXT-FIG. 3.3. Illustration of the variation within the newly diagnosed acritarch species (all x 1000, also see Plate 19). *Dilatisphaera quadratica*: A, holotype, DG00LK1.227npg1-U42, Upper Visby beds; B, DG00LK1.223npg1-R40, Upper Visby Beds; *Elektoriskos longispinosa*: C, DG00LK1.167npg1-M43, 3, Upper Visby Beds; D, holotype, DG00LK1.171npg1-O42, Upper Visby beds; *Micrhystridium* sp.A: E, DG00LH2.17npg1-J32, 1, Upper Visby beds; F, DG00LK1.112npg1-O36, Upper Visby beds; *Pterospermella saturniforme*: G, holotype, DG00LK1.56npg1-N34, 4, Lower Visby beds; H, DG00LK1.40npg1-M36, 4, Lower Visby beds; *Buedingiisphaeridium? globulosum*: I, holotype, DG00LK1.183npg1-R38, Upper Visby beds; J, DG00LK1.72npg1-J48, 3, Lower Visby beds.

## RESULTS

Prior to this study, the palynology of the Lower Silurian of Gotland had not been investigated in detail. The analysis of Gotland palynomorphs conducted by Le Hérissé (1989) was the first real glimpse of the turnover in palynoflora at this time, but only five samples from the Visby Beds were analysed and little quantitative analysis was done. Here, 87 samples have been statistically analysed over the same interval in the Visby Beds.

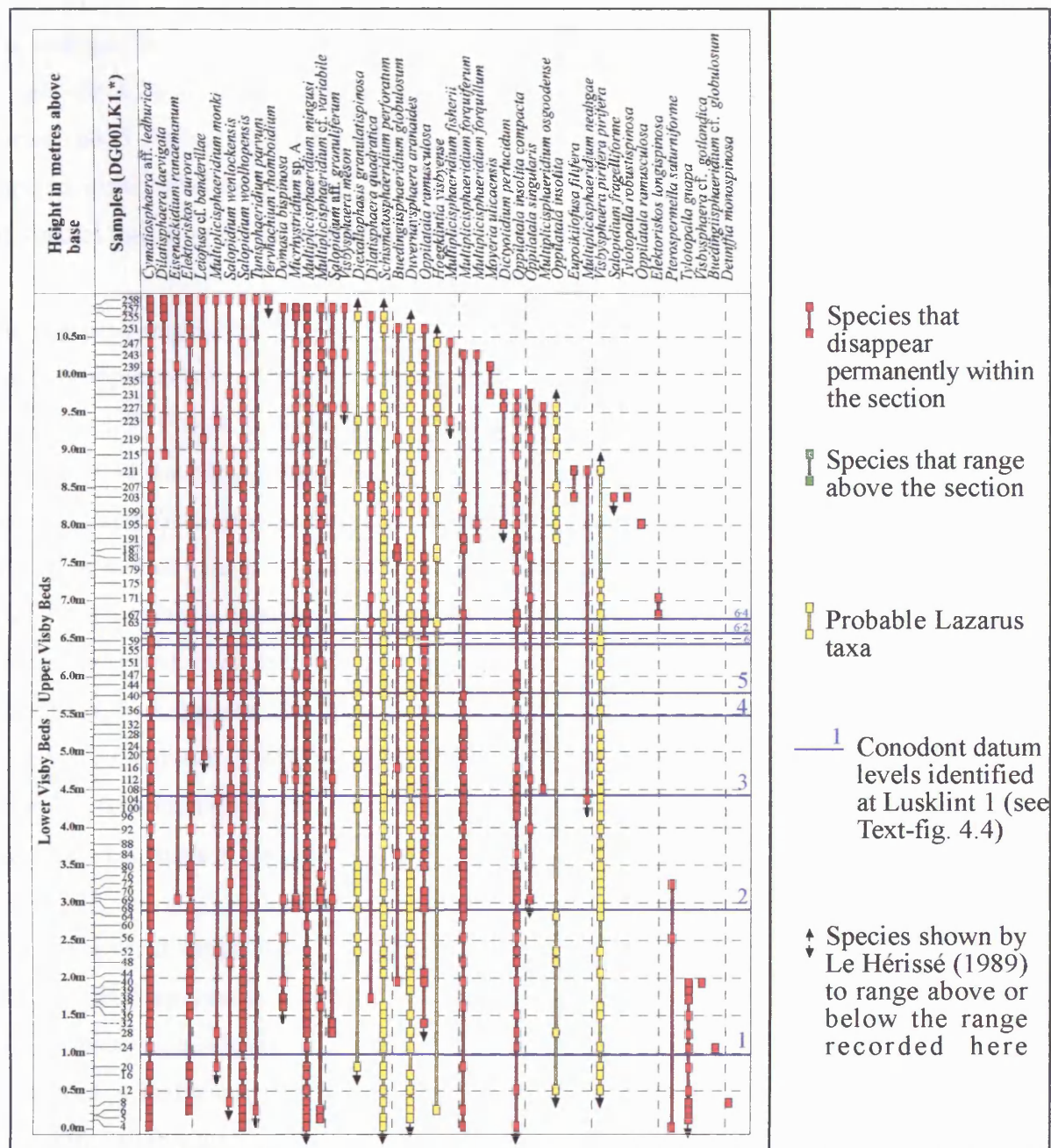
## EXTINCTION, ORIGINATION AND ABUNDANCE CHANGE DATA

*Palynomorph extinction and origination data*

One of the main aims of this study was to analyse the extinction and origination patterns seen in the palynomorphs through the Ireviken Event. To achieve this, stratigraphic range plots have been constructed based on presence/absence data. Many of the species recorded range above and below the section analysed, so have been removed from the plots (see Appendices 1 and 2 for the stratigraphic range plot for the whole data set). To avoid complications arising from possible palynomorph migrations in and out of Gotland at this time, the species ranges have only been extended if this was confirmed by the stratigraphic ranges recorded by Le Hérissé (1989); comparison to other Silurian palynomorph data sets is made later in this chapter. Here, two types of Lazarus taxa have been identified: taxa that suddenly disappear from the record after a relatively common occurrence and then occur at a higher level (such as *Schismatiosphaeridium perforatum*); or taxa that are less common, but highly distinctive, and disappear from the record, to re-occur at a higher level (such as *Visbysphaera pirifera*). The whole data set for both sections, comprising the samples analysed, number of palynomorphs of a species per gram of sediment and percent of that species of the assemblage in a sample, is listed in Appendices 3 and 4.

*Palynomorph extinctions*

The dominant pattern shown by the palynomorph species that show range tops in the section at Luskint 1 is a gradual disappearance, occurring very late in the Ireviken Event (Text-fig. 4.1). 86.3% of the species that disappear, do so in the top four metres of the section (the rest are spread roughly evenly across the rest of the section). This signal is probably partly due to the close proximity to the top of the section; it may be possible to extend the range of some of the species on analysis of higher samples. The position of the palynomorph last appearances is largely independent of the conodont extinction datum levels.



TEXT-FIG. 4.1. Stratigraphic range diagram plotted for Luskint 1, showing the species that disappear permanently in the section and the probable Lazarus taxa, relative to the conodont extinction datum levels.

44 species show range tops in this in the section, 23 of which also show a first appearance here. Eight species were lost from the genus *Multiplicisphaeridium*, five from the genus *Oppilatala*, four from *Salopidium* and three from *Visbysphaera*. Four genera lost two species and sixteen genera lost one.

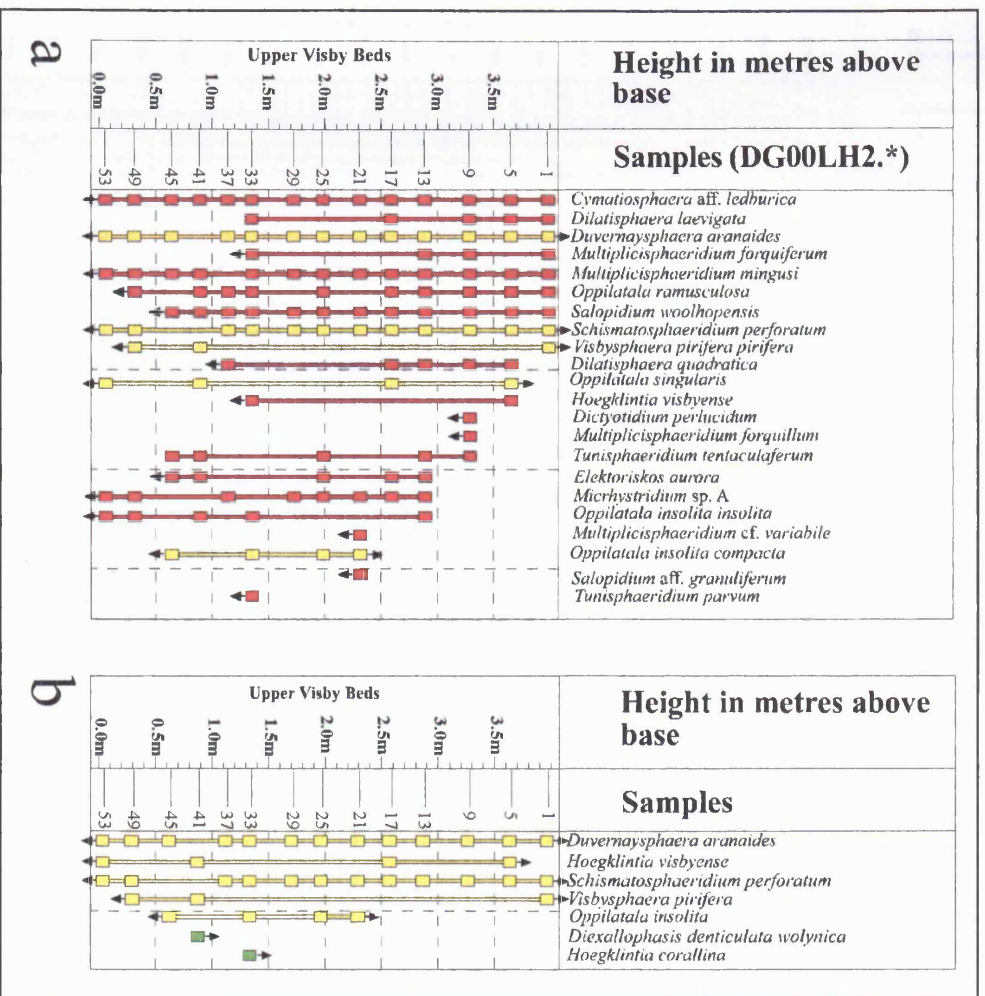
The stratigraphic range plot for the species that show range tops at Lickershamn 2 can be seen in Text-fig. 4.2a. Of the 72 species recorded, 22 disappear within the section (including the Lazarus taxa). As at Luskint 1, *Multiplicisphaeridium* and *Oppilatala* are most strongly affected, losing four species each. Three genera lost two species and eight lost one. Two of the species that show range tops in this section also show a first appearance here.

#### *Palynomorph originations*

The first appearances at Luskint 1 show a different pattern from that of the last appearances (Text-fig. 4.3). Firstly, they are more numerous (54 species first appear in the section as opposed to 44 that show range ends) and secondly, they occur right through the whole of the Ireviken Event. There is an uneven distribution across the event, with a slightly convex pattern seen. This pattern is partly due to a number of species that seem to first appear at the base of the section; at least some of these ranges would probably be extended if lower strata were investigated. Even when this is considered, there is a definite drop in the number of species that first appear in the upper parts of the section, from 42 first appearances below 3.5m and 13 above. It is difficult to identify any relationship in the first appearances to the conodont extinction steps, but it could be argued that the number of originations reduces when the main steps in the conodont extinction begin.

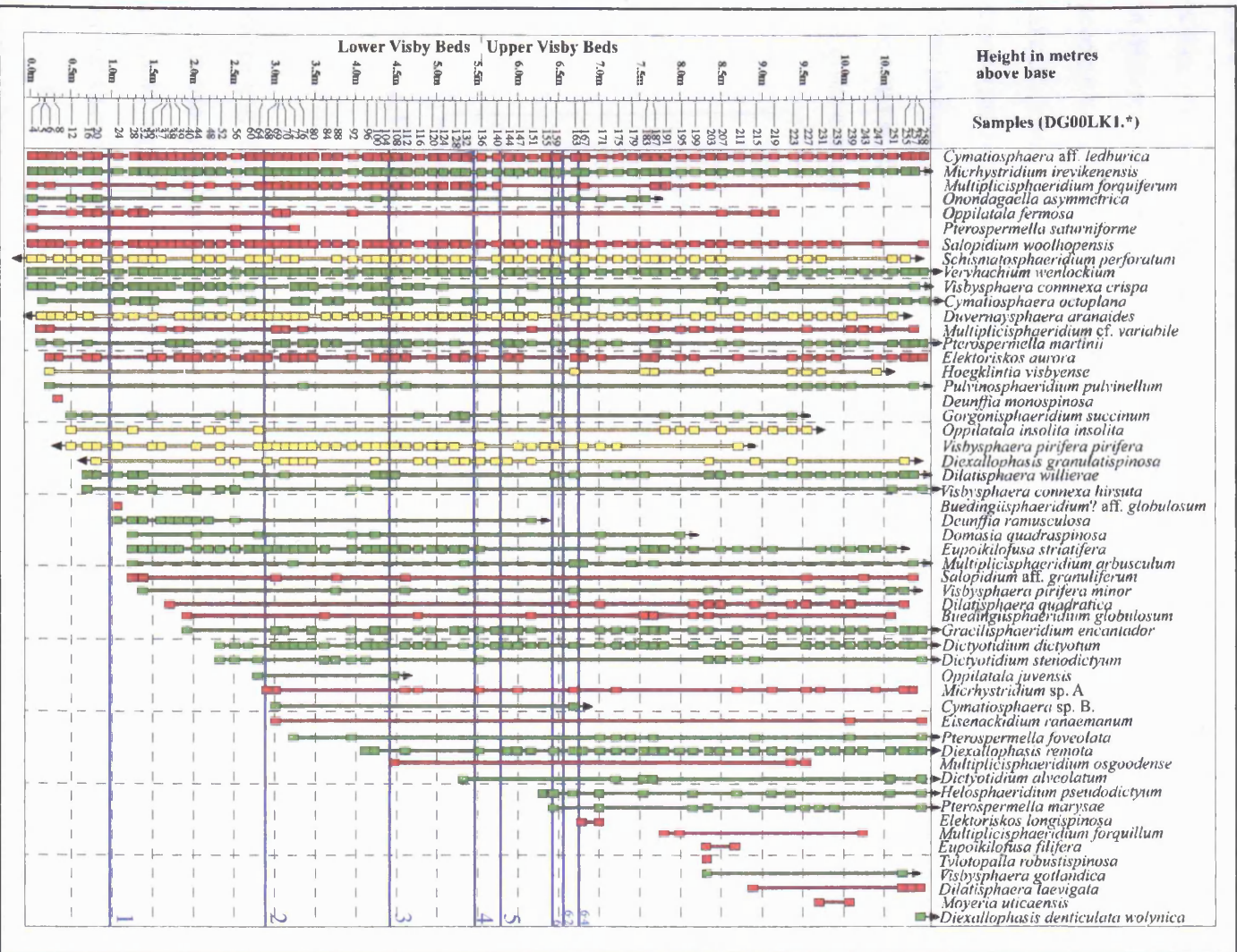
Five species first appear from each of the genera *Multiplicisphaeridium* and *Visbysphaera*, four from *Pterospermella*, and three each from *Cymatiosphaera*, *Dictyotidium*, *Diexallophasis*, *Dilatisphaera*, *Eupiokliofusa* and *Oppilatala*. Four genera gained two species and fifteen gained one. Of the 54 species that first appear, 26 have range tops in the section (including Lazarus taxa).

Of the 72 species recorded at Lickershamn 2 (Text-fig. 4.2b), seven show first appearances in the section. Two species from the genus *Hoegklintia* show first appearances. The other five genera gain one species in this section.



TEXT—FIG. 4.2. Stratigraphic range diagram plotted for Lickersham 2: (a). showing the species that disappear permanently in the section and the probable Lazarus taxa; (b). showing the species that first appear within the section and the probable Lazarus taxa. See Text—fig. 4.1 for key.

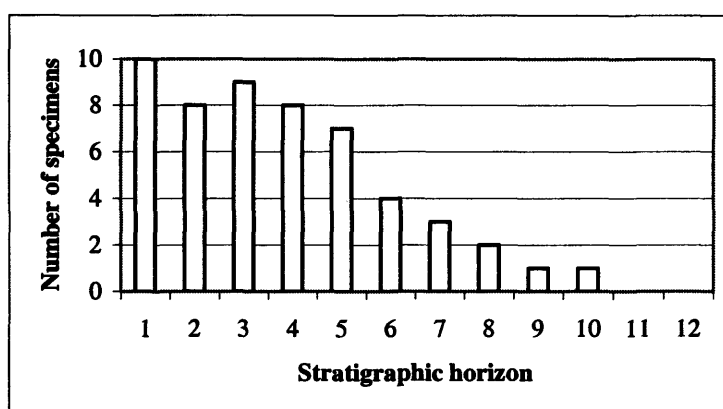




TEXT-FIG. 4.3. Stratigraphic range diagram plotted for Luskint 1, showing the species that first appear within the section and the probable Lazarus taxa relative to the conodont extinction datum levels. See Text-fig. 4.1 for key.

*Range end confidence limits*

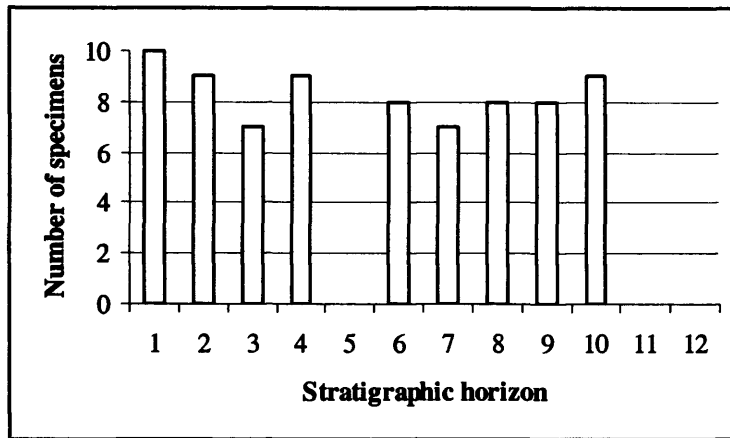
Local stratigraphic ranges of species are likely to underestimate the true extent of the range. Therefore, a number of quantitative methods for estimating the likely true range ends have been developed. All these methods (commonly used ones are outlined in Marshall 1998, p. 23–53) rely on the recorded stratigraphic range (usually several hundred metres) and the distribution of samples containing, or not containing, the particular species with that range. They do not take into account the gradual or sudden nature of the range end, which is very important in determining confidence limits. For example, if a species were present in ten equally spaced samples in the lowermost ten metres of a twelve metre section, under the conventional calculations the range end would be given a high confidence compared to a species that occurred in fewer than ten samples within the same range. If this species had a gradual decline in numbers to the end of its range (Text-fig. 4.4), it is likely that specimens that define the real range end have been missed in a higher horizon (such as horizon eleven or twelve). This gives a deceptively high level of confidence.



TEXT-FIG. 4.4. Graph showing a species that occurs in every sample within its range, but has a gradual decline in numbers.

Equally, a range end that has very sharp decline in numbers should be regarded with greater confidence than one with a gradual decline. For example, in Text-fig. 4.5, the conventional calculations would regard the last appearance level of this species as having a lower confidence limit than that seen in Text-fig. 4.4, as it does not occur in every sample within its range. However, the sudden disappearance of this previously abundant species means that it is unlikely that it has been missed in horizon eleven. The recorded range end can therefore be considered as having a higher range end confidence level.





TEXT-FIG. 4.5. Graph showing a species that does not occur in every sample within its range, but is abundant in most of the section and has a sudden decline in numbers.

The Luskint 1 and Lickershamn 2 datasets are rather different from those normally used in range end calculations. The data collected on Gotland is from a very restricted stratigraphic interval and presence/absence data have been collected in conjunction with highly detailed abundance data. The calculations outlined in Marshall (1998) were applied to the data collected in Gotland (see example in Text-fig. 4.6). The calculations proved inconclusive, often giving calculated extensions range ends that were greater than the entire recorded species range.

Species	Height extended (m)	Species	Height extended (m)
<i>C. aff. ledburica</i>	4.50	<i>H. visbyense</i>	7.20
<i>D. laevigata</i>	3.82	<i>D. perlucidum</i>	0.00
<i>D. aranaides</i>	4.55	<i>M. forquillum</i>	0.00
<i>M. forquiferum</i>	3.82	<i>T. tentaculaferum</i>	4.12
<i>M. minguisi</i>	4.55	<i>E. aurora</i>	3.45
<i>O. ramusculosa</i>	4.46	<i>M. sp. A</i>	3.73
<i>S. woolhopensis</i>	3.90	<i>O. insolita insolita</i>	4.35
<i>S. perforatum</i>	4.61	<i>M. cf. variabile</i>	0.00
<i>V. pirifera pirifera</i>	6.60	<i>O. insolita compacta</i>	2.25
<i>D. quadratica</i>	3.90	<i>S. aff. granuliferum</i>	0.00
<i>O. singularis</i>	4.62	<i>T. parvum</i>	0.00

TEXT-FIG. 4.6. Table showing the calculated distance the range ends of the species at Lickershamn 2 should be extended, according to point estimates of the true stratigraphic range ends (see Marshall 1998, p. 24).

A more complex method has been developed to try and address some of the problems encountered above (see discussion in Hayek and Bura 2001). As yet, it has not been established if this method will be fruitful here and this is identified as a line of future work.

*The fraction below 7µm in size*

To test for missed species occurrences and range ends, the fraction below 7µm in size was monitored through the whole of both the sections (as outlined in Chapter 2). One in four of the samples processed were analysed. The number of specimens recorded was minimal, never reaching more than 0.8 specimens per gram of sediment; three of the twenty-two samples investigated had no specimens in this fraction. The palynomorphs recovered were dominated by small leiospheres (at 62% of all the specimens recovered from all the samples). Most of the other palynomorphs were specimens of *Domasia trispinosa* and *Veryhachium wenlockium*, which due to their pointed form are more likely than the stellate forms to slip through the 7µm sieve mesh. The topmost samples analysed generally contain several more specimens and species than the lower samples (e.g. sample DG00LK1.257 contained 33 specimens from six species and DG00LK1.48 contained three specimens from two species).

*The conodont extinction pattern*

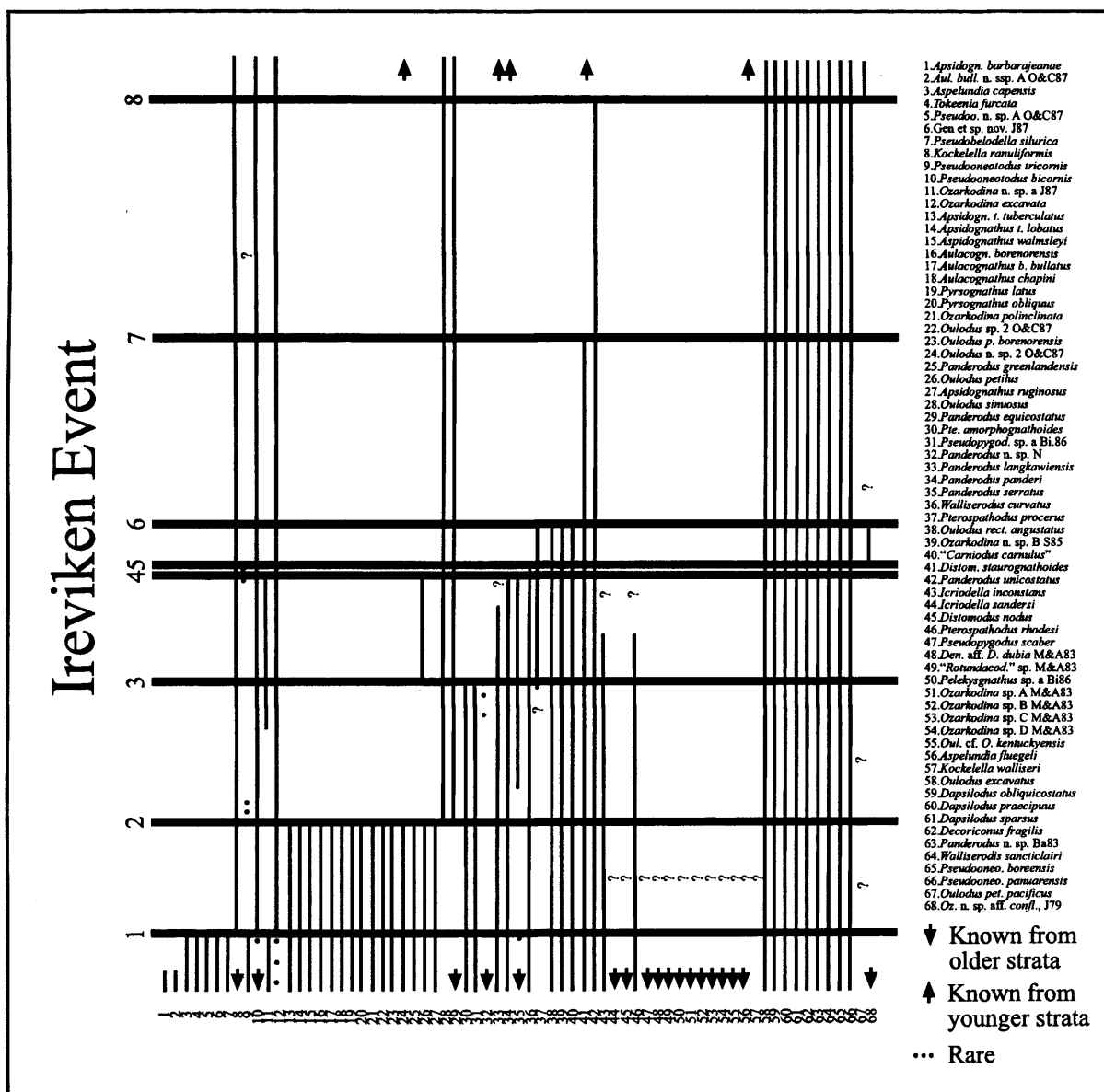
There is a pronounced step-wise extinction pattern seen in the conodonts through the Ireviken Event (Text-fig. 4.7) (Aldridge *et al.* 1993, Jeppsson 1997). The importance of this data set lies in the large turnover and its high resolution (samples were collected at around ten centimetre intervals, about half the resolution of sampling in this study). The extinction pattern is recognised as a worldwide event (Jeppsson 1997).

*The palynomorph abundance data*

The subtle changes in abundance recorded in this study tell a very complex story. To determine any pattern in these data they have been analysed qualitatively and quantitatively through multivariate analysis. The absolute and relative frequency data for taxa in the sections at Luskint 1 and Lickershamn 2 are listed in Appendices 3–8.

*General trends seen at Luskint 1*

The majority of the species that make up the assemblage recorded at Luskint 1 maintain a consistent percentage of the whole assemblage through the section. For example *Diexallophasis gotlandica* has a percent abundance record with a standard deviation of 2.4%, *Micrhystridium eatonensis* 0.6% and *Veryhachium wenlockium* 8.4%. Major changes in the absolute abundance data are not accompanied by changes in the relative proportions (for example the high number of palynomorphs per gram of sediment in sample DG00LK1.187 causes a marked peak in the absolute abundance data, whilst the percentage abundance data change little). Most of the species recorded are rare and occur at fewer than ten per thousand



TEXT-FIG. 4.7. Stratigraphic range diagram for the conodonts through the Ireviken Event, adapted from Jeppsson (1997, fig. 17.2). This diagram represents a composite of the conodont data from several sections, not all from Gotland. The extinction datum levels are numbered. The precise datum levels identified at Luskint 1 are marked on Text-figs 4.1 and 4.3.

logged. The palynomorph assemblage at Lusklint 1 is dominated by *M. stellatum*, *S. granuliferum*, *V. wenlockium*, *D. trispinosa* and leiospheres to varying degrees.

In some species the contrasts in abundance between the top, middle and base of the section are marked. This is particularly seen in *Micrhystridium stellatum*, *Salopidium granuliferum* and *Veryhachium wenlockium*. *M. stellatum* has a high level of abundance in the lowermost and uppermost samples (Appendix 6), with a peak of 49.07% in DG00LK1.8 and a peak of 31.75% in sample DG00LK1.243. The samples collected in the middle part of the section show consistently low relative numbers of *M. stellatum* (especially between samples DG00LK1.112 and 159 which are all below 5.5%).

*Salopidium granuliferum* is recorded at a plateau of around 22% in the lowermost samples. In contrast to *M. stellatum*, the relative numbers then fall to a level consistently below 10% above sample DG00LK1.183.

*V. wenlockium* has a similar pattern to that of *M. stellatum*, but not as pronounced. From the base of the section until sample DG00LK1.28 the relative frequency of *V. wenlockium* is never higher than 10%. Between samples DG00LK1.32 and 88 a peak is recorded at around 20%. Above this, the percentage abundance varies around 10–15%, until the uppermost part of the section where a plateau of around 30% is reached between samples DG00LK1.211 and 235.

The top of the section contains higher levels of *Cymatiosphaera* aff. *ledburica* and *Veryhachium trispinosum*. *C. aff. ledburica* maintains a near constant 1–2% relative frequency in most of the section sharply rising to a peak of 12% in DG00LK1.257. *V. trispinosum* has a slightly more gradual rise over six samples, from 1% or less, (or often not recorded) to a peak of 9% in DG00LK1.258. The leiospheres have a generally slightly higher abundance in the Upper Visby Beds at around 10% in each of the four categories (around 5% in each category is recorded in the Lower Visby Beds).

A number of species occur in nearly every sample, but only in very low numbers (usually only two or three specimens). For example, *Duvernaysphaera aranaides* and *Pterospermella martini* occur through most of the section, but at never more than 1% of the total assemblage.

More subtle morphological variations were also observed. In samples DG00LK1.112, 116 and 128 (Pl.18, fig.7) the *Visbysphaera pirifera pirifera* specimens have markedly longer

processes than those from the base and top of the section (Pl. 18, fig. 6). In sample DG00LK1.144 (Pl.3, fig. 15) *D. aranaides* has wider process bases.

It is difficult to find patterns in much of the abundance data, with many species (e.g. *Multiplicisphaeridium minguisi*) having an apparently random distribution pattern.

#### *General trends seen at Lickershamn 2*

General trends in the abundance of species at Lickershamn 2 are particularly hard to discern, mainly because of the short height of the section. As at Lusklint 1, all the samples are dominated by a combination of leiospheres, *M. stellatum*, *V. wenlockium*, *S. granuliferum* and *D. trispinosa*, which vary little in relative abundance through the section. Again, most of the species recorded are very low in number, but occur consistently.

#### *Multivariate analysis*

To investigate patterns in the data, correspondence analysis and cluster analysis were undertaken. To avoid unnecessary spread in the plots, outliers (species that occur in less than five percent of the samples and samples that contain less than five percent of the species) were removed from the dataset (see discussion in Shi 1993, p. 204). The data were also transformed to a logarithmic scale to minimise the tendency of all the most abundant species to cluster together.

The transformed dataset was investigated using correspondence analysis and cluster analysis. Correspondence analysis is an ordination technique, but unlike other methods assigns differential weights to samples, thereby maximising the correlation between samples or taxa. Plots of the spatial relationship in three–dimensions between samples or taxa are produced, grouping together similar samples (see discussion in Shi 1993, p. 221). There are a number of cluster analysis methods, which emphasise different aspects of similarity and dissimilarity within a dataset (see discussion in Etter 1999, p. 305–311). Here, Morisita's index is used because it is recommended by Etter (1999) as the best overall measure of similarity.

The correspondence analysis for the samples at Lusklint 1 (Text–fig. 4.8) shows that most of the samples cluster in one group around 0, with relatively small variance. A number of outliers (sample numbers shown) are located slightly away from the main group. No discrete groups can be distinguished from these plots.



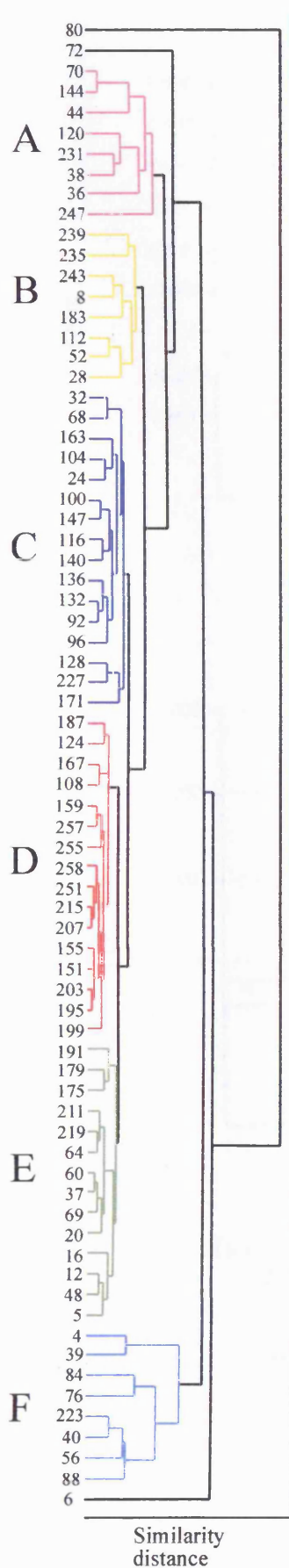
Using the Morisita cluster analysis method (Text–fig. 4.9) six distinct groups of samples at Luskint 1 are identified (defined by the colours and letters). When plotted against the samples in stratigraphic order (Text–fig. 4.10) the groupings are less clear, but three broader groups can be identified: a lower group (below sample LK1.92) characterised by some of the samples from group E and group B and most of the samples from group F, a middle group (samples LK1.92–215) characterised by samples from group C, group D and group A and a upper group (above sample LK1.215) mostly made up of the remaining group E and group B samples. These groups are remarkably similar to those observed in the general trends section above (picked out by species such as *M.stellatum*, *S. granuliferum* and *V. wenlockium*). This method can potentially pick out repetitions of samples with similar characteristics reflecting otherwise hidden cyclicity and this seems to be the case here. Both the bottom and the top of the section are dominated by samples from groups B and E, though the restricted height of the section means the full extent of a potential cycle is not seen.

The correspondence analysis for the species at Luskint 1 (Text–fig. 4.11) shows they mostly cluster in one group around zero, with relatively small variance. A number of outliers (species names shown) are located away from the main group; all but two of these outliers (*D. granulatispinosa*, from the F cluster and *H. pseudodictyum*, from the G cluster) lie within the D cluster identified on Text–fig. 4.12 through cluster analysis.

Cluster analysis (Text–fig. 4.12) identifies seven groups of species with similar distributions at Luskint 1. The major factors associating the species into groups relate to the part of the section where species co-occur in similar numbers and to how commonly the species occur through the whole section. Using Text–fig. 4.11 and 4.12 together, it can be suggested that most of the species occur in the same relative numbers in all samples, apart from the most numerous species (many of which plot as outliers in Text–fig. 4.11, and within group D in Text–fig. 4.12), which have a more variable distribution.

The smaller dataset collected for Lickershamn 2 was treated in exactly the same way as the Luskint 1 data and the results from correspondence analysis and Morisita cluster analysis plotted.

The correspondence analysis for the samples at Lickershamn 2 (Text–fig. 4.13) shows a much more widely spaced distribution than that seen at Luskint 1 (Text–fig. 4.8). There is no central cluster of very similar samples and when the clusters groups identified from the cluster analysis dendrogram (Text–fig. 4.14) are added, four distinct groups (A to D) are identified.

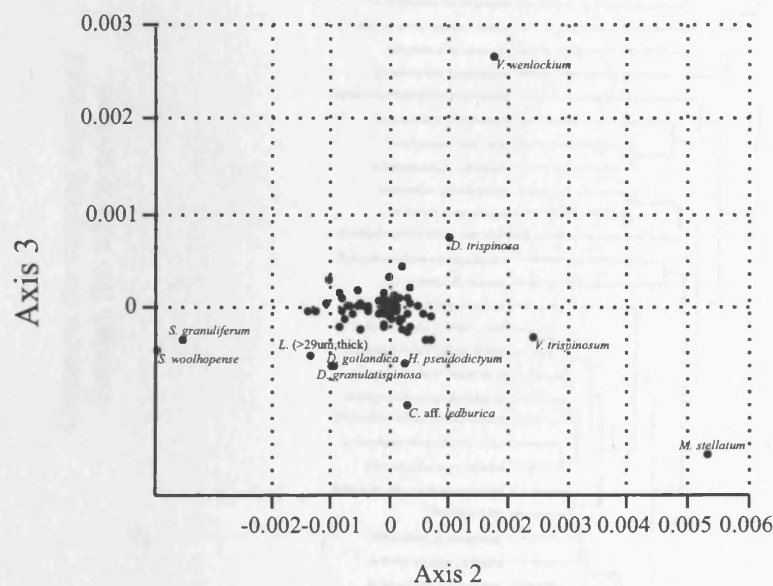
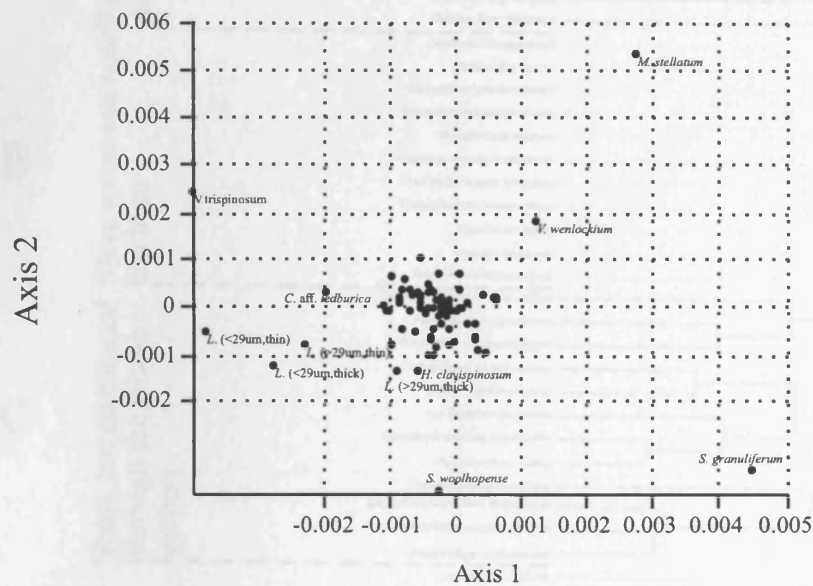


TEXT-FIG. 4.9. Cluster analysis dendrogram for samples from Luskint 1.  
Colours have been used to differentiate groups with common characteristics.

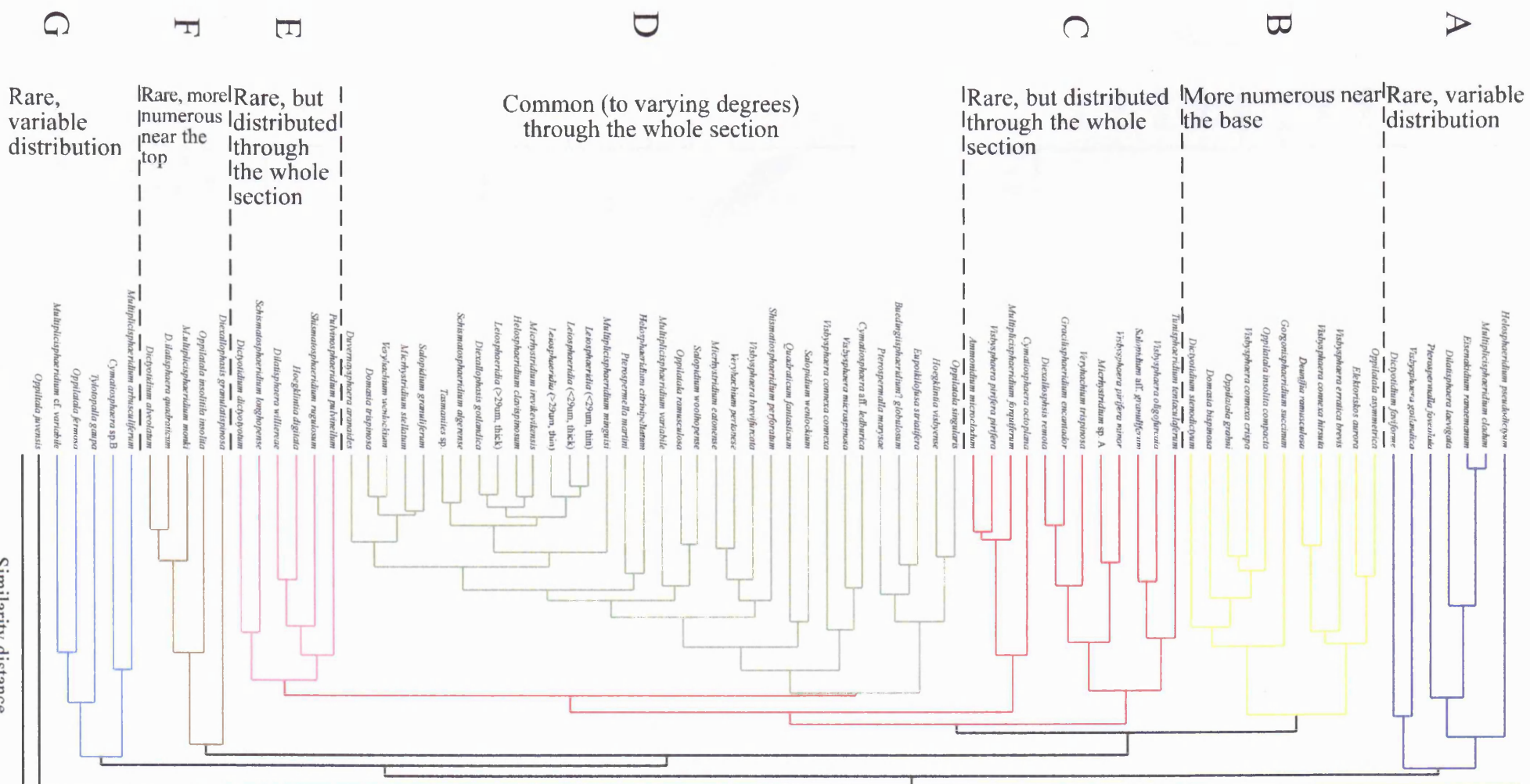
LK1.258	
LK1.257	
LK1.255	
LK1.251	
LK1.247	
LK1.243	
LK1.239	
LK1.235	
LK1.231	
LK1.227	
LK1.223	
LK1.219	
LK1.215	
LK1.211	
LK1.207	
LK1.203	
LK1.199	
LK1.195	
LK1.191	
LK1.187	
LK1.183	
LK1.179	
LK1.175	
LK1.171	
LK1.167	
LK1.163	
LK1.159	
LK1.155	
LK1.151	
LK1.147	
LK1.144	
LK1.140	
LK1.136	
LK1.132	
LK1.128	
LK1.124	
LK1.120	
LK1.116	
LK1.112	
LK1.108	
LK1.104	
LK1.100	
LK1.96	
LK1.92	
LK1.88	
LK1.84	
LK1.80	
LK1.76	
LK1.72	
LK1.70	
LK1.69	
LK1.68	
LK1.64	
LK1.60	
LK1.56	
LK1.52	
LK1.48	
LK1.44	
LK1.40	
LK1.39	
LK1.38	
LK1.37	
LK1.36	
LK1.32	
LK1.28	
LK1.24	
LK1.20	
LK1.16	
LK1.12	
LK1.8	
LK1.6	
LK1.5	
LK1.4	

TEXT-FIG. 4.10. Table showing the cluster analysis groups identified on text-fig. 4.9 relative to the Luskint 1 samples in stratigraphic order.

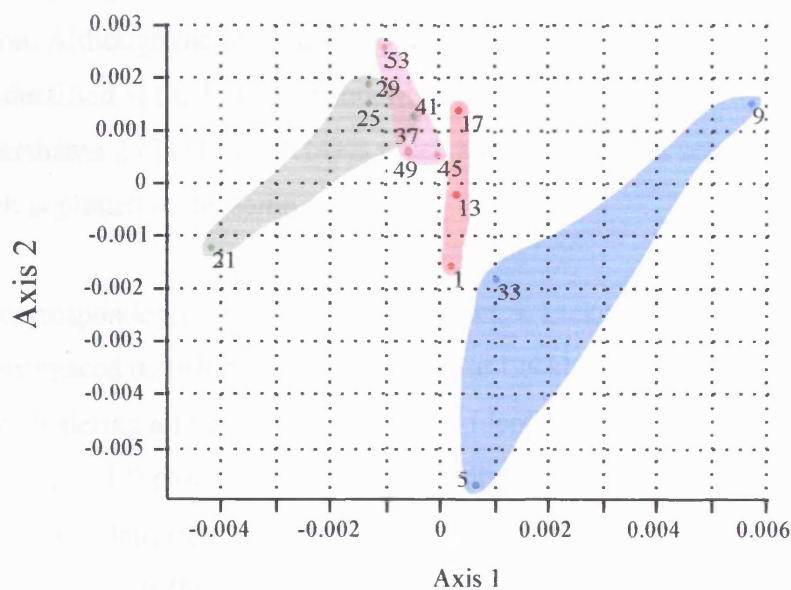




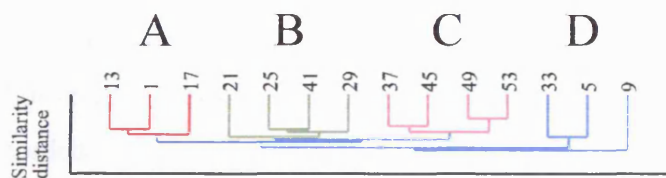
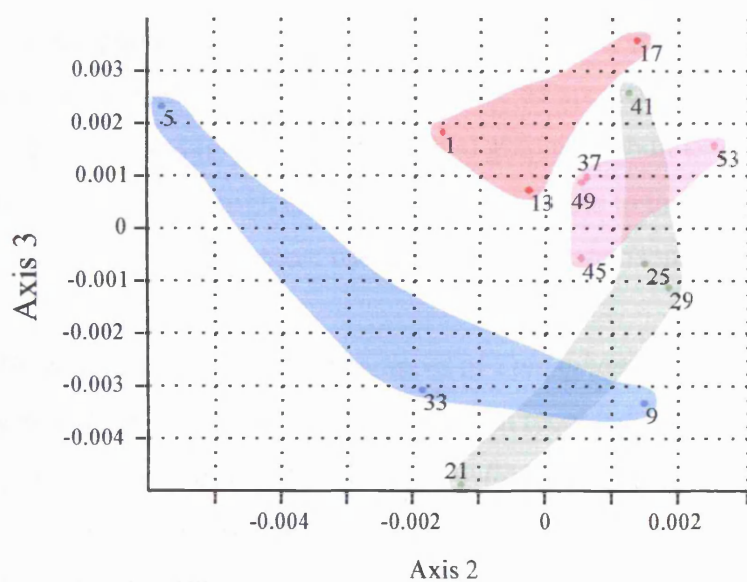
TEXT—FIG. 4.11. Plots showing the three-dimensional distribution of the species at Lusklint 1 after correspondence analysis (the species names for the tightly clustered samples on the plot have been removed for clarity).



TEXT-FIG. 4.12. Cluster analysis dendrogram for species from Luskint 1.  
Colours have been used to differentiate the clusters with common characteristics.



TEXT-FIG. 4.13. Plots showing the three-dimensional distribution of the samples at Lickershamn 2 after correspondence analysis (sample numbers have been included). Colours relate to clusters identified in Text-fig. 4.14



TEXT-FIG. 4.14. Cluster analysis dendrogram of samples from Lickershamn 2. Colours have been added to differentiate the clusters with common characteristics.

LH2.1	■
LH2.5	■
LH2.9	■
LH2.13	■
LH2.17	■
LH2.21	■
LH2.25	■
LH2.29	■
LH2.33	■
LH2.37	■
LH2.41	■
LH2.45	■
LH2.49	■
LH2.53	■

TEXT-FIG. 4.15. Table showing the cluster analysis groups identified on Text-fig. 4.14 relative to Lickershamn 2 samples in stratigraphic order

When plotted in stratigraphic order (Text-fig. 4.15) the four groups can be identified as group C, which characterises the lower samples, the group B, which characterises the central samples and groups A and D, which mostly characterise samples from the upper part of the section. Although the individual groups appear to be much more clearly distinguished than any identified at Luskint 1, it should be noted that the similarity distance between samples at Lickershamn 2 (Text-fig. 4.14) is much smaller than that seen at Luskint 1 (Text-fig. 4.9, which is plotted at the same scale).

The correspondence analysis for the species at Lickershamn 2 (Text-fig. 16), again has a more widely spaced distribution than that seen at Luskint 1 (Text-fig. 4.11). Although there is some clustering around zero, the clusters identified from the cluster analysis dendrogram (Text-fig. 4.17) plot as overlapping, but distinct groups. The specific characteristics of the clusters are identified in Text-fig. 4.17. The similarity distance recorded for the species at Lickershamn 2 is the same as for Luskint 1 (Text-fig. 4.12).

#### COMPARISON TO OTHER PALYNOLOGICAL STUDIES OUTSIDE OF GOTLAND

In 1974, Hill published the stratigraphic ranges of palynomorphs from the type area of the Llandovery and the Welsh Borderland. Of the 69 species recorded by Hill, 38 have been recorded on Gotland in this study. Minimal graphical abundance data were presented by Hill (1974) which is not of high enough detail to compare to the data presented here. The range end diagrams provide the most useful basis for comparison.

Hill (1974) recorded the last appearances of *Tunisphaeridium parvum* and *Visbysphaera meson* below the Telychian, much earlier than recorded on Gotland where they were found at the top of the Visby Beds. *Dilatisphaera williereae* and *D. laevigata* were recorded as starting at a much lower level by Hill (in the Fronian and early Telychian respectively). On Gotland, *D. williereae* first appears in the Lower Visby Beds and *D. laevigata* in the Upper Visby Beds. Hill recorded a near identical level of origination for *Deunffia monospinosa* as that seen in Gotland, but recorded it disappearing at a lower level in type area. *Hoegklintia corallina* was only recorded in the late Llandovery Hughley Shales by Hill, but is not recorded until the early Wenlock Upper Visby Beds in this study. *Deunffia ramusculosa* was reported to have a slightly earlier origination than in Gotland, where it ranges from near the base of the section studied here. *Cymatiosphaera octoplana* and *Pterospermella foveolata* have roughly the same level of origination. Most of the species ranges identified by Hill are not comparable to those on Gotland and many have been extended in subsequent studies.







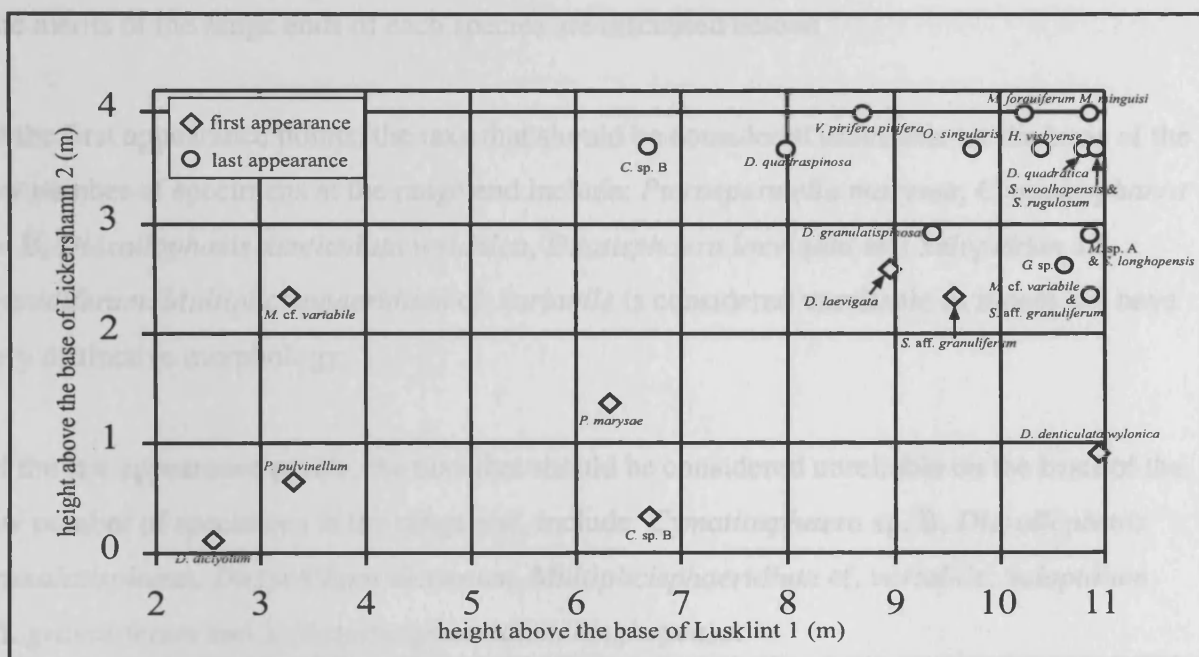
Dorning (1981a) also provided comparable data for the boundary beds of the Llandovery and Wenlock type areas, but gave no abundance figures. Of the 63 species he recorded in the late Llandovery Hughley Shales and the early Wenlock Buildwas Formation, 30 species are common to Gotland.

Dorning (1981a) reported *Multiplicisphaeridium neaghiae* as last appearing in Shropshire in the Llandovery, whereas it is recorded high in the Upper Visby Beds in Gotland. Similarly, *Visbysphaera meson* disappears in Shropshire in the lowermost Wenlock before its last recorded occurrence at the top of Luskint 1 in Gotland. *Elektoriskos aurora* and *Domasia bispinosa* begin at a similar level in both Gotland and Shropshire. Dorning recorded *Pterospermella foveolata* originating a little earlier than reported in Gotland. *Eupoikilofusa striatifera*, *Tylotopalla robispinosa* and *Helosphaeridium pseudodictyum* all have their first and last appearances in Shropshire before and after those seen in Gotland. The last appearances of *Salopidium wenlockensis* and *Deunffia ramusculosa* are recorded at a much higher level in Shropshire, as late as the Ludlow. *S. woolhopensis* was similarly recorded with a range end at a higher level in Shropshire than in Gotland.

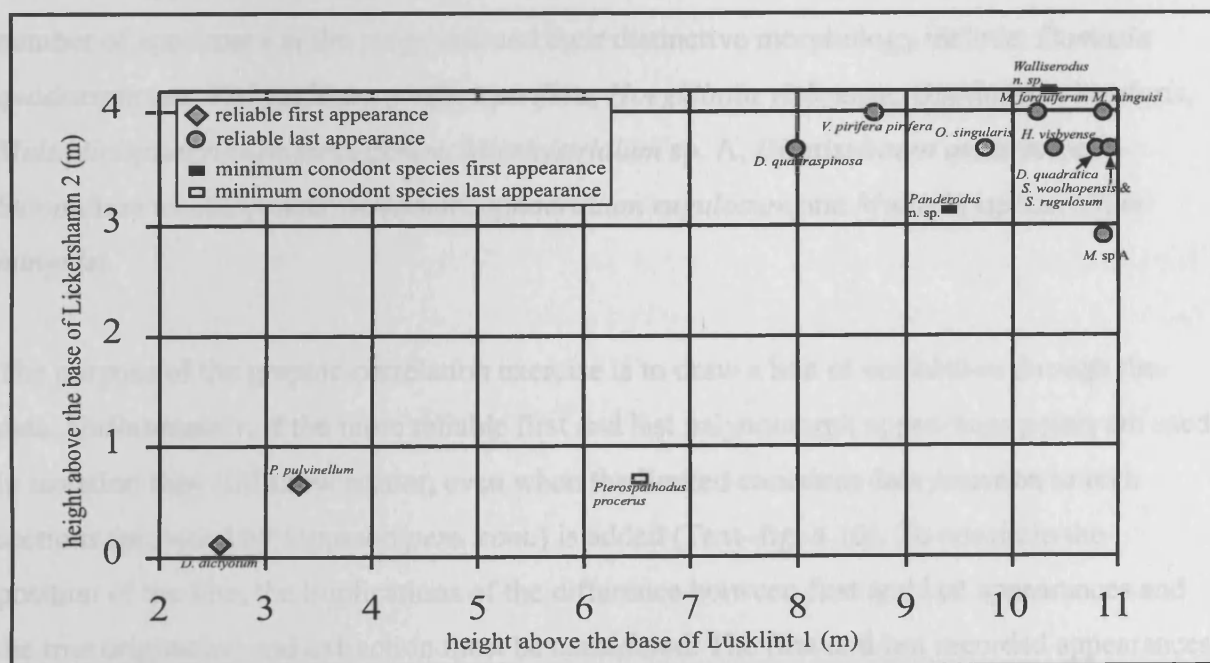
Mabillard and Aldridge (1985) recorded 62 palynomorph species in the Llandovery/Wenlock boundary type section, 26 of which are found at the same interval on Gotland. Many of the range ends are not comparable with those recorded here, as they have been extended in subsequent studies. Those that can be compared are: *Domasia ramusculosa* and *Domasia quadrispinosa* which appear slightly earlier in Gotland and *Gracilisphaeridium encantador* and *Dictyotidium dictyotum* which first appear at about the same level in both localities.

#### GRAPHIC CORRELATION

A scatter graph was plotted for graphic correlation (see Shaw 1964), using the stratigraphic levels of the first and last appearances of palynomorphs recorded both at Luskint 1 and Lickershamn 2 (Text-fig. 4.18). The data points are scattered, making it impossible to place a line of correlation. The level of scatter is surprising, as the sections are very close to each other (about 4km apart) and the sampling was of higher resolution than that of most studies used for graphic correlation. (Much of the scatter can probably be explained by the fact that samples were not collected high or low enough at Lickershamn 2). It is therefore necessary to reassess the data points. Data for species that occur in extremely low numbers or for species that gradually tail off from a previously high abundance are less reliable than those for more numerous species and for those that decline rapidly (see range end discussion above). Species



TEXT-FIG. 4.18. Graph showing all the first and last palynomorph appearance points common to both Luskint 1 and Lickershamn 2.



TEXT-FIG. 4.19. Graph showing the reliable first and last palynomorph appearance points and conodont first and last appearance points common to both sections.



that were difficult to identify have less reliable range ends than those that are easily identified.

The merits of the range ends of each species are discussed below:

Of the first appearance points, the taxa that should be considered unreliable on the basis of the low number of specimens at the range end include: *Pterospermella marysae*, *Cymatiosphaera* sp. B, *Diexallophasis denticulata wylonica*, *Dilatisphaera laevigata* and *Salopidium* aff. *granuliferum*. *Multiplicisphaeridium* cf. *variabile* is considered unreliable as it does not have very distinctive morphology.

Of the last appearance points, the taxa that should be considered unreliable on the basis of the low number of specimens at the range end, include: *Cymatiosphaera* sp. B, *Diexallophasis granulatispinosa*, *Dictyotidium dictyotum*, *Multiplicisphaeridium* cf. *variabile*, *Salopidium* aff. *granuliferum* and *Schismatiosphaeridium longhopense*.

The reliable first appearance points are those of *Dictyotidium dictyotum*, which is both numerous and distinctive and *Pulvinosphaeridium pulvinellum*, which although occurring in low numbers is highly distinctive.

Of the last appearance points, the taxa that should be considered reliable on the basis of the number of specimens at the range end and their distinctive morphology include: *Domasia quadraspinosa*, *Visbysphaera pirifera pirifera*, *Hoegklintia visbyense*, *Oppilatala singularis*, *Multiplicisphaeridium forquiferum*, *Micrhystridium* sp. A, *Dilatisphaera quadratica*, *Salopidium woolhopensis*, *Schismatiosphaeridium rugulosum* and *Multiplicisphaeridium minguisi*.

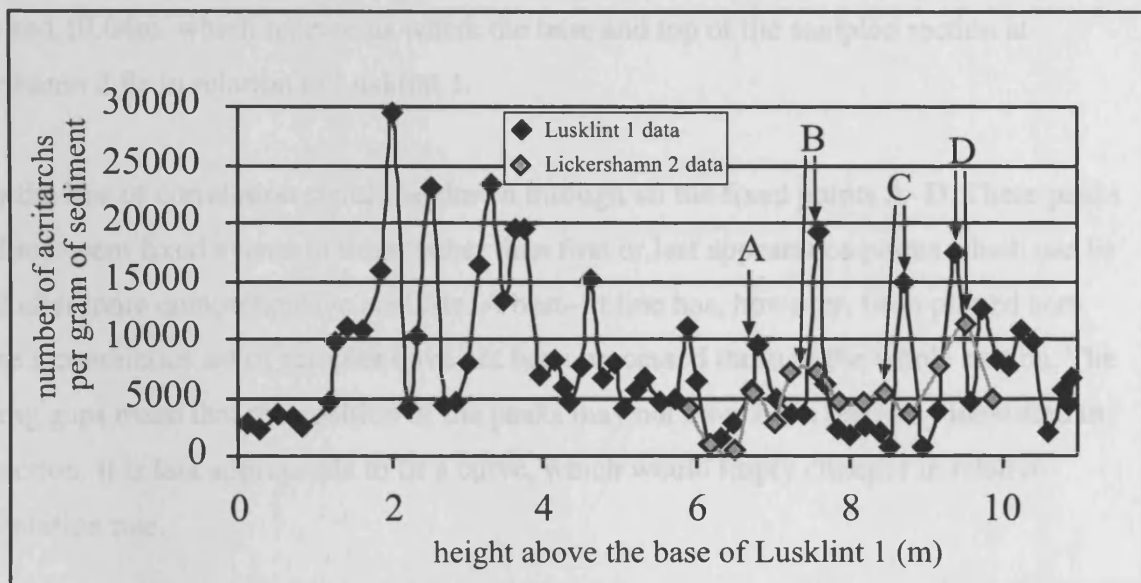
The purpose of the graphic correlation exercise is to draw a line of correlation through the data. Unfortunately, if the more reliable first and last palynomorph appearance points are used in isolation they still show scatter, even when the limited conodont data common to both sections (provided by Jeppsson *pers. com.*) is added (Text-fig. 4.19). To constrain the position of the line, the implications of the difference between first and last appearances and the true origination and extinction must be considered. The first and last recorded appearances of a species are unlikely to be the true levels of origination or extinction, which would be at some point earlier or later in time. The line should therefore lie below the first appearance points and above the last appearance points. Uncertainty still lies in how much the range might be extended and in which section it should be extended (it is very unlikely it would be extended by the same amount in both sections).

To further constrain the line of correlation, alternative correlation points that are represented in both sections must be sought. Unfortunately, the relative abundance data are too complex to single out precise levels that are apparent in both sections. However, the data for the number of acritarchs per gram of sediment contains four distinct peaks in the upper part of Luskint 1, which can be matched with smaller peaks in the number of acritarchs per gram data for Lickershamn 2 (Text-fig. 4.20 peaks A–D). When these data points are plotted they follow a near linear pattern (Text-fig. 4. 21).

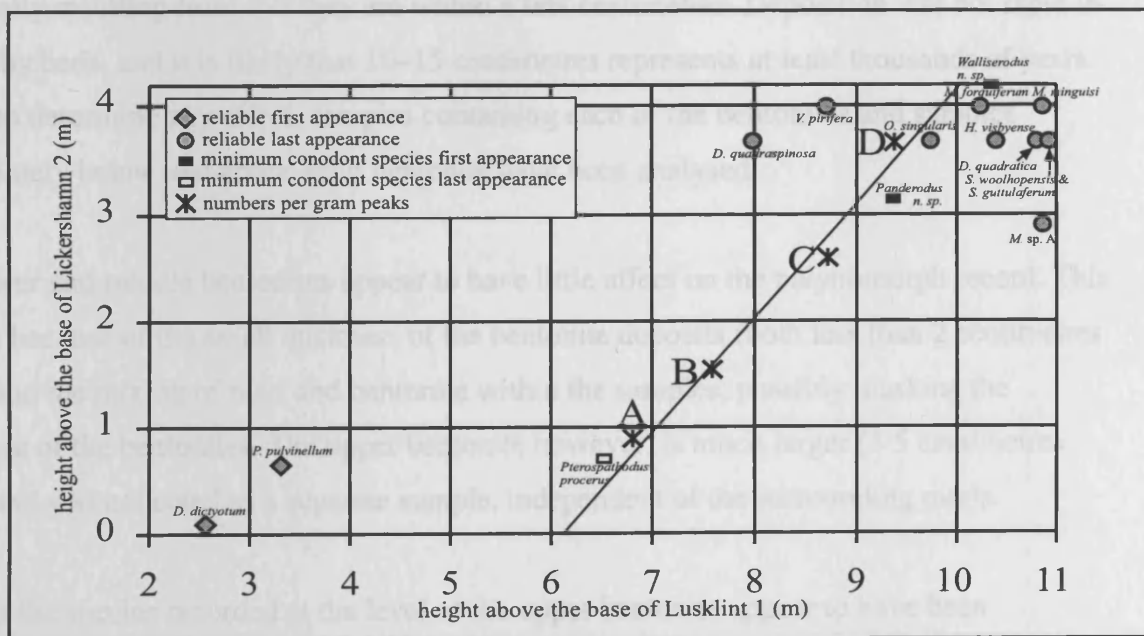
At first glance, the correlation line drawn on Text-fig. 4.21 appears to solve the correlation problem, but the peaks in the number of palynomorphs per gram of sediment should be treated with caution. These points would be usable if they result purely from changes in productivity, but this may not be the case. The number of palynomorphs per gram of sediment is dependent on many factors, such as preservation potential, sedimentation rate, and nutrient levels, but most of all it is dependent on lithology. Limestones are much more competent than marls and therefore undergo much less compaction than the same original thickness of marl. A given thickness of limestone today, therefore represents a shorter period of time than the equivalent thickness of marl. The smaller the amount of time represented, the fewer the number of palynomorphs. Hence, the peaks could merely represent changes in lithology between limestone and marl, which occur regularly through the whole of both sections.

At Luskint 1, peak A is formed by sample DG00LK1.167, which is a marl. The sample directly before that is another marl, but the two samples below that (forming the trough on Text-fig. 4.20) are both limestones. Above peak A, the three samples are all limestones. Peak B (sample DG00LK1.183, a marl), is preceded by the same three limestone samples (forming the trough) and followed by three marl samples. Peak C (sample DG00LK1.211, a marl) is preceded by three limestone samples and followed by a limestone/marl sample. Peak D (sample DG00LK1.223), contrary to the prediction of the peaks being made up of marl surrounded by limestone samples, is a limestone preceded by a marl and a limestone/marl sample. Above this are two limestone samples. All the samples analysed at Lickershamn 2 (apart from two limestone/marl samples) are limestone.

Shaw (1964) used least squares linear regression to calculate the line of correlation, but this method does not take into account the relative significance of appearances, or disappearances of different species (see discussion in MacLeod & Keller 1991, p. 1442). The line drawn here cannot be fully trusted, but it is a best estimate with the available data and fits with the



TEXT-FIG. 4.20. Graph showing the number of palynomorphs per gram of sediment at Luskint 1 and Lickershamn 2. The Lickershamn 2 data has been superimposed (at the same scale) onto the Luskint 1 plot. Peaks common to both sections have been labelled).



TEXT-FIG. 4.21. Graph showing the reliable first and last palynomorph appearance points, conodont first and last appearance points and number of palynomorphs per gram of sediment peaks common to both sections. A correlation line has been drawn based upon points A-D.

conodont first and last appearance points. The gradient of the line is  $45.8^\circ$ , which forms a ratio for Luskint 1 to Lickershamn 2 of 1:1.03. The correlation line intercepts the Luskint 1 axis at 6.08m and 10.04m, which represents where the base and top of the sampled section at Lickershamn 2 lie in relation to Luskint 1.

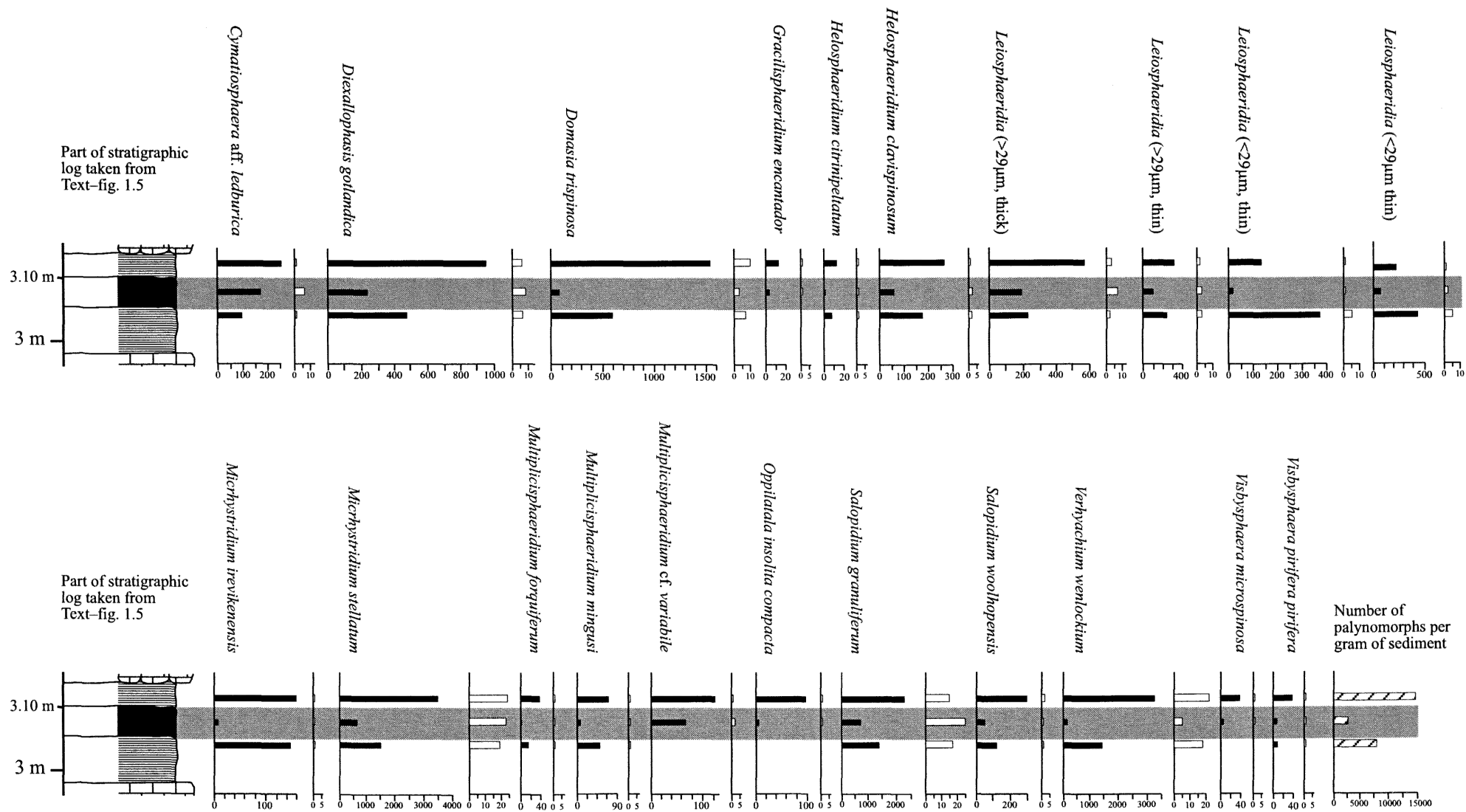
Ideally the line of correlation should be drawn through all the fixed points A–D. These peaks should represent fixed events in time, rather than first or last appearance points which can be moved after more comprehensive analysis. A best-fit line has, however, been plotted here because a continuous set of samples have not been processed through the whole section. The sampling gaps mean that the position of the peaks may not have been precisely identified in each section. It is less appropriate to fit a curve, which would imply changes in relative sedimentation rate.

#### THE EFFECT OF BENTONITE DEPOSITION ON THE PALYNOMORPH RECORD

In the context of the changes in the palynomorphs during the Ireviken Event, the effect of bentonite deposition is difficult to decipher. Any variations in the abundances before, or directly leading up to, the deposition can be regarded as influenced by factors other than the bentonite. Variations occurring after the deposition of the bentonite can only be regarded as potentially resulting from it if they are within a few centimetres. Deposition was not rapid in the Visby beds, and it is likely that 10–15 centimetres represents at least thousands of years. To try to determine any effect, samples containing each of the bentonites and samples immediately below and above each bentonite have been analysed.

The lower and middle bentonites appear to have little affect on the palynomorph record. This may be because of the small thickness of the bentonite deposits (both less than 2 centimetres thick) and the mixing of marl and bentonite within the samples, possibly masking the influence of the bentonites. The upper bentonite however, is much larger (5.5 centimetres thick) and was collected as a separate sample, independent of the surrounding marls.

Most of the species recorded at the level of the upper bentonite appear to have been unaffected by the ash fall; species that show a detectable abundance change have been plotted on Text-fig. 4.22. The number of palynomorphs per gram of sediment shows a sharp drop



TEXT-FIG.4.22. Graph showing the absolute abundance of selected species (black bars), percentage abundance of selected species (white bars) and number of palynomorphs per gram of sediment (patterned bars), across the upper bentonite.

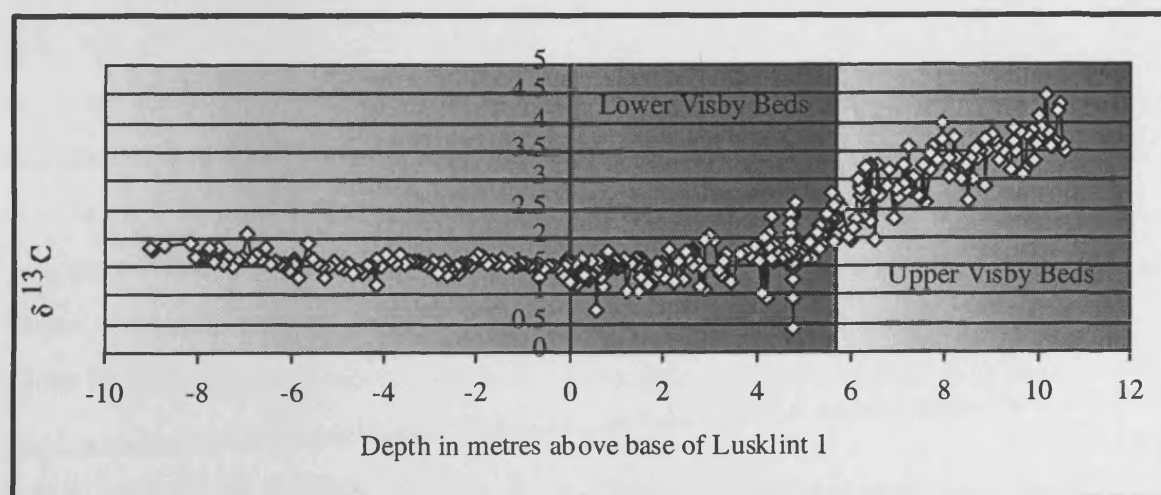
from 7755 before the bentonite to 1656 within the bentonite, then rising to 14670 after. Most species reflect these figures without changes in relative abundance, which are only apparent in a few taxa. *Cymatiosphaera* aff. *ledburica* shows a slight increase from 1.29% before the bentonite, to 6.74% in it, falling to 1.81% after. *Micrhystridium stellatum* and *Salopidium granuliferum* also show an increase in percent abundance within the bentonite. This level is maintained in *M. stellatum*, but falls again to 15.61% in *S. granuliferum*. *Veryhachium wenlockium* has a fall in percent abundance at the bentonite, from 18.0% to just 5.35%. The proportion instantly recovers to previous levels above. *Domasia trispinosa* falls from 7.92% before the bentonite to 3.16% within it, but again recovers to 10.87% after.

#### THE GEOCHEMICAL RECORD

##### *Stable carbon and oxygen isotope data for Luskint 1*

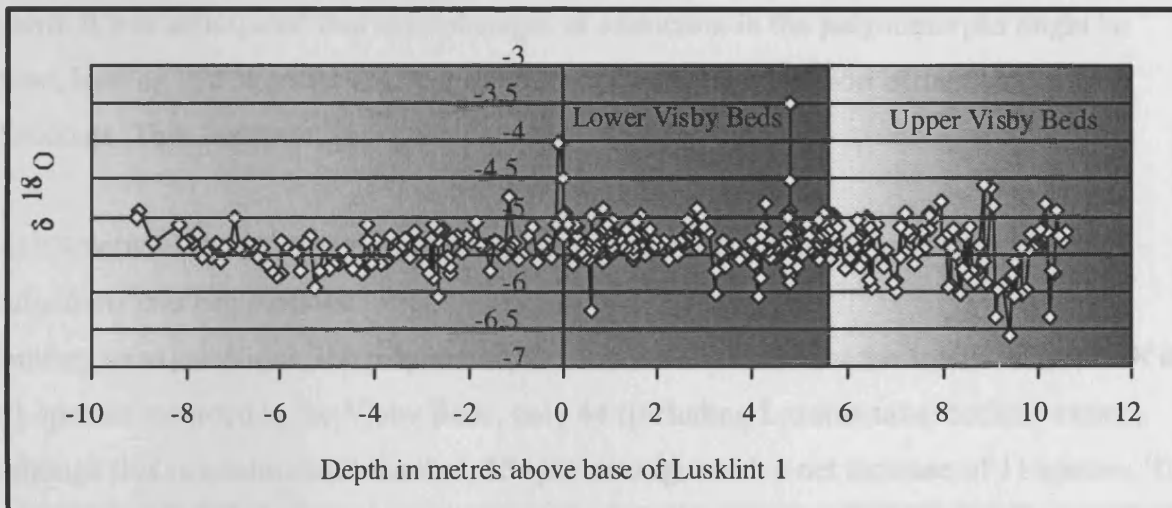
Dr. Richard Corfield and Dr. Derek Siveter of the University of Oxford have collected samples for analysis of stable carbon and oxygen isotopes, from Luskint 1. Their samples were collected from 8.75m below the base of the section sampled here, to 10.89m above (see Appendix 9). Corfield and Siveter have kindly made their data available for comparison with the acritarch record.

Between -8m and 4m, the carbon stable isotope data (Text-fig. 4.23) shows a roughly consistent signature, with a  $\delta^{13}\text{C}$  value of around 1.5. The samples below -8m have  $\delta^{13}\text{C}$  values of around 1.8. Above 4m the samples show a rising trend, from around 1.6 to 4.2. The  $\delta^{13}\text{C}$  values in the upper part of Luskint 1 are more variable than those from the lower part of the section.



TEXT-FIG. 4.23. Graph showing the  $\delta^{13}\text{C}$  whole rock analysis relative to the base of the section sampled for this study, data provided by Corfield and Siveter.

The oxygen stable isotope data (Text-fig. 4.24) show a roughly consistent signature mostly falling within the -5 to -6 range. There are a number of outliers (e.g. the sample at 4.79 m has a value of -3.5), which can probably be disregarded as an experimental error. The main deviation from the steady state values occurs at around 9m to 9.5m, where a fall to a  $\delta^{18}\text{O}$  value of around -6 and subsequent rise to previous levels, is recorded.



TEXT-FIG. 4.24. Graph showing the  $\delta^{18}\text{O}$  whole rock analysis relative to the base of the section sampled for this study (data provided by Corfield and Siveter).

## DISCUSSION AND CONCLUSION

The main aims of this study were to investigate the palynomorph record through the Ireviken Event and to endeavour to relate the changes recorded to possible climate and sea-level changes and to the highly detailed conodont record for this time. The presumption was that the devastating extinction seen in the conodonts would be mirrored in the palynomorph record. It was anticipated that several stages of extinction in the palynomorphs might be found, leading to a stepwise collapse in the food-web and knock-on extinctions in the conodonts. This, however, is not the case.

## PALYNOMORPH EXTINCTIONS, ORIGINATIONS, ABUNDANCE CHANGES AND MIGRATIONS

*Extinctions and originations*

Contrary to expectations, the palynomorphs were not devastated at the Ireviken Event. Of the 111 species recorded in the Visby Beds, only 44 (including Lazarus taxa) became extinct. Although this is a substantial number, 55 species originated, a net increase of 11 species. The turnover in palynomorph species is dramatic over this interval, but diversity increases rather than decreases. The stratigraphic range plots constructed by Le Hérisse (1989) for the Visby Beds also show this pattern, with 43 species becoming extinct and 54 originating.

Most of the species that originated and/or became extinct are from the genera *Multiplicisphaeridium*, *Oppilatala*, *Pterospermella*, *Salopidium*, and *Visbysphaera*. It is suggested that these genera contain species that lie at the very edge of their environmental tolerances. The species that became extinct would have found it difficult to tolerate environmental change and the species that originated were probably pioneers moving into new niches that the more established species could not tolerate. Although these complex patterns are difficult to explain, it is possible that changing sea-level and environment were gradually creating new global and local niches through the whole of the Ireviken Event. The gentle pace of these changes enabled a steady increase in the number of species. The absence of a gradual extinction pattern may be because the palynomorphs could tolerate small gradual changes without becoming extinct, but once the cumulative effect of these changes had become large enough, a more sudden and concentrated set of extinctions took place.

Alternatively, environmental changes may have been gradual through most of the event (stimulating the gradual originations as new niches opened up), apart from the end where more severe changes took place. The palynomorphs may have been able to tolerate the gradual changes, but not the more severe later stage ones.



A further line of evidence to suggest that the palynomorphs were more environmentally tolerant than previously suggested lies in the relationship with the conodonts. At the outset of this study, the hypothesis was forwarded that the extinction of palynomorph species might have directly, or indirectly caused the extinction of conodont species. For this, a step-wise extinction pattern, close to that of the conodonts would be predicted. The original hypothesis assumed that the acritarchs were more climate sensitive than the conodonts and became extinct first, but the data show that the palynomorph extinctions followed those of the conodonts. This suggests the conodonts were more environmentally sensitive than the palynomorphs.

#### *Range end confidence limits*

Graphic correlation between Lickershamn 2 and Luskint 1 suggested that in many cases the recorded palynomorph range end points are not representative of the true range ends (especially where the range end currently lie at the position of the highest or lowest sample in either section). The range end statistical analyses attempted in this study proved inconclusive; future analysis utilising all available data is suggested.

#### *Multivariate analysis*

The multivariate analysis carried out on the abundance data from Luskint 1 shows three distinct groups of samples in the bottom, middle and top of the section. The base is dominated by higher *M. stellatum*, *V. wenlockium* and *S. granuliferum*; the middle by low levels of *M. stellatum* and *V. wenlockium* and a higher number of *S. granuliferum*; the top by abundant *M. stellatum* and *V. wenlockium* and less abundant *S. granuliferum*. These variations are independent of lithology (which is very different at the top and bottom of Luskint 1) and may reflect changes in sea level or climate. Seven groups of species with comparable distributions were identified at Luskint 1, the largest of which is made up of the most common species. The apparent sensitivity of the commonly occurring species over others to the changes occurring at this time may be a reflection of their greater number, but may also reflect a relatively enhanced sensitivity to sea level and environmental change.

The repetition of cluster analysis sample groups at both the base and the top of Luskint 1, suggests the possibility of a cycle. It is difficult to identify the cause, but a cyclic change in sea level, or climate may be responsible. Until the analysis of samples that extend the stratigraphic range of the section is conducted the extent and reliability of this signal cannot be assessed.

The multivariate analysis carried out for Lickershamn 2 gave much more distinct patterns, probably because of the smaller number of samples analysed. The samples could be split into three similar groups, again representing the bottom, middle and top of the section. These groups probably reflect a lower number of the more common species at the base of the section, slightly higher in the central section and higher still in the top part of the section. Four groups of species with similar distributions in Lickershamn 2 were identified, mostly characterised by a similarly rare or similarly common occurrence.

#### *Comparison to other palynological studies outside of Gotland*

There are three main problems associated with comparisons to other palynological studies: the unprecedented high resolution of sampling in this study, the level of detail recorded when the samples were logged and the unknown level of the Llandovery/Wenlock boundary and graptolite zones on Gotland.

A summary of the probable migrations between Gotland and the Welsh Basin is made in Text-fig. 5.1, although these may be revised with more precise data from the British sections. Migrations into Gotland are classed as species that are first recorded in the Welsh Basin and later in time in Gotland. Migrations into the Welsh Basin are classed as species that are first recorded in Gotland and then later in time in the Welsh Basin. At present, this comparison suggests there were a slightly more migrations out of Gotland to the Welsh Basin (seven out and three into Gotland).

Author	Migration	
	To Gotland	To the Welsh Basin
Hill 1974	<i>D. laevigata</i> <i>D. williereae</i> <i>H. corallina</i>	<i>D. ramusculosa</i>
Dorning 1981a		<i>D. ramusculosa</i> <i>P. foveolata</i> <i>S. wenlockense</i> <i>S. woolhopensis</i>
Mabillard & Aldridge 1985		<i>D. quadrispinosa</i> <i>D. ramusculosa</i>

TEXT-FIG. 5.1. Summary of the apparent migrations in and out of Gotland and the Welsh Basin at the Llandovery/Wenlock boundary.

This comparison is very limited and without reliable abundance data for both areas an estimation of how favourable the conditions in each area was, cannot be made.

The mostly consistent pattern of earlier originations than in Gotland recorded by Hill (1974), suggests that at least three species migrated into the Baltic once they had become established in the type area. When the results of Dorning (1981a) are compared to the data presented here it is found that four species originated earlier in Gotland and then presumably migrated to the Welsh Basin.

The work of Mabillard and Aldridge (1985) was of high resolution (about half that of this study), but of the 62 species recorded, only 26 are found at the same interval on Gotland. On comparison to the present study two originations appear earlier in Gotland suggesting these species migrated from Gotland to the Welsh Basin at this time.

#### THE RESPONSE OF THE PALYNOMORPHS TO THE DEPOSITION OF THE UPPER BENTONITE

The palynomorphs recovered from the bentonite sample show a marked drop in the number per gram of sediment. In the sample above, collected from the following few centimetres, a marked rise in number is recorded. Most species simply reflect this by increasing in number and do not change their relative abundance. The change in number is probably mostly a result of the different amounts of time being sampled. The bentonite most likely represents a single eruption, at most lasting several years, whereas the subsequent marl deposit probably represents hundreds, if not thousands of years. Alternatively, the change in number may in part be a direct result of the deposition of the bentonite. During bentonite deposition the short-term oceanic conditions may not have been very good for the palynomorphs, blocking out light and smothered them. In the slightly longer term the fertilizing potential of the bentonite could have caused a recovery, with numbers reaching a higher level than before the bentonite. *Cymatiosphaera* aff. *ledburica*, *Micrhystridium stellatum*, *Salopidium granuliferum*, *Domasia trispinosa* and *Veryhachium wenlockium* are most affected by the bentonite. *C.* aff. *ledburica*, *M.* *stellatum*, and *S.* *granuliferum* all increase their percent abundance in the bentonite sample and *D.* *trispinosa* and *V.* *wenlockium* decrease their percent abundance. All the species apart from *M.* *stellatum* (which continues to increase in percent abundance) return to their previous abundance levels after the eruption. It can therefore be concluded that these five species are the most bentonite sensitive. The lower and middle bentonites have no observed affect on the palynomorph record. There are no originations or extinctions specifically associated with any of the bentonites, other than those consistent with the patterns associated with the whole section.

Very few studies have been published on the effects of bentonites on planktonic communities. Perhaps the publication most applicable to this study is by Rigby and Davies (2000), who analysed the response of graptolites to the introduction of ash to the Llandovery ocean. They reported a plankton bloom immediately above a bentonite horizon (as reported here) and suggested this was stimulated by an influx of nitrogen, phosphates and silicon, in conjunction with the increased micronutrients including iron. 'Fresh' iron (hydrolysed  $\text{Fe}^{3+}$ ) is more readily absorbed by plankton, rather than the older iron, which, becomes progressively more colloidal and less reactive (Davis 1967). The influx of ash into the ocean system would be a ready source of  $\text{Fe}^{3+}$  and a massive bloom stimulant. It has been shown by Watson (1997), that inputs of volcanogenic iron (in this case from Mount Pinatubo into the Southern Ocean where iron is limiting) produce a huge rise in primary productivity. Ash from the Iceland 2000 Hekla eruption (Frogner 2001) has been shown to produce a rapid release of 'bioactive trace metals... available to support primary production'. Strong (1993) reported observations that show the eruption of El Chichón in 1982 produced a rapid and dramatic reduction in phytoplankton concentrations in the summer and autumn of that year. The longer-term effects were not discussed.

Botting (1999) suggested that volcanic eruptions in the Ordovician did not generate an instant response in the plankton (in this case graptolites and pseudoplanktic inarticulate brachiopods). An increase in absolute abundance was calculated to have occurred 100–200 years later (determined from the mean sedimentation rate calculated from the duration and thickness of the *teretiusculus* Biozone). This abundance increase was suggested to have been caused by an upwelling of nutrients initiated by the descent of dense ash-rich water. Contrary to the interpretations made here, the nutrient rich ash was suggested to have generated no direct response. Botting (1999, p. 502) argued that a feedback loop is likely to have been set up whereby plankton blooms produced a high influx of nutrients to the benthos, which then perpetuated the benthos and promoted continued circulation. The mechanism by which the benthos perpetuated the circulation was not discussed.

It is possible that a delayed response of the plankton to the deposition of volcanic ash, as reported by Botting, might be present at Lusklint 1 (the signal could be included within the sample directly above the bentonite and now seen in the absolute abundance data). At present it is not possible to confirm this, as the thickness of sediment at Lusklint 1 represented by 100–200 years is unknown. A comparison to the patterns Botting recorded is further complicated because graptolites and pseudoplanktic inarticulate brachiopods are unlikely to

have reacted in the same way as palynomorphs to a volcanic eruption. The volcanic deposit is likely to be different at different localities, varying in chemistry, grain size and residence time in the water column, which would all make a significant difference to the response of the plankton. It is possible that the feedback loop suggested by Botting occurred on Gotland, but at this stage this is impossible to test.

Around the Llandovery/Wenlock boundary volcanism was geographically widespread, ranging from Gotland (Laufeld 1976), to the British Isles (Fortey *et al.* 1996), to Australia (Jones *et al.* 1995). It was also temporally widespread through the Silurian; for example, there are numerous bentonites in the Ludlow (Mullins 2001). The volcanism seen at Luskint 1 was probably not significant enough to cause extinctions. Most of the palynomorph extinctions recorded are significantly later than the bentonite layers and bentonites recorded elsewhere in the Silurian are not associated with extinctions.

#### GRAPHIC CORRELATION

One of the main conclusions that can be drawn from the graphic correlation exercise is that the sections are not long enough for reliable results, especially as there are no common marker horizons. The other main conclusion is, that if the correlation line is correct or even roughly correct, the sampled interval at Lickershamn 2 does not extend Luskint 1; it just repeats part of it. The 45.8° angle of the correlation line suggests that the overall sedimentation rate at the two sections is almost identical with a slightly faster rate at Lickershamn 2. If the correlation line is correct, the range ends of the conodonts are more reliable for correlation than those of the acritarchs. Further sampling above and below both sections needs to be carried out to determine precisely the correlation of the sections. Using another analytical method such as magnetic susceptibility (Ellwood *et al.* 2001) may be an alternative way of solving the problem.

#### THE GEOCHEMICAL RECORD

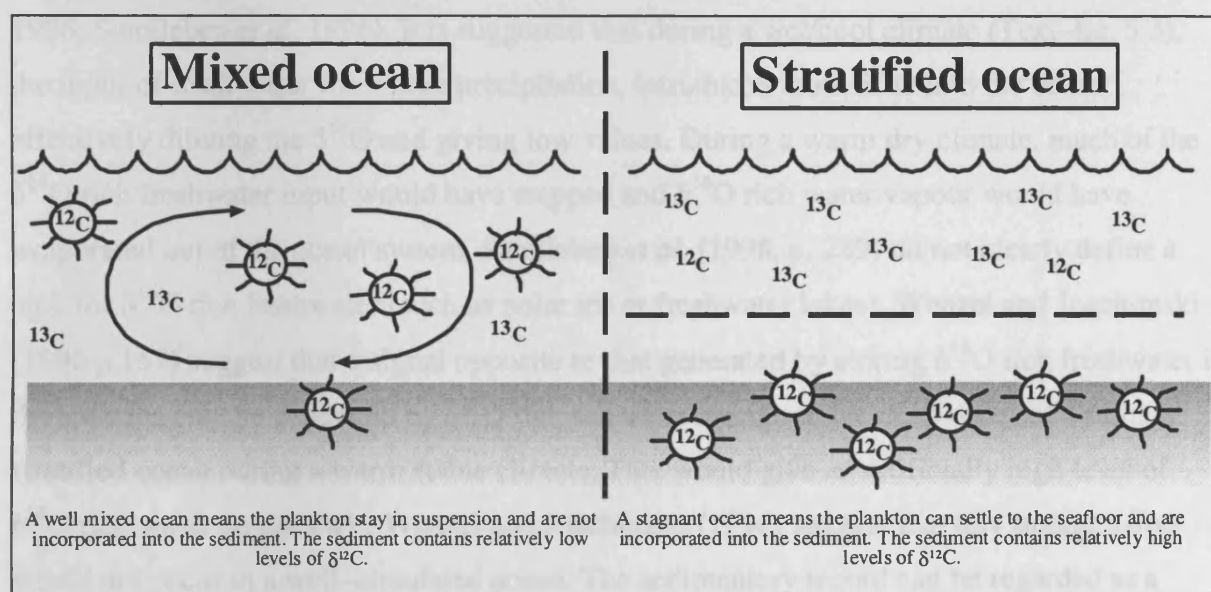
##### *Stable carbon and oxygen isotope data for Luskint 1*

The stable isotope data, provided by Corfield and Siveter and used here, are derived from the analysis of whole rock samples and reflect the nature of the isotopes buried in the sediment not those present in the ocean.

Plankton preferentially incorporate  $\delta^{12}\text{C}$  rather than  $\delta^{13}\text{C}$  during photosynthesis, providing a mobile sink for  $\delta^{12}\text{C}$ . When the ocean was well mixed (Text-fig. 5.2) low levels of plankton were incorporated into the sediment, as there was little opportunity for them to settle to the

seafloor. Relatively low levels of  $\delta^{12}\text{C}$  were incorporated into the sediment (i.e. whole rock samples), whereas high levels might have occurred in the ocean (and be reflected in samples purely analysed from brachiopod shells secreted in equilibrium with the oceanic water).

When the ocean became stratified (Text-fig. 5.2) undisturbed settling of plankton to the seafloor occurred, favouring incorporation of plankton into the sediment. The removal of plankton (rich in  $\delta^{12}\text{C}$ ) from the ocean system, would have given a relatively rich  $\delta^{13}\text{C}$  ocean (recorded in brachiopod shell samples) and a  $\delta^{12}\text{C}$  rich sediment (recorded in whole rock samples). Therefore, the sedimentary  $\delta^{12}\text{C}/\delta^{13}\text{C}$  ratio in both oceanic circulation states was very different from that of the ocean.



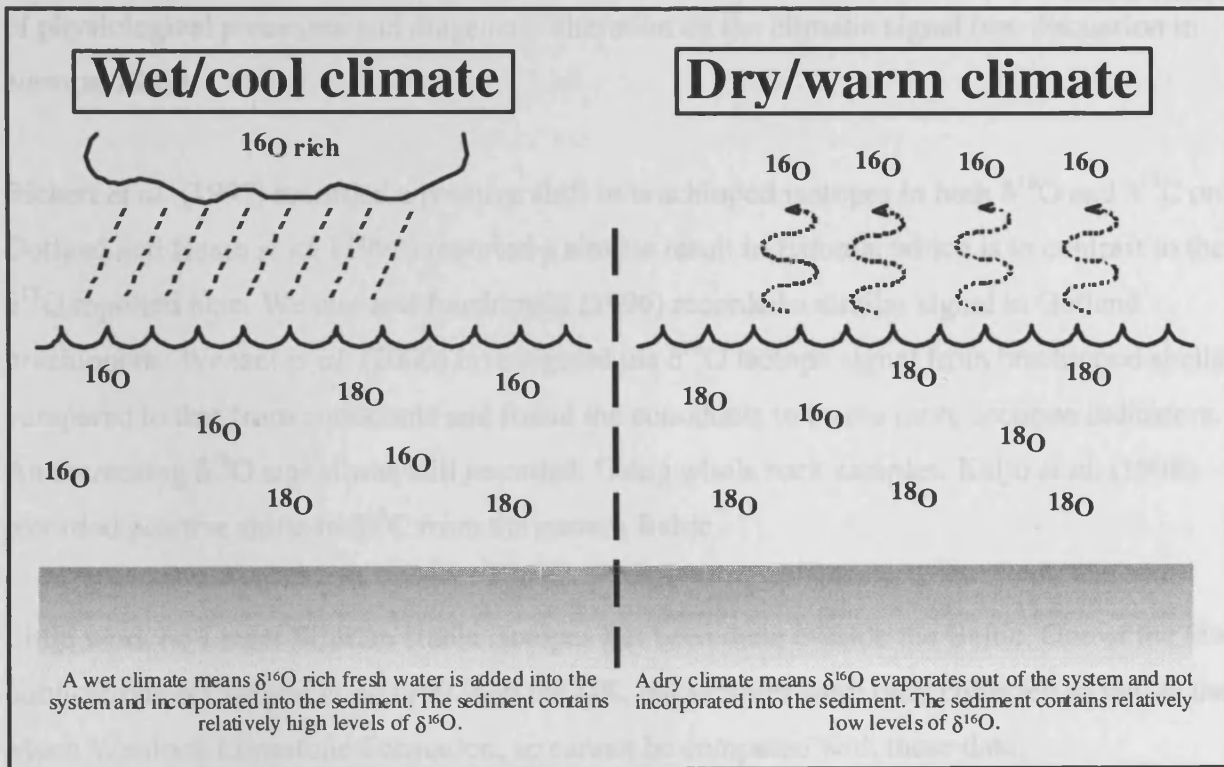
TEXT-FIG. 5.2. Cartoon showing the relative levels of  $\delta^{12}\text{C}$  incorporation into oceanic sediment, in a well-mixed and a stratified ocean.

Primary productivity undoubtedly had a very large influence on the preserved carbon isotope record. If many more plankton were present in the oceans at a particular time, the amount that became incorporated in the sediment must have been greater than during times of lower productivity, independent of the oceanic circulation conditions. This would increase the resulting  $\delta^{12}\text{C}$  value, as a greater number of  $\delta^{12}\text{C}$  rich plankton would be incorporated into the sediment. It cannot be assumed that the productivity through the entire Ireviken Event was constant; most likely it changed with climate and/or sea level changes.

For much of the geological record, the oxygen stable isotope record is interpreted as indicative of palaeotemperature. It is suggested that during glacial periods the oceans become progressively depleted in  $\delta^{16}\text{O}$ . This is because the lighter  $\delta^{16}\text{O}$  is preferentially removed from

the oceans during evaporation, rather than the heavier  $\delta^{18}\text{O}$ .  $\delta^{16}\text{O}$  rich water is then precipitated as snow to form glacier ice and ice caps. The more severe the glaciation, the larger the ice caps, and the greater the  $\delta^{18}\text{O}$ :  $\delta^{16}\text{O}$  ratio in the ocean. During non-glacial periods, the  $\delta^{16}\text{O}$  has the opportunity to return to the oceans through rainfall and melt-water (see discussion in Railsback, 1990). It is thought that after the demise of the end Ordovician glaciation, little or no ice persisted into the early Silurian (see discussion later in this chapter). Most authors therefore suggest an alternative explanation for the Silurian stable oxygen isotope record.

If oxygen stable isotopes are interpreted as a palaeosalinity record, the major controls on  $\delta^{18}\text{O}$ /  $\delta^{16}\text{O}$  levels were fresh water input and rates of evaporation (Wenzel and Joachimski 1996, Samtleben *et al.* 1996). It is suggested that during a wet/cool climate (Text-fig. 5.3), the input of fresh water from high precipitation, introduced more  $\delta^{16}\text{O}$  into the ocean, effectively diluting the  $\delta^{18}\text{O}$  and giving low values. During a warm dry climate, much of the  $\delta^{16}\text{O}$  rich freshwater input would have stopped and  $\delta^{16}\text{O}$  rich water vapour would have evaporated out of the ocean system. Samtleben *et al.* (1996, p. 289) do not clearly define a sink for  $\delta^{16}\text{O}$  rich freshwater (such as polar ice or freshwater lakes). Wenzel and Joachimski (1996 p.157) suggest that a signal opposite to that generated by storing  $\delta^{16}\text{O}$  rich freshwater in the ice caps may be generated by  $\delta^{18}\text{O}$  rich saltwater storage in the deep water of a salinity stratified ocean during a warm stable climate. This would give an artificially high level of  $\delta^{16}\text{O}$  rich water on the shelf. Wenzel and Joachimski (1996) suggest that this storage effect would not occur in a well-circulated ocean. The sedimentary record can be regarded as a measure of the oceanic  $\delta^{18}\text{O}$ /  $\delta^{16}\text{O}$  levels on the shelf, along with a signal from all the diagenetic depositional carbonate phases in the sample (Heath *et al.* 1998).



TEXT-FIG. 5.3. Cartoon showing the relative levels of  $\delta^{16}\text{O}$  incorporation into oceanic sediment, in a wet/cool and dry/warm climate.

The rise in  $\delta^{13}\text{C}$  may simply reflect the rise in the occurrence of limestones (which rapidly develop into more continuous and thicker units higher in the Upper Visby Beds). The limestones would have had a much greater bioclastic input. If the bioclastic sediment were partly from organisms which constructed calcite shells in areas that were characterised by the  $\delta^{13}\text{C}$  rich ocean and these were then transported further out onto the shelf into the area of Lusklint 1, the sedimentary record would be altered accordingly. Equally,  $\delta^{12}\text{C}$  rich organic debris may have been winnowed out of the bioclastic limestones, which may therefore give a false indication of the buried carbon.

The stable oxygen isotope record suggests that the changes in precipitation and evaporation across the Ireviken Event are very minor and are only picked up in the sedimentary record as a more variable isotope pattern in the Upper Visby Beds. It may also imply there was little change in deepwater circulation and storage effects across the Ireviken Event (Wenzel and Joachimski 1996).

It is difficult to compare Corfield and Siveters' isotope data to other studies because nothing has been published on the same scale. Many other studies use brachiopod shells to derive isotope values which, in recent years has been brought into question because of the influence



of physiological processes and diagenetic alteration on the climatic signal (see discussion in Newton 1997).

Bickert *et al.* (1997) recorded a positive shift in brachiopod isotopes in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  on Gotland and Heath *et al.* (1998) reported a similar result in Estonia, which is in contrast to the  $\delta^{18}\text{O}$  reported here. Wenzel and Joachimski (1996) recorded a similar signal in Gotland brachiopods. Wenzel *et al.* (2000) investigated the  $\delta^{18}\text{O}$  isotope signal from brachiopod shells compared to that from conodonts and found the conodonts to be the more accurate indicators. An increasing  $\delta^{18}\text{O}$  signal was still recorded. Using whole rock samples, Kaljo *et al.* (1998) recorded positive shifts in  $\delta^{13}\text{C}$  from the eastern Baltic.

Little work on Lower Silurian stable isotopes has been done outside the Baltic. One of the few publications is Corfield *et al.* (1992) on the UK, but samples were only collected as low as the Much Wenlock Limestone Formation, so cannot be compared with these data.

#### MODELS FOR THE PALAEOZOIC

Several assumptions have to be made when formulating models to explain the acritarch record in the Palaeozoic. It has to be assumed that the preserved record is an accurate representation of the phytoplankton community. It is reasonable to assume that modern dinoflagellates are analogous to Palaeozoic acritarchs. They have a broadly similar morphology, having for example, similar processes and excystment mechanisms, they are both cyst forming, and acritarchs have a dinoflagellate like, planktonic distribution. Dinoflagellates show no simple cause and effect relationship between environmental factors and morphology; morphology reflects a very complex interplay of factors such as temperature, salinity, nutrient supply and genetics. An equal complexity between acritarch morphology and these factors must therefore be assumed.

If it is assumed dinoflagellates are analogous to acritarchs it is important to know the function of the cyst in modern dinoflagellates. Reviewing opinions at that time, Evitt (1985) suggested that cysts are the resistant housings of hypnozygotes i.e. zygotic cells which are in a non-motile resting stage after sexual reproduction e.g. during the winter months or during adverse conditions. Cysts have been recorded as the benthic resting stage of the life cycle (Dale 1977). Many acritarchs probably did not produce cysts (only around 15% of modern dinoflagellates are cyst producing), but I have assumed the preserved record reflects patterns of primary productivity.

A number of studies that relate modern and Cenozoic dinoflagellates to ecological preferences (such as temperature and nutrient supply) have been published (e.g. Versteegh and Zonneveld 1994, Devillers and de Vernal 2000). The unknowns involved are too great to apply the same principles to the Gotland palynomorphs. Attempts have been made to relate modern dinoflagellates to fossil acritarch species (Dale, 1977), but cannot be applied here because comparable species to the palynomorphs presented here were not used.

The preservation potential throughout the sections is assumed to be the same and the general rate of deposition is assumed to be constant (although it is accepted that marlstones have more potential for compaction than the limestone and therefore represent greater periods of time). The samples processed are assumed to be unbiased, yielding a representative palynomorph population from each level. All these assumptions are difficult to test.

A major assumption made in formulating a model for the Silurian is that changes in atmospheric CO<sub>2</sub> result in changes in climate. The relationship between palaeotemperature changes and changes in CO<sub>2</sub> level is close for much of the Palaeozoic (Berner 1992). The direction of a cause and effect relationship is difficult to distinguish. A major assumption that is usually made when suggesting a model for climate change is that high atmospheric CO<sub>2</sub> levels produce a warm climate. This may not always be the case; Crowley and Baum (1995) suggested that high atmospheric CO<sub>2</sub> levels do not necessarily indicate a warm climate, citing the Late Ordovician glaciation as an example. They considered that the Gondwana plate configuration at that time (which was at a tangent to the South Pole) created a situation where a glaciation occurred during a period of high atmospheric CO<sub>2</sub> levels. This was probably coupled with other factors such as changes in ocean circulation. The glaciation under these conditions was short lived and such an event may be unlikely under most circumstances.

#### *Extinction mechanisms*

Ever since Alvarez *et al.* (1980), published their theory of an extraterrestrial cause for the Cretaceous-Tertiary (K/T) mass extinction, a bolide impact has been a popular mass extinction scenario. The evidence for an impact at the K/T boundary (and perhaps at some other extinction events (Becker *et al.* 2001)) is strong, but it is difficult to implicate an impact at the Llandovery/Wenlock boundary. There are no documented impact structures and there is no chemical evidence (such as an iridium anomaly) for an impact at the Ireviken Event.

It has been established that eruption of voluminous flood basalts is coincident with a number extinction events, for example at the Cretaceous/Tertiary and Permian/ Triassic boundaries

(Kerr 2000). This is often cited as a major causal mechanism for extinctions. There is no evidence for similar occurrences in the Silurian.

There is good evidence for glaciation in the early Silurian (Hambrey 1985, Grahn and Caputo 1992, Caputo 1998). Unfortunately, accurate dating of the glacial events is notoriously problematic. There are glacial deposits of suggested latest Llandovery and earliest Wenlock age (Grahn and Caputo 1992) but the date of these can only be approximately constrained by evidence of the age of overlying strata. The build-up of ice at this time may have caused a small sea level fall, but probably not of enough magnitude to cause an extinction event. At the Llandovery/Wenlock boundary, the ice levels would have been minor (confined to South America), compared to those seen late Ordovician and early Llandovery, when the ice was more widespread covering West Africa, South Africa, the Arabian Peninsula, eastern North America, west and central South America and Europe (Hambrey 1985).

Gas hydrates have been implicated in climate change theories by a number of authors (see discussion in Weissert 2000). The hypothesis involves sudden release of methane from sedimentary gas hydrate deposits, initiated by a warming of the deep ocean (which could be argued to have occurred in an S-state). Methane escape would be reflected by a negative carbon isotope anomaly, which would return to a higher level than the original values as the sedimentary processes responded by burying more organic carbon. The carbon isotope data recorded from Luskint 1 (Corfield and Siviter *pers. com.*) show a gradually increasing positive carbon-isotope anomaly; this suggests methane release was unlikely at this time.

Major tectonic changes were happening globally at the time of the Ireviken Event and throughout the whole Silurian. Although the exact timing is controversial, the early Silurian saw the collision of Baltica and Avalonia with Laurentia (Torsvik *et al.* 1990). The tectonic changes must have had an effect on local sea level, but it is unclear what effect these changes had on the palynomorphs at the Ireviken Event. The effects would have been highly dependent on the timing of the collision and the speed at which it took place, both of which are unclear. The consequences would have been wide ranging altering currents, nutrient supplies and local weather patterns.

All the above factors appear inadequate or insufficiently concentrated to cause the Ireviken Event. There remain two models cited in recent literature: sea level change (Loydell 1998) and the transition from a P to an S state (Jeppsson 1997). These mechanisms are reviewed below.

*Sea level change*

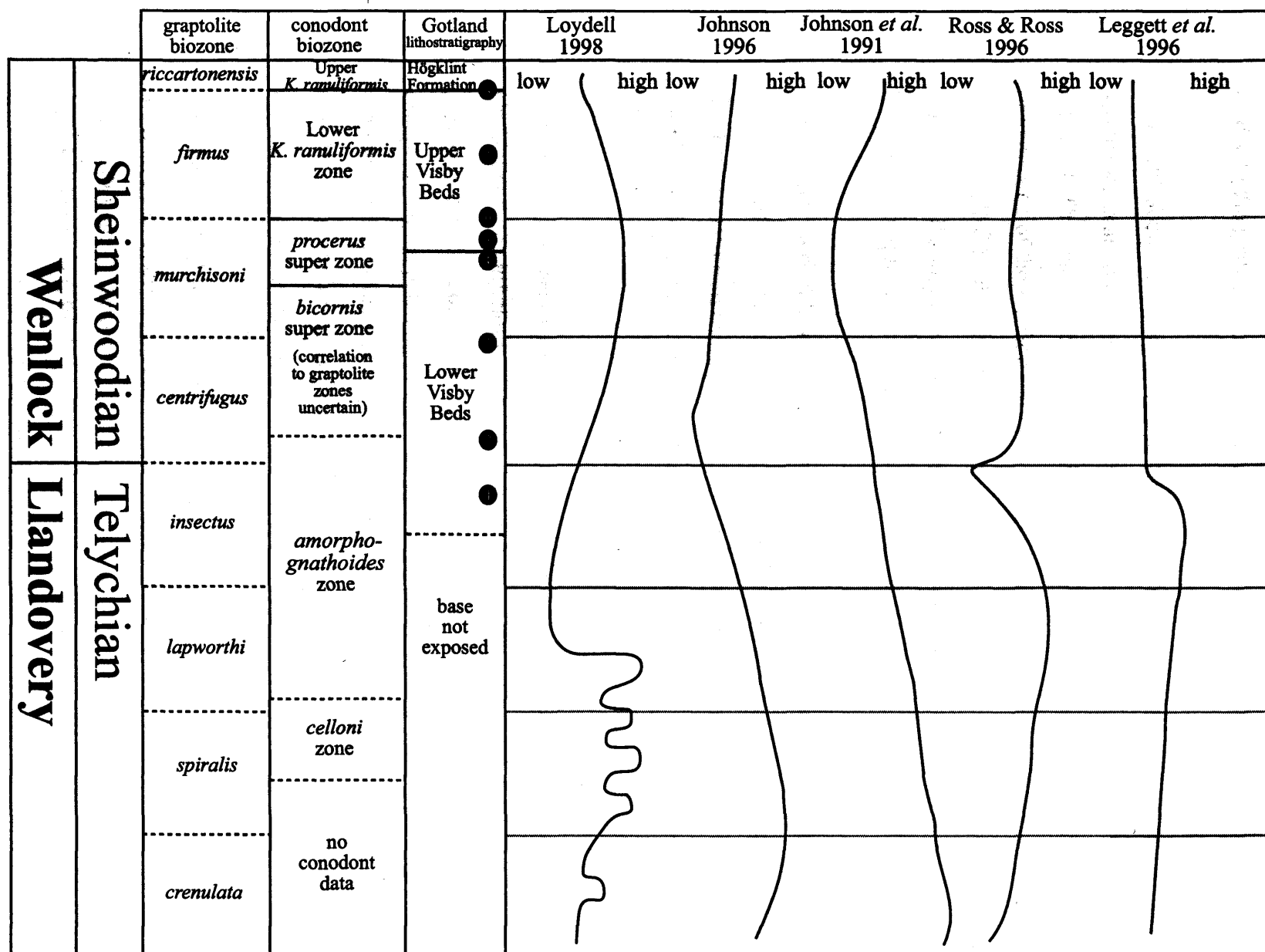
Before 1990 (when Jeppsson published his P and S model), sea level change was the most cited explanation proposed for the faunal and floral changes observed in the Silurian.

Presently, many authors (e.g. Johnson *et al.* 1991, 1996, Loydell 1994, 1998) still regard sea level change as the main causal mechanism for the extinctions recorded. Not all the interpretations of the magnitude and direction of sea level change agree, especially at the Llandovery/Wenlock boundary (Text-fig. 5.4).

The sea level curve signals are highly dependent on the method used to calculate them and the amount of data available to the authors. For example, Johnson *et al.* (1991) published a generalised sea level curve for the Silurian showing a gradual sea level fall across the Llandovery/Wenlock boundary. In the light of a larger database (Johnson 1996) this pattern was revised to show a marked fall in the late Llandovery and a rise in the early Wenlock.

Unfortunately, one of the more detailed curves must be treated with caution. Loydell (1998) constructed his curve on the basis of graptolite diversity and sedimentary carbon content, there are a number of problems with both lines of evidence. Firstly, it is unclear whether the graptolites themselves have been used when the inshore and outer shelf environments have been defined. If they have, the argument becomes circular (Jeppsson and Aldridge 2001). Factors other than sea level that may have affected graptolite diversity were not considered. These factors include nutrient supply, water temperature, oceanic circulation, graptolite food supply and predator-prey relationships (Jeppsson and Aldridge 2000, p. 1137, Jeppsson and Aldridge 2001). The absence of any direct living relatives of the graptolites means there is no direct evidence to suggest their ecological preferences. Loydell's assertion that sea level was the primary control on graptolite distribution may be correct, but it could equally be argued that any of the other factors mentioned above could have been a more dominant influence. The curve also relies on the preservation potential, the sedimentation rate and the level of bioturbation remaining constant at different levels. Loydell (2001) cited numerous authors who have reported 'decades of consistent observations' on graptolite diversity and sea level, but as Jeppsson and Aldridge (2001) point out, we have to assume that all the datasets are statistically reliable and that different sample sizes have been taken into account. This is not often the case.

Text-fig. 5.4 graphically illustrates that there are major mismatches between Loydell's (1998) curve and that of other authors. Loydell attributed these differences to the inaccurate dating



TEXT-FIG. 5.4. Diagram showing a comparison of the commonly used sea level curves for the lower Silurian. The graptolite zones identified from the UK (Loydell 1998, Mabillard and Aldridge 1985), the conodont zones from Gotland (datum levels marked with a black circle) (Jeppsson 1997) and the Gotland lithostratigraphy are shown. Dashed lines are used for the boundaries between the graptolite zones because their correlation to the stages are unknown. Dashed lines are used in the conodont zonation where their position relative to the Gotland lithostratigraphy is unknown. The correlation between the conodont biozones and graptolite biozones is taken from Loydell *et al.* (1998).

and correlation of graptolites used in other curves, some of which have subsequently been reassessed by Loydell (1992, Loydell *et al.* 1998). As Loydell (2001, p. 731) suggested, the differences in the sea level curves may be resolved when more precise dating using graptolites is conducted on the datasets used in other studies. Equally these differences in the curves may be due to the problems encountered when graptolites are used as sea level indicators.

As a control on his sea level interpretation, Loydell (1998) used increased carbon content of sediments as an indicator of transgressive sequences, but again this is not solely dependent on sea level. The amount of organic carbon fixed in sediments is greatly influenced by oxygenation of the sea floor and nutrient availability (Hay 1988). Sea floor oxygenation is in turn controlled by dissolved oxygen in the water and oceanic circulation of the bottom waters. Nutrient availability controls the level of photosynthesis and the amount of carbon fixation from the atmosphere.

Burial histories of Silurian coastal topographies have been used to determine sea level changes (Johnson *et al.* 1998). This provides another potential independent test for the sea level curve produced by Loydell (1998). Unfortunately this method involves biostratigraphic correlation of Silurian rocky shorelines, which is notoriously difficult (Jeppsson and Aldridge 2001).

The lithological record provides a possible source of information about sea level variations. On Gotland, the lithology of the late Llandovery is dominated by calcareous marls, which gradually become dominated by argillaceous limestones in the early Wenlock. It is generally accepted that the patch reef formation that occurred in the early to mid Wenlock represented a shallow shelf environment (Watts and Riding 2000). A somewhat simplistic interpretation is that the change in lithology reflects a gradual relative drop in water depth where the increasingly shallow water created a reef community niche.

A potentially highly sensitive and detailed record of sea level variations might be recorded in the acritarchs. Interpreting relative water depths from acritarchs is difficult, as sea level is one of probably many factors that influenced the palynomorph record. Working on Ludlow material, Dorning (1981b) produced a summary of the palynomorph assemblages likely to be recorded at different proximities to the shoreline. Generalised nearshore, offshore and deep-water palynomorph communities were described. The usefulness of these generalisations in the present study is limited, as the assemblages analysed all fall within the offshore category. Using Palaeozoic material from Libya, Al-Ameri (1983) produced a generalised diagram

(similar to that of Dorning (1981b)) where six acritarch zones related to water depth were identified. No specific depth information was suggested and most of the acritarchs discussed by Al–Ameri and in the present study are within his Zone 4.

Le Hérissé and Gourvennec (1995) suggested that *Deunffia-Domasia* dominated assemblages, such as those reported for the Llandovery/Wenlock boundary in the Welsh Borderland (Hill & Dorning 1984), are indicative of outer-shelf environments. This interpretation is difficult to apply to Gotland; the occurrences of *Deunffia* are very rare and the relative abundance of *Domasia* varies little between samples. If Le Hérissé and Gourvennec (1995) are correct, the relative stasis of *Deunffia-Domasia* numbers across the Llandovery/Wenlock boundary on Gotland could be used to suggest that sea level change was small. Richardson and Rasul (1990) suggested that an inshore index calculation could be used to estimate shore proximity/water depth. The concept relied on the acanthomorph/netromorph etc. classification, the groupings of which were then used as a proxy for environment. This assumption is flawed. Richardson and Rasul (1990) used the groups to suggest specific environmental conditions, but the groups include very diverse species, with probably very different environmental tolerances.

It is very likely that sea level change was an important factor in the Silurian, and lithological and palaeontological changes support this view. Problems arise when sea level is invoked as the only cause of the biotic turnover. If sea level change were the only mechanism affecting the biota in the Silurian it must be assumed that either the climate was in steady state or that climate change did occur, but had no influence over the biota. Given the massive climate change that has taken place in the last few million years (even the last ten thousand years) it is difficult to believe that the climate was stable for the whole of the lower Silurian. It appears that the proponents of a single cause and effect sea level hypothesis are suggesting that the biota was unresponsive to climate change during the Silurian. This is difficult to believe.

#### *P and S cyclicity*

P and S cyclicity was first proposed by Jeppsson (1990) as an explanation of biotic and sedimentological changes throughout the Silurian (see Jeppsson 1998 for a summary).

According to the model, (Text–fig. 5.5) P–states such as that occurring in the late Llandovery were characterised by a wet climate, with high runoff and high sediment influx into the ocean; marls were deposited on the shelf. The deep oceans were well mixed due to the heating and

upwelling in the tropics of dense cold water currents (which supply nutrients). The cool temperatures caused a slight thermal contraction of the oceans and consequent regression.

S-states such as that envisaged for the early Wenlock were characterised by a dry climate with low runoff and high evaporation. The sediment influx into the oceans stopped, the water became clear and limestones developed on the shelf. The cold dense water current switched off and salinity stratification developed. The higher temperatures would have caused thermal expansion of the oceans and a slight transgression.

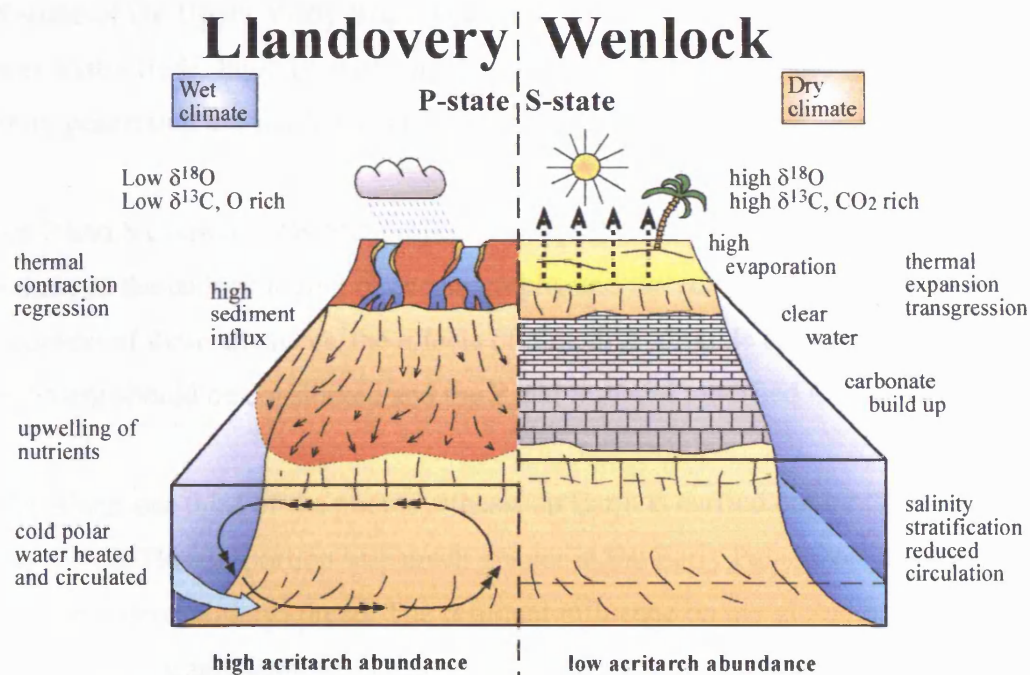
At the transition between the P and S-states (Text-fig. 5.6) the ocean reached CO<sub>2</sub> saturation point and changed from being a carbon sink to a carbon source (Jeppsson 1990). The increased CO<sub>2</sub> pumped into the atmosphere is thought to have been one of the main warming mechanisms.

The P and S model predicts a high rate of vertical advection of nutrients to the surface waters and increased weathering in the P-state and a stratified ocean in the S-state; this predicts a high planktonic production in the P-state and low in the S-state (only a tenth of that in the P-state (Jeppsson 1990)).

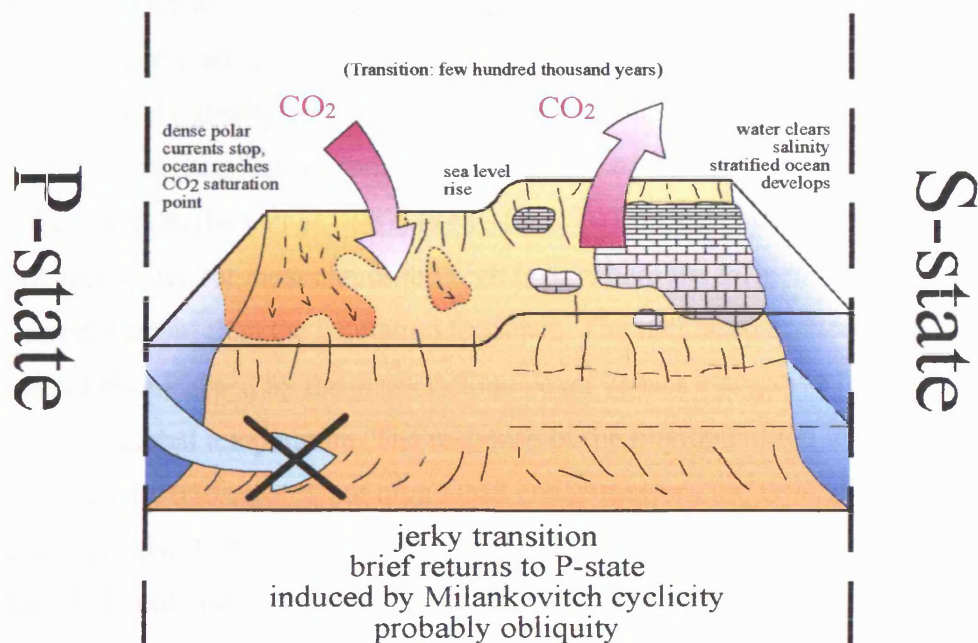
The acritarch record at Lusklint 1 and Lickerhamn 2 shows no unequivocal evidence for the existence of P and S cycles, but merely that this was a time of turnover associated with probable climatic and sea level changes. Although the P and S model does not successfully explain some of the patterns observed in this study, it is the best model available that encompasses the complexities of sea level change and climate variability. The predictive power of the model can only improve as the more speculative parts are constrained.

The mixed and stratified ocean and wet/cool and dry/warm climate scenarios discussed above for stable carbon and oxygen isotopes could be regarded as a proxy for the P and S climate states respectively, of Jeppsson (1990) (see discussion in Wenzel and Joachimski 1996). The complex interplay of factors that control isotope composition in the sediment means it is difficult to suggest whether the predictions of the P and S model are correct. If oceanic circulation was the dominant factor, the model predicts lower relative values of  $\delta^{13}\text{C}$  in the S-state of the Upper Visby Beds where we see the opposite in a rising trend, implying a better-circulated ocean. Equally productivity and fractionation of  $\delta^{12}\text{C}$  into the acritarchs could have been more dominant. The model predicts a decrease in productivity in the Upper Visby Beds, which could generate the rising signal observed, due to lower level of removal of  $\delta^{12}\text{C}$ . If a





Text-fig.5.5. Cartoon showing the characteristics of the late Llandovery P-state and the early Wenlock S-state (after Jepps 1990).



Text-fig. 5.6. Cartoon showing the characteristics of the transition between the late Llandovery P-state and the early Wenlock S-state (after Jepps 1990).

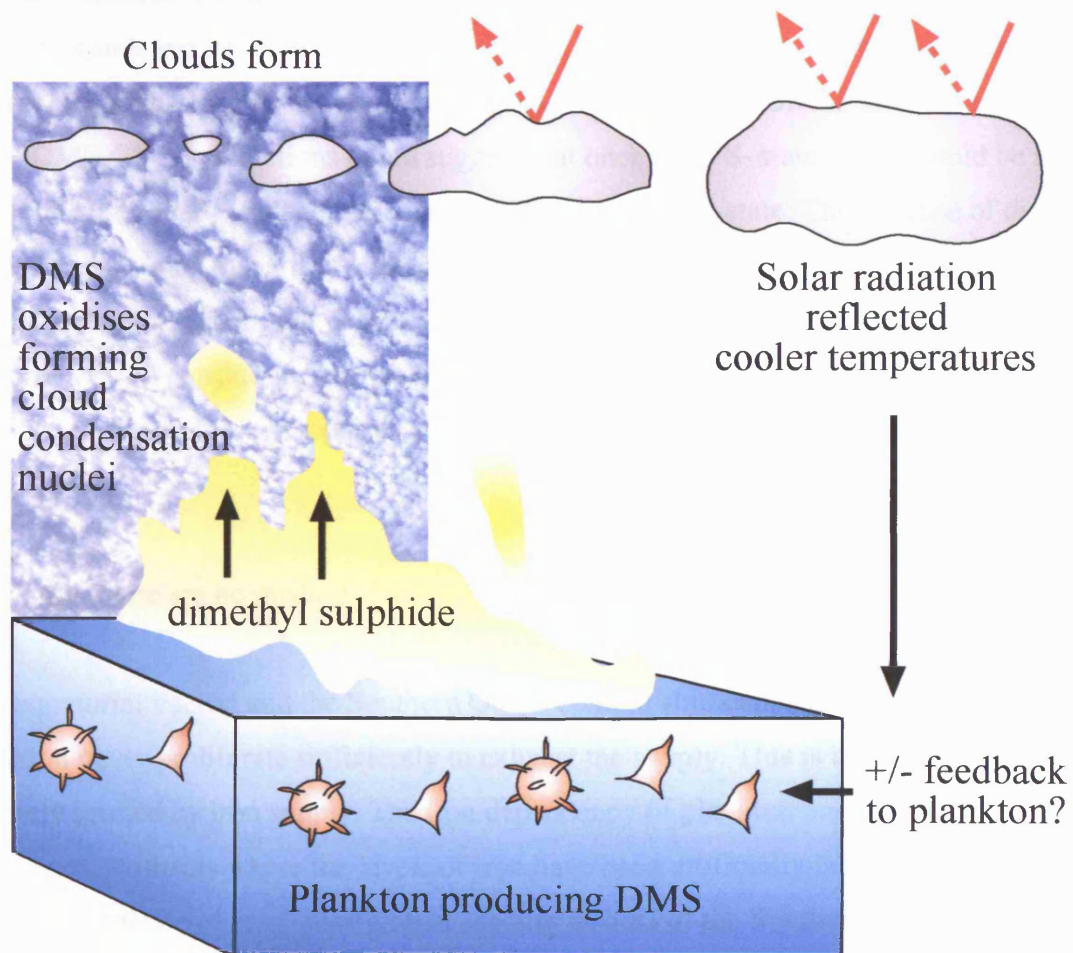
change in temperature and/or salinity took place, the model predicts increased levels of  $\delta^{18}\text{O}$  in S-state of the Upper Visby Beds, where we see very little change from the record of the Lower Visby Beds. Equally, there may have been little or no change in temperature and salinity generating the stable signal observed.

Since P and S cyclicity was first proposed (Jeppsson 1990), there have been a number of advances in the understanding of oceanography and the ecology of modern phytoplankton. In the context of these advances, the effects of dimethyl sulphide emissions and of iron enrichment should be considered and the P and S model modified in response.

Today about one third of the photosynthesis on Earth is carried out by the phytoplankton (King 1975). This proportion was much greater in the Early Palaeozoic as land plants were primitive and not widely spread. The resultant influence on the global biosphere of oceanic photosynthesis was, therefore, considerably greater than it is today.

Many modern planktonic algae generate dimethyl sulphide (DMS) from a dimethylsulphonium propionate (DMSP) precursor, produced in osmoregulation, during grazing, autolysis and bacterial or viral attack. Coccoliths have been recorded as having the highest rate of DMS excretion per unit biomass at the present day (Charlson *et al.* 1987, p. 656), but it is widely accepted that dinoflagellate DMS production is important in modern oceans and possibly greatly underestimated (Steinke *et al.* 2002). DMS oxidises in the atmosphere to form sulphate aerosols, a major source of cloud condensation nuclei (CCN) over the oceans (Charlson *et al.* 1987) (Text–fig 5.7). Low-level clouds generally have an insulating influence, but most clouds are high level where the influence on planetary albedo is much more dominant than the insulation feedback. The increased scattering and absorbing of the sun's radiation caused by the greater cloud cover causes a negative feedback response decreasing the global temperature. The response of the phytoplankton to the temperature change is not fully understood, but high DMS concentrations are typically observed in warm surface waters (Idso 1992). Therefore, in a high productivity P-state there would be feedback to prolong that cool climate.

Mixing in the water column is extremely important in the conversion of DMSP to DMS (Simó & Pedrós-Alió 1999). Minimum yield of DMS is achieved at a mixing depth of 15–20m, higher yields are recorded at deeper mixing layer depths and near 100% conversion at extremely shallow depths of circulation. If DMS production is introduced as a major factor in the P and S model, the depth of vertical mixing will be one of the dominant influences on its



Text-fig. 5.7 Cartoon showing the relationship between DMS production in plankton and increased cloud cover.

production and by inference, on global temperature.

Simó & Pedrós-Alió (1999) suggested that in winter and early spring when the climate is cooler (perhaps analogous to P-state), mixed waters are characterised by blooms of large diatoms. These have a large biomass, but produce little DMS as most large diatoms produce little DMSP. The stratification that occurs in the late spring (perhaps analogous to an S-state) lowers the phytoplankton biomass and favours small flagellates, coccolithophores and dinoflagellates, which all have a strong DMS producing potential. The food web seems to alternate between the two states. During the mixed waters of winter and spring, the primary producers sink and swim in and out of the photic zone, but during the stratified late spring an internal recycling loop develops producing a faster turnover of DMSP and, after a short lag-time, DMS. These predictions could suggest that once in an S-state, there would be a strong (biologically driven) tendency to change back to a cooler P-state. The absence of diatoms in the Palaeozoic may mean that these conclusions are irrelevant. The response of dinoflagellates to similar conditions has not been investigated, but could be quite different and may be more important when considering acritarchs. No changes in size distribution between large and small acritarch species (as reported by Simó and Pedrós-Alió (1999) for diatoms) are reported here.

Currently, there are no methods for testing the level of DMS in the Palaeozoic ocean.

The equatorial Pacific and the Southern Ocean contain abundant essential nutrients, but plankton never proliferate sufficiently to exhaust the supply. This is because productivity is severely limited by iron supply. The iron dependency of plankton has been illustrated in seeding experiments where the levels of iron have been artificially increased in particular areas. In 2000, Boyd *et al.* showed that seeding an area of the Southern Ocean with iron stimulated the phytoplankton to produce an elevated draw-down of CO<sub>2</sub> from the atmosphere, increase the utilization of nutrients and elevate DMS levels after only 13 days. Others (e.g. Turner *et al.* 1996), have shown that experiments which mimic natural iron enrichment increase DMS production by a factor of 3·5. A dramatic illustration of the influence of iron enrichment can be seen in Text-fig. 5.8., which shows a chlorophyll rich plume stimulated by iron enrichment (Martin *et al.* 1994).

If the P and S climate model is correct, it would be expected that during the wet climate of a P-state there would be little opportunity for wind blown dust to enter the atmosphere. Elevated iron levels would only be observed around the mouths of rivers and would be a very

localised phenomenon. The alluvial iron would be quickly removed from the ocean system in various oxidation reactions (Cranfield 1988) and would be buried in the rapidly accumulating sediment; much of the iron would be attached to clay particles, which tend to flocculate in brackish conditions. In modern oceans more than 90% of fluvial sediment (containing most of the iron) is deposited in coastal areas and on continental margins; of the majority of elements in the sediment, only 20% are suspended and carried out to sea (Lisitzin 1996).

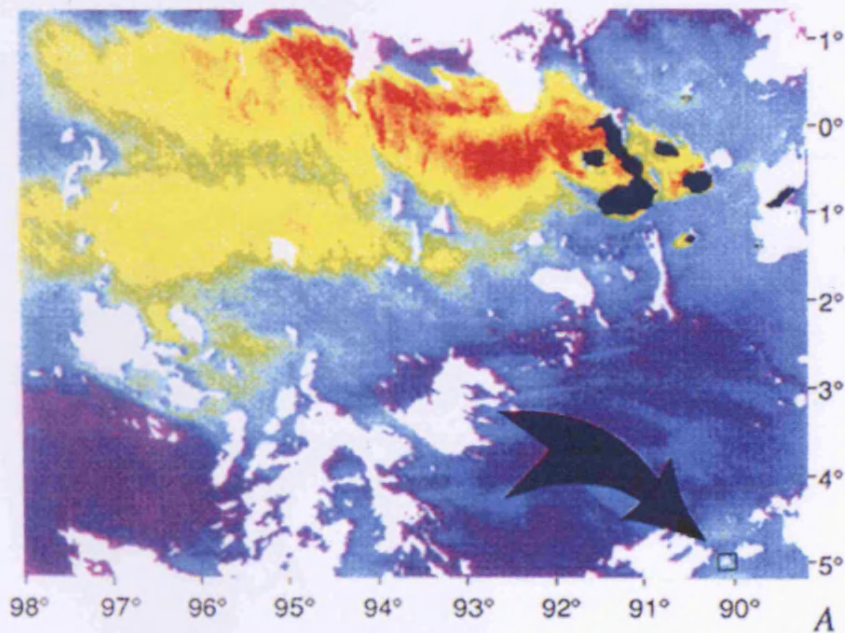
In the open ocean sediments, aeolian and glacial sources contribute 3·1 billion tons to the world's oceans every 1000 years, but fluviogenic sources supply only 1·7 billion tons every 1000 years (Lisitzin 1996). In the P and S model the arid S-state would provide a source of widespread airborne iron-rich dust (as is exemplified by the iron fertilization stretching west into the Atlantic Ocean and into the Mediterranean from the Sahara desert (Text-fig.5.9; Dulac *et al.* 1996)). The major source and sink areas are shown in Text-fig. 5.10 (Lisitzin 1996). It should also be noted that modern day aeolian dust is mainly concentrated between the tropics, the same latitude as that suggested for the Baltic in the early Wenlock (Torsvik *et al.* 1990). Tappan (1986) emphasized the importance of terrestrial weathering as a plankton nutrient source, to the extent that land plant evolution has had a massive influence on planktonic evolution through the nutrient retention of land plant biomass; the nutrients would otherwise have been available to be recycled back into the oceans. Several studies have reported an order of magnitude decrease in atmospheric dust loads during the transition between arid glacial environments and wet interglacial environments (see Idso 1992 for a summary). The decrease in iron available to the phytoplankton carried in atmospheric dust during interglacial conditions is suggested to greatly reduce their planktonic productivity rates.

It could be argued that the Silurian plankton of the Baltic were not iron limited. This may be the case, but the location of the Baltic near to the equator means that the plankton were likely to have behaved as they do today in the equatorial Pacific and the Southern Ocean.

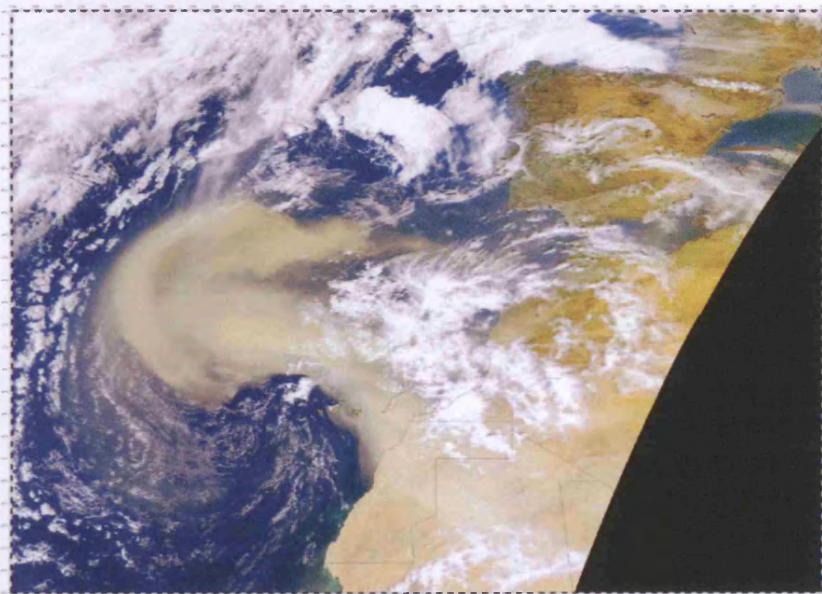
There are currently no methods for estimating iron levels of the Palaeozoic ocean.

The gradual acritarch species originations that occur through most of the Ireviken Event may be a reflection of gradually increasing available iron during the transition from a P to an S-state. The number of acritarchs per gram of sediment shows no increasing or decreasing trend through the sections. The warmer more arid S-state would have provided a larger source of iron, which in turn should increase the phytoplankton biomass and induce a negative feedback

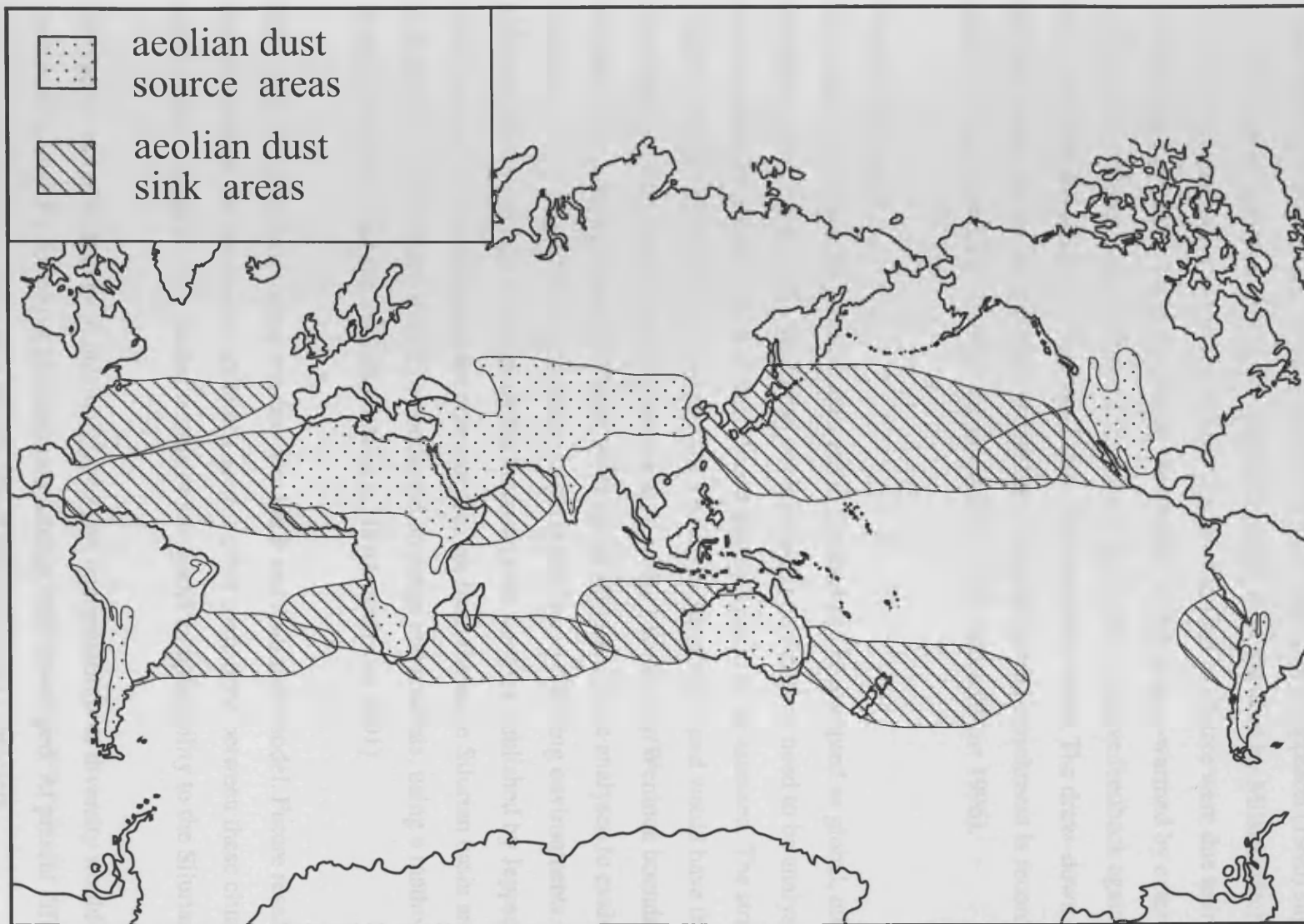




TEXT-FIG. 5.8. False-colour image from the Coastal Zone Colour Scanner on the Nimbus 7 satellite, October 1983. This image indicates the chlorophyll-rich plume extending west from the Galapagos Islands after iron seeding (red colour indicates higher chlorophyll concentrations). Fig. 1. A, from Martin *et al.* 1994.



TEXT-FIG. 5.9. Satellite image showing a massive sandstorm blowing off north-western Africa, enveloping hundreds of thousands of square km of the eastern Atlantic Ocean. This storm, recorded on the 26th of February 2000, by the SeaWiFS project stretches more than 1600km out to sea. (Source: SeaWiFS project, NASA (<http://seawifs.gsfc.nasa.gov>))



TEXT-FIG. 5.10. Map showing the large extent of the planet affected by deposition of wind blown dust. After Lisitzin (1996).

from increased DMS production (in contrast to the predictions made by Simó and Pedrós-Alió (1999) for an increased biomass of diatoms). This would cause indirect cooling (Turner *et al.* 1996) and a possible return to the cooler P-state. The Jeppsson model does not predict this. The influence of iron induced DMS negative feedback may be important in explaining the transition from P to S-state, which is thought to have been jerky. Jeppsson (1990) suggested the brief returns to P-state during the transition period were induced by Milankovitch cyclicity. An alternative explanation is that the brief returns to P-state were due to iron induced DMS negative feedback cooling the climate, which was re-warmed by external forcing from increasing atmospheric CO<sub>2</sub> only to induce the negative feedback again, until a threshold level was reached where the S-state could be maintained. The draw-down of CO<sub>2</sub> into the oceans during increased photosynthesis induced by iron enrichment is recorded as only having a small negative effect on atmospheric CO<sub>2</sub> values (Frost 1996).

#### FUTURE RESEARCH

Before the phytoplankton patterns observed in Gotland can be accepted as global, other localities, which have similar depth and environmental parameters, need to be analysed. This would enable the provincialism of the Silurian phytoplankton to be assessed. The stratotype at Hughley Brook (Shropshire) would provide a suitable comparison and would have the added advantage of better constraining the precise level of the Llandovery/Wenlock boundary on Gotland. The patterns present in deeper water facies also need to be analysed to evaluate the variability of the palynomorph responses to the extinction in differing environments. To maintain the consistency of this study the Estonian core samples published by Jeppsson (1993), could be used (although the core samples are from the same Silurian basin and facies as Gotland). Further work should be conducted on range end analysis, using a method which is more inclusive of all the available data (e.g. Hayek and Bura 2001)

The acritarchs provide a unique window into the P and S climate model. Future research should compare the patterns of acritarchs seen at other transitions between these climate states, which would provide further testing of the model's applicability to the Silurian.

The usefulness of acritarchs in biostratigraphy and interpretations of diversity would be greatly enhanced if a definitive classification scheme were developed. At present different authors place different importance on individual morphological characters.

The value of the data collected on Gotland would be enhanced if it were accurately correlated with the Llandovery/Wenlock boundary at the type section. There are two main ways this



might be achieved: a statistical reassessment of the palynological samples collected from the Llandovery/Wenlock boundary type section by Mabillard and Aldridge (1985), or through a magnetic susceptibility survey. Palynological correlation is problematic due to regional assemblage variations, but magnetic susceptibility correlations have successfully been used on Lower Devonian sections (Ellwood *et al.* 2001). Accurate correlation (independent of the conodont zonation) would be useful in comparing Lusklint 1 with Lickersham 2.

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## Appendix 1

### STRATIGRAPHIC RANGE DIAGRAM FOR ALL THE SPECIES RECORDED AT LUSKLINT 1

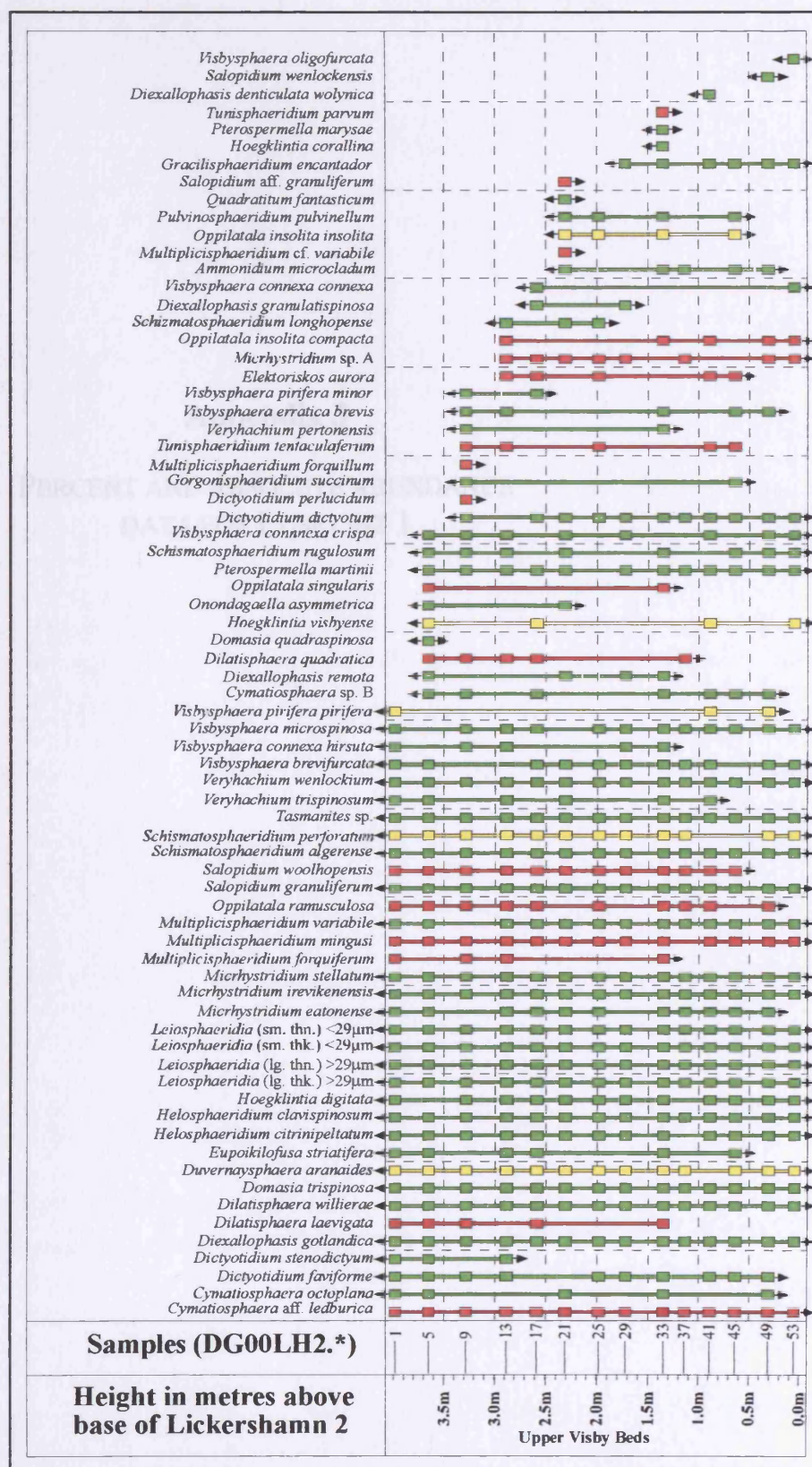






## **Appendix 2**

### **STRATIGRAPHIC RANGE DIAGRAM FOR ALL THE SPECIES RECORDED AT LICKERSHAMN 2**



Appendix 2. Stratigraphic range diagram for all the species recorded at Lickersham 2.

### **Appendix 3**

#### **PERCENT AND ABSOLUTE ABUNDANCE DATA FOR LUSKLINT 1**

[illegible]

**Appendix 3.** The percent abundance for each species (on the top row) and the absolute abundance (on the bottom row) in the samples at Lusklin1.





Species	Sample DG00* (metres)																								
		0.00	6.74	0.00	0.19	0.00	0.19	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Leucosia cf. hundertlii</i>	LK1.69	0.00	6.74	0.00	0.19	0.00	0.19	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Leucosia parvicornis</i>	3.06-3.11	0.00	179	0	5	0	5	0	5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.68	0.00	1.29	0.00	0.00	0.00	0.00	0.00	1.08	0.00	0.00	0.10	1.19	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	3.02-3.06	0.00	100	0	0	0	0	0	84	0	0	0	8	92	31	0	0	0	0	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.64	0.00	1.20	0.00	0.00	0.00	0.00	0.00	0.28	0.91	0.00	0.00	1.83	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	2.85-2.89	0.00	55	0	0	0	0	0	13	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.60	0.00	1.69	0.20	0.00	0.00	0.09	0.00	0.00	0.29	0.00	0.00	0.09	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
<i>Heogobius vitiensis</i>	2.70-2.73	0.00	75	9	0	0	4	0	0	13	0	0	0	4	35	0	0	0	0	0	0	0	0	0	4
<i>Heogobius vitiensis</i>	LK1.56	0.00	1.25	0.00	0.00	0.00	0.10	0.00	0.19	0.39	0.00	0.10	0.87	0.29	0.00	0.00	0.00	0.00	0.19	0.00	0.10	0.00	0.48	1.25	0.00
<i>Heogobius vitiensis</i>	2.53-2.57	0.00	288	0	0	0	22	0	0	44	89	0	22	0	67	22	200	67	0	0	0	44	0	0	0
<i>Heogobius vitiensis</i>	LK1.52	0.00	0.65	0.10	0.00	0.00	0.10	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	2.35-2.40	0.00	67	10	0	0	10	0	0	10	0	10	0	0	57	19	0	0	0	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.48	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	2.21-2.24	0.00	19	0	0	0	0	0	0	19	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.44	0.00	0.43	0.08	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.43	0.08	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	2.02-2.06	0.00	127	25	0	0	0	0	0	102	0	0	0	127	25	0	0	0	76	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.40	0.00	1.01	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.18	0.00	0.09	0.55	0.09	0.09	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.87-1.93	0.00	161	0	0	0	0	0	29	0	29	0	0	15	88	15	15	0	0	15	0	0	15	0	0
<i>Heogobius vitiensis</i>	LK1.39	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.09	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.78-1.83	0.00	114	0	0	0	0	0	33	0	16	0	0	163	0	0	0	0	33	0	0	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.38	0.00	1.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	1.92	0.00	0.00	0.00	0.28	0.00	0.10	0.00	0.10	0.28	0.00	0.00
<i>Heogobius vitiensis</i>	1.72-1.78	0.00	180	0	0	0	0	0	0	17	0	0	0	180	0	0	0	0	26	0	9	0	9	0	0
<i>Heogobius vitiensis</i>	LK1.37	0.00	1.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.82	0.00	0.00	0.00	0.00	0.25	0.00	0.17	0.00	9.66	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.68-1.72	0.00	258	0	0	0	0	0	0	0	0	0	0	237	0	0	0	0	32	0	22	0	1259	0	0
<i>Heogobius vitiensis</i>	LK1.36	0.00	1.64	0.19	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	2.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	6.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.62-1.68	0.00	176	20	0	0	0	0	10	0	0	0	0	215	10	0	0	0	0	0	0	645	0	10	0
<i>Heogobius vitiensis</i>	LK1.32	0.00	1.10	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.37	0.00	0.09	0.00	0.00	0.09	0.00	0.00	0.00	6.59	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.41-1.45	0.00	121	10	0	0	0	0	0	0	0	0	0	151	0	10	0	0	10	0	0	726	0	10	0
<i>Heogobius vitiensis</i>	LK1.28	0.00	3.34	0.09	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	1.43	0.00	0.09	0.00	0.00	0.57	0.00	0.00	0.00	4.86	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.27-1.37	0.00	328	9	0	0	0	0	9	0	0	0	0	141	0	9	0	0	56	0	9	0	478	0	0
<i>Heogobius vitiensis</i>	LK1.24	0.00	3.71	0.38	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	1.47	0.00	0.00	0.11	0.00	0.11	0.00	0.00	0.00	6.15	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	1.08-1.14	0.00	174	18	0	0	0	0	9	0	0	0	0	69	0	5	0	5	0	32	0	288	0	0	0
<i>Heogobius vitiensis</i>	LK1.20	0.00	1.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	1.79	0.00	0.00	0.00	0.00	0.12	0.00	0.00	6.76	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.82-0.89	0.00	48	0	0	0	0	0	0	0	0	0	0	3	46	0	0	0	3	0	0	174	0	3	0
<i>Heogobius vitiensis</i>	LK1.16	0.00	1.78	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.19	0.00	0.00	1.59	0.09	0.00	0.00	0.00	0.00	0.00	8.27	0.19	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.71-0.74	0.00	57	0	0	0	0	0	3	0	6	0	0	51	3	0	0	0	0	0	0	265	0	6	0
<i>Heogobius vitiensis</i>	LK1.12	0.00	2.40	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	1.63	0.00	0.00	0.00	0.00	0.00	0.00	6.15	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.51-0.55	0.00	87	0	0	0	0	0	0	3	0	0	0	59	0	0	0	0	0	0	0	223	0	0	0
<i>Heogobius vitiensis</i>	LK1.8	0.00	1.82	0.34	0.00	0.00	0.00	0.00	0.43	0.00	0.09	0.00	0.00	0.95	0.09	0.00	0.00	0.09	0.00	0.00	4.16	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.30-0.33	0.00	102	19	0	0	0	0	24	0	5	0	0	53	5	0	0	5	0	0	0	233	0	5	0
<i>Heogobius vitiensis</i>	LK1.6	0.00	4.08	0.00	0.00	0.00	0.10	0.00	0.38	0.00	0.00	0.00	0.00	7.02	0.00	0.00	0.00	0.00	0.00	0.00	3.61	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.18-0.25	0.00	513	0	0	0	12	0	0	48	0	0	0	0	883	0	0	0	0	0	0	454	0	60	0
<i>Heogobius vitiensis</i>	LK1.5	0.00	3.95	0.10	0.00	0.00	0.14	0.00	0.00	0.10	0.00	0.19	0.00	0.00	1.58	0.00	0.00	0.00	0.00	0.00	6.04	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.17-0.18	0.00	164	4	0	0	6	0	4	0	8	0	0	66	0	0	0	0	0	0	251	0	0	0	0
<i>Heogobius vitiensis</i>	LK1.4	0.00	1.38	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.11	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	8.06	0.00	0.00	0.00	0.00
<i>Heogobius vitiensis</i>	0.11-0.15	0.00	38	0	0	0	0	0	0	0	3	0	0	55	0	0	0	0	0	0	222	0	0	0	0

Appendix 3. The percent abundance for each species (on the top row) and the absolute abundance (on the bottom row) in the samples at Luskint 1.



Species	Sample DG00* (metres)	1.69	1.71	1.73	1.75	1.77	1.79	1.81	1.83	1.85	1.87	1.89	1.91	1.93	1.95	1.97	1.99	2.01	2.03	2.05	2.07	2.09	2.11	2.13	2.15	2.17	2.19	2.21	2.23	2.25	2.27	2.29	2.31	2.33	2.35	2.37	2.39	2.41	2.43	2.45	2.47	2.49	2.51	2.53	2.55	2.57	2.59	2.61	2.63	2.65	2.67	2.69	2.71	2.73	2.75	2.77	2.79	2.81	2.83	2.85	2.87	2.89	2.91	2.93	2.95	2.97	2.99	3.01	3.03	3.05	3.07	3.09	3.11	3.13	3.15	3.17	3.19	3.21	3.23	3.25	3.27	3.29	3.31	3.33	3.35	3.37	3.39	3.41	3.43	3.45	3.47	3.49	3.51	3.53	3.55	3.57	3.59	3.61	3.63	3.65	3.67	3.69	3.71	3.73	3.75	3.77	3.79	3.81	3.83	3.85	3.87	3.89	3.91	3.93	3.95	3.97	3.99	4.01	4.03	4.05	4.07	4.09	4.11	4.13	4.15	4.17	4.19	4.21	4.23	4.25	4.27	4.29	4.31	4.33	4.35	4.37	4.39	4.41	4.43	4.45	4.47	4.49	4.51	4.53	4.55	4.57	4.59	4.61	4.63	4.65	4.67	4.69	4.71	4.73	4.75	4.77	4.79	4.81	4.83	4.85	4.87	4.89	4.91	4.93	4.95	4.97	4.99	5.01	5.03	5.05	5.07	5.09	5.11	5.13	5.15	5.17	5.19	5.21	5.23	5.25	5.27	5.29	5.31	5.33	5.35	5.37	5.39	5.41	5.43	5.45	5.47	5.49	5.51	5.53	5.55	5.57	5.59	5.61	5.63	5.65	5.67	5.69	5.71	5.73	5.75	5.77	5.79	5.81	5.83	5.85	5.87	5.89	5.91	5.93	5.95	5.97	5.99	6.01	6.03	6.05	6.07	6.09	6.11	6.13	6.15	6.17	6.19	6.21	6.23	6.25	6.27	6.29	6.31	6.33	6.35	6.37	6.39	6.41	6.43	6.45	6.47	6.49	6.51	6.53	6.55	6.57	6.59	6.61	6.63	6.65	6.67	6.69	6.71	6.73	6.75	6.77	6.79	6.81	6.83	6.85	6.87	6.89	6.91	6.93	6.95	6.97	6.99	7.01	7.03	7.05	7.07	7.09	7.11	7.13	7.15	7.17	7.19	7.21	7.23	7.25	7.27	7.29	7.31	7.33	7.35	7.37	7.39	7.41	7.43	7.45	7.47	7.49	7.51	7.53	7.55	7.57	7.59	7.61	7.63	7.65	7.67	7.69	7.71	7.73	7.75	7.77	7.79	7.81	7.83	7.85	7.87	7.89	7.91	7.93	7.95	7.97	7.99	8.01	8.03	8.05	8.07	8.09	8.11	8.13	8.15	8.17	8.19	8.21	8.23	8.25	8.27	8.29	8.31	8.33	8.35	8.37	8.39	8.41	8.43	8.45	8.47	8.49	8.51	8.53	8.55	8.57	8.59	8.61	8.63	8.65	8.67	8.69	8.71	8.73	8.75	8.77	8.79	8.81	8.83	8.85	8.87	8.89	8.91	8.93	8.95	8.97	8.99	9.01	9.03	9.05	9.07	9.09	9.11	9.13	9.15	9.17	9.19	9.21	9.23	9.25	9.27	9.29	9.31	9.33	9.35	9.37	9.39	9.41	9.43	9.45	9.47	9.49	9.51	9.53	9.55	9.57	9.59	9.61	9.63	9.65	9.67	9.69	9.71	9.73	9.75	9.77	9.79	9.81	9.83	9.85	9.87	9.89	9.91	9.93	9.95	9.97	9.99	10.01	10.03	10.05	10.07	10.09	10.11	10.13	10.15	10.17	10.19	10.21	10.23	10.25	10.27	10.29	10.31	10.33	10.35	10.37	10.39	10.41	10.43	10.45	10.47	10.49	10.51	10.53	10.55	10.57	10.59	10.61	10.63	10.65	10.67	10.69	10.71	10.73	10.75	10.77	10.79	10.81	10.83	10.85	10.87	10.89	10.91	10.93	10.95	10.97	10.99	11.01	11.03	11.05	11.07	11.09	11.11	11.13	11.15	11.17	11.19	11.21	11.23	11.25	11.27	11.29	11.31	11.33	11.35	11.37	11.39	11.41	11.43	11.45	11.47	11.49	11.51	11.53	11.55	11.57	11.59	11.61	11.63	11.65	11.67	11.69	11.71	11.73	11.75	11.77	11.79	11.81	11.83	11.85	11.87	11.89	11.91	11.93	11.95	11.97	11.99	12.01	12.03	12.05	12.07	12.09	12.11	12.13	12.15	12.17	12.19	12.21	12.23	12.25	12.27	12.29	12.31	12.33	12.35	12.37	12.39	12.41	12.43	12.45	12.47	12.49	12.51	12.53	12.55	12.57	12.59	12.61	12.63	12.65	12.67	12.69	12.71	12.73	12.75	12.77	12.79	12.81	12.83	12.85	12.87	12.89	12.91	12.93	12.95	12.97	12.99	13.01	13.03	13.05	13.07	13.09	13.11	13.13	13.15	13.17	13.19	13.21	13.23	13.25	13.27	13.29	13.31	13.33	13.35	13.37	13.39	13.41	13.43	13.45	13.47	13.49	13.51	13.53	13.55	13.57	13.59	13.61	13.63	13.65	13.67	13.69	13.71	13.73	13.75	13.77	13.79	13.81	13.83	13.85	13.87	13.89	13.91	13.93	13.95	13.97	13.99	14.01	14.03	14.05	14.07	14.09	14.11	14.13	14.15	14.17	14.19	14.21	14.23	14.25	14.27	14.29	14.31	14.33	14.35	14.37	14.39	14.41	14.43	14.45	14.47	14.49	14.51	14.53	14.55	14.57	14.59	14.61	14.63	14.65	14.67	14.69	14.71	14.73	14.75	14.77	14.79	14.81	14.83	14.85	14.87	14.89	14.91	14.93	14.95	14.97	14.99	15.01	15.03	15.05	15.07	15.09	15.11	15.13	15.15	15.17	15.19	15.21	15.23	15.25	15.27	15.29	15.31	15.33	15.35	15.37	15.39	15.41	15.43	15.45	15.47	15.49	15.51	15.53	15.55	15.57	15.59	15.61	15.63	15.65	15.67	15.69	15.71	15.73	15.75	15.77	15.79	15.81	15.83	15.85	15.87	15.89	15.91	15.93	15.95	15.97	15.99	16.01	16.03	16.05	16.07	16.09	16.11	16.13	16.15	16.17	16.19	16.21	16.23	16.25	16.27	16.29	16.31	16.33	16.35	16.37	16.39	16.41	16.43	16.45	16.47	16.49	16.51	16.53	16.55	16.57	16.59	16.61	16.63	16.65	16.67	16.69	16.71	16.73	16.75	16.77	16.79	16.81	16.83	16.85	16.87	16.89	16.91	16.93	16.95	16.97	16.99	17.01	17.03	17.05	17.07	17.09	17.11	17.13	17.15	17.17	17.19	17.21	17.23	17.25	17.27	17.29	17.31	17.33	17.35	17.37	17.39	17.41	17.43	17.45	17.47	17.49	17.51	17.53	17.55	17.57	17.59	17.61	17.63	17.65	17.67	17.69	17.71	17.73	17.75	17.77	17.79	17.81	17.83	17.85	17.87	17.89	17.91	17.93	17.95	17.97	17.99	18.01	18.03	18.05	18.07	18.09	18.11	18.13	18.15	18.17	18.19	18.21	18.23	18.25	18.27	18.29	18.31	18.33	18.35	18.37	18.39	18.41	18.43	18.45	18.47	18.49	18.51	18.53	18.55	18.57	18.59	18.61	18.63	18.65	18.67	18.69	18.71	18.73	18.75	18.77	18.79	18.81	18.83	18.85	18.87	18.89	18.91	18.93	18.95	18.97	18.99	19.01	19.03	19.05	19.07	19.09	19.11	19.13	19.15	19.17	19.19	19.21	19.23	19.25	19.27	19.29	19.31	19.33	19.35	19.37	19.39	19.41	19.43	19.45	19.47	19.49	19.51	19.53	19.55	19.57	19.59	19.61	19.63	19.65	19.67	19.69	19.71	19.73	19.75	19.77	19.79	19.81	19.83	19.85	19.87	19.89	19.91	19.93	19.95	19.97	19.99	20.01	20.03	20.05	20.07	20.09	20.11	20.13	20.15	20.17	20.19	20.21	20.23	20.25	20.27	20.29	20.31	20.33	20.35	20.37	20.39	20.41	20.43	20.45	20.47	20.49	20.51	20.53	20.55	20.57	20.59	20.61	20.63	20.65	20.67	20.69	20.71	20.73	20.75	20.77	20.79	20.81	20.83	20.85	20.87	20.89	20.91	20.93	20.95	20.97	20.99	21.01	21.03	21.05	21.07	21.09	21.11	21.13	21.15	21.17	21.19	21.21	21.23	21.25	21.27	21.29	21.31	21.33	21.35	21.37	21.39	21.41	21.43	21.45	21.47	21.49	21.51	21.53	21.55	21.57	21.59	21.61	21.63	21.65	21.67	21.69	21.71	21.73	21.75	21.77	21.79	21.81	21.83	21.85	21.87	21.89	21.91	21.93	21.95	21.97	21.99	22.01	22.03	22.05	22.07	22.09	22.11	22.13	22.15	22.17	22.19	22.21	22.23	22.25	22.27	22.29	22.31	22.33	22.35	22.37	22.39	22.41	22.43	22.45	22.47	22.49	22.51	22.53	22.55	22.57	22.59	22.61	22.63	22.65	22.67	22.69	22.71	22.73	22.75	22.77	22.79	22.81	22.83	22.85	22.87	22.89	22.91	22.93	22.95	22.97	22.99	23.01	23.03	23.05	23.07	23.09	23.11	23.13	23.15	23.17	23.19	23.21	23.23	23.25	23.27	23.29	23.31	23.33	23.35	23.37	23.39	23.41	23.43	23.45	23.47	23.49	23.51	23.53	23.55	23.57	23.59	23.61	23.63	23.65	23.67	23.69	23.71	23.73	23.75	23.77	23.79	23.81	23.83	23.85	23.87	23.89	23.91	23.93	23.95	23.97	23.99	24.01	24.03	24.05	24.07	24.09	24.11	24.13	24.15	24.17	24.19	24.21	24.23	24.25	24.27	24.29	24.31	24.33	24.35	24.37	24.39	24.41	24.43	24.45	24.47	24.49	24.51	24.53	24.55	24.57	24.59	24.61	24.63	24.65	24.67	24.69	24.71	24.73	24.75	24.77	24.79	24.81	24.83	24.85	24.87	24.89	24.91	24.93	24.95	24.97	24.99	25.01	25.03	25.05	25.07	25.09	25.11	25.13	25.15	25.17	25.19	25.21	25.23	25.25	25.27	25.29	25.31	25.33	25.35	25.37	25.39	25.41	25.43	25.45	25.47	25.49	25.51	25.53	25.55	25.57	25.59	25.61	25.63	25.65	25.67	25.69	25.71	25.73	25.75	25.77	25.79	25.81	25.83	25.85	25.87	25.89	25.91	25.93	25.95	25.97	25.99	26.01	26.03	26.05	26.07	26.09	26.11	26.13	26.15	26.17	26.19	26.21	26.23	26.25	26.27	26.29	26.31	26.33	26.35	26.37	26.39	26.41	26.43	26.45	26.47	26.49	26.51	26.53	26.55	26.57	26.59	26.61	26.63	26.65	26.67	26.69	26.71	26.73	26.75	26.77	26.79	26.81	26.83	26.85	26.87	26.89	26.91	26.93	26.95	26.97	26.99	27.01	27.03	27.05	27.07	27.09	27.11	27.13	27.15	27.17
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Species	Sample DG00* (metres)	<i>Veryhachium rhomboidium</i>	<i>Veryhachium trispinosum</i>	<i>Veryhachium wenlockium</i>	<i>Visbysphaera brevivirgata</i>	<i>Visbysphaera connexa connexa</i>	<i>Visbysphaera connexa crispata</i>	<i>Visbysphaera connexa hirsuta</i>	<i>Visbysphaera erratica brevis</i>	<i>Visbysphaera gottlandica</i>	<i>Visbysphaera meson</i>	<i>Visbysphaera microspinosa</i>	<i>Visbysphaera oligofurcata</i>	<i>Visbysphaera pirifer pirifer</i>	<i>Visbysphaera pirifer minor</i>	<i>Visbysphaera cf. gottlandica</i>
LK1.288	0.11	9.89	2.70	0.60	0.11	0.00	0.11	0.00	0.11	0.11	0.00	0.10	0.00	0.00	0.00	0.00
10.91-10.97	7	648	177	39	7	0	7	7	0	0	0	72	0	0	0	0
LK1.287	0.00	4.39	4.68	0.30	0.00	0.09	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10.88-10.93	0	192	205	13	0	4	0	17	0	0	0	0	0	0	0	0
LK1.285	0.00	5.69	12.98	0.36	0.18	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10.82-10.84	0	320	779	20	0	0	0	0	0	0	0	20	0	0	0	5
LK1.284	0.00	6.29	7.34	0.29	0.00	0.00	0.19	0.19	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00
10.61-10.69	0	132	154	6	0	0	4	0	0	0	0	4	0	0	0	2
LK1.287	0.00	4.06	13.04	0.67	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.00
10.42-10.45	0	399	1281	66	0	0	0	28	0	0	0	28	0	0	0	0
LK1.283	0.00	4.33	17.03	0.19	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
10.26-10.30	0	460	1810	20	0	0	0	0	0	0	0	10	51	41	0	10
LK1.289	0.00	2.45	22.14	0.28	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
10.10-10.14	0	185	1669	21	0	0	0	7	0	0	0	7	7	0	0	7
LK1.215	0.00	1.63	29.25	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.92-9.99	0	132	2367	31	0	0	0	0	0	0	0	0	0	0	0	0
LK1.231	0.00	2.51	25.10	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.74-9.79	0	313	3129	0	0	0	0	13	0	0	0	0	0	0	0	13
LK1.227	0.00	1.31	20.52	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
9.56-9.61	0	58	906	21	0	0	0	0	0	0	0	4	12	4	0	0
LK1.223	0.00	1.77	33.33	0.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.38-9.42	0	306	5749	113	0	0	0	0	0	0	0	0	0	0	0	0
LK1.219	0.00	2.04	32.62	0.48	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.15-9.19	0	81	1298	19	0	4	0	0	0	0	0	15	0	0	0	4
LK1.215	0.00	4.91	22.51	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
8.93-8.97	0	43	197	0	0	0	0	1	0	0	0	1	1	0	0	0
LK1.211	0.00	2.64	29.84	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.72-8.75	0	393	4448	41	0	0	0	0	0	0	0	14	27	14	28	0
LK1.207	0.00	0.80	27.81	0.64	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00
8.51-8.58	0	5	173	4	1	1	0	0	0	0	0	1	0	0	0	0
LK1.203	0.00	1.21	15.80	0.31	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.37-8.43	0	23	301	6	0	0	0	0	0	0	0	2	0	0	0	2
LK1.199	0.00	1.22	12.84	0.00	0.36	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.18-8.20	0	31	325	0	9	0	0	5	0	0	0	0	2	0	0	0
LK1.195	0.00	1.02	17.72	0.30	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.01-8.05	0	17	294	5	8	0	0	0	0	0	0	0	0	0	0	0
LK1.191	0.00	1.73	14.78	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7.82-7.87	0	40	341	2	2	0	0	0	0	0	0	0	0	0	0	0
LK1.187	0.00	0.10	9.91	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7.67-7.74	0	6	605	18	0	0	0	0	0	0	0	0	0	0	0	0
LK1.183	0.00	0.56	10.10	0.19	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00
7.59-7.62	0	107	1937	36	36	0	0	0	0	0	0	36	0	0	0	0
LK1.179	0.00	0.46	15.18	0.37	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7.41-7.44	0	16	533	13	16	0	0	0	0	0	0	0	0	0	0	0
LK1.175	0.00	0.00	7.66	0.17	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7.23-7.28	0	0	269	6	16	0	0	0	0	0	0	0	0	0	0	0
LK1.171	0.00	0.11	18.76	0.19	1.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7.01-7.08	0	5	889	9	55	0	0	0	0	0	0	0	0	0	0	0
LK1.167	0.00	0.08	18.39	0.25	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6.92-6.97	0	8	1748	24	55	0	0	0	0	0	0	0	0	0	0	0

Appendix 3. The percent abundance for each species (on the top row) and the absolute abundance (on the bottom row) in the samples at Luskint 1.



Sample DG00* (metres)	Species	<i>Veryhachium rhomboidium</i>	<i>Veryhachium trispinosum</i>	<i>Veryhachium wenlockium</i>	<i>Visbysphaera brevifurcata</i>	<i>Visbysphaera connexa connexa</i>	<i>Visbysphaera connexa crispata</i>	<i>Visbysphaera connexa hirsuta</i>	<i>Visbysphaera erratica brevis</i>	<i>Visbysphaera goilandica</i>	<i>Visbysphaera meson</i>	<i>Visbysphaera microspinosa</i>	<i>Visbysphaera oligofurcata</i>	<i>Visbysphaera pirifera pirifera</i>	<i>Visbysphaera pirifera minor</i>	<i>Visbysphaera cf. goilandica</i>
LK1.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
306-311	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
302-306	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
285-289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
270-273	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
253-257	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
235-240	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
221-224	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
202-206	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
187-193	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
178-183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
172-178	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
168-172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
162-168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
141-145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
127-137	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
108-114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
082-089	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
071-074	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
051-055	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
030-033	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
018-025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
017-018	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LK1.4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
011-015	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3. The percent abundance for each species (on the top row) and the absolute abundance (on the bottom row) in the samples at Luskint 1.

## **Appendix 4**

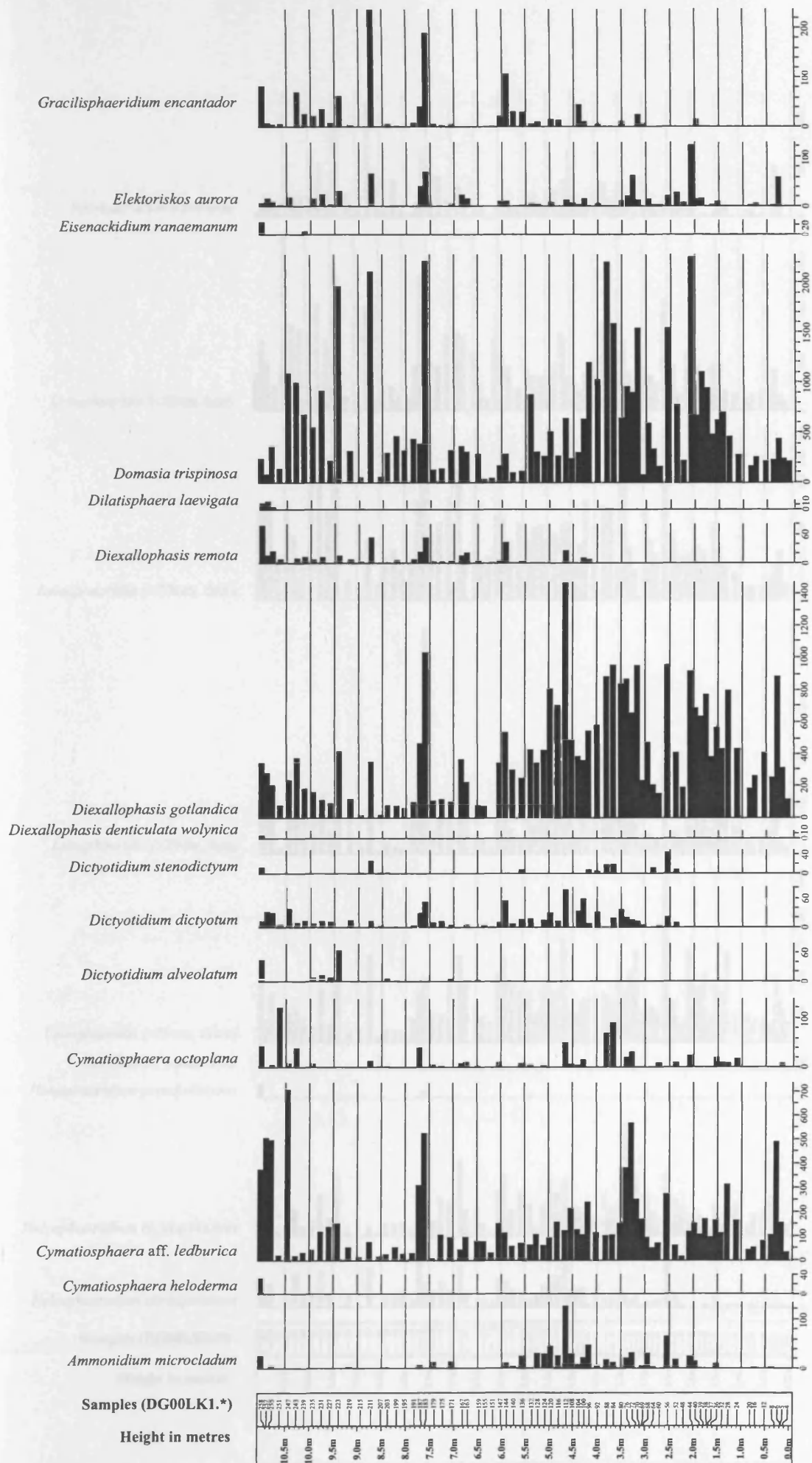
### **PERCENT AND ABSOLUTE ABUNDANCE DATA FOR LICKERSHAMN 2**





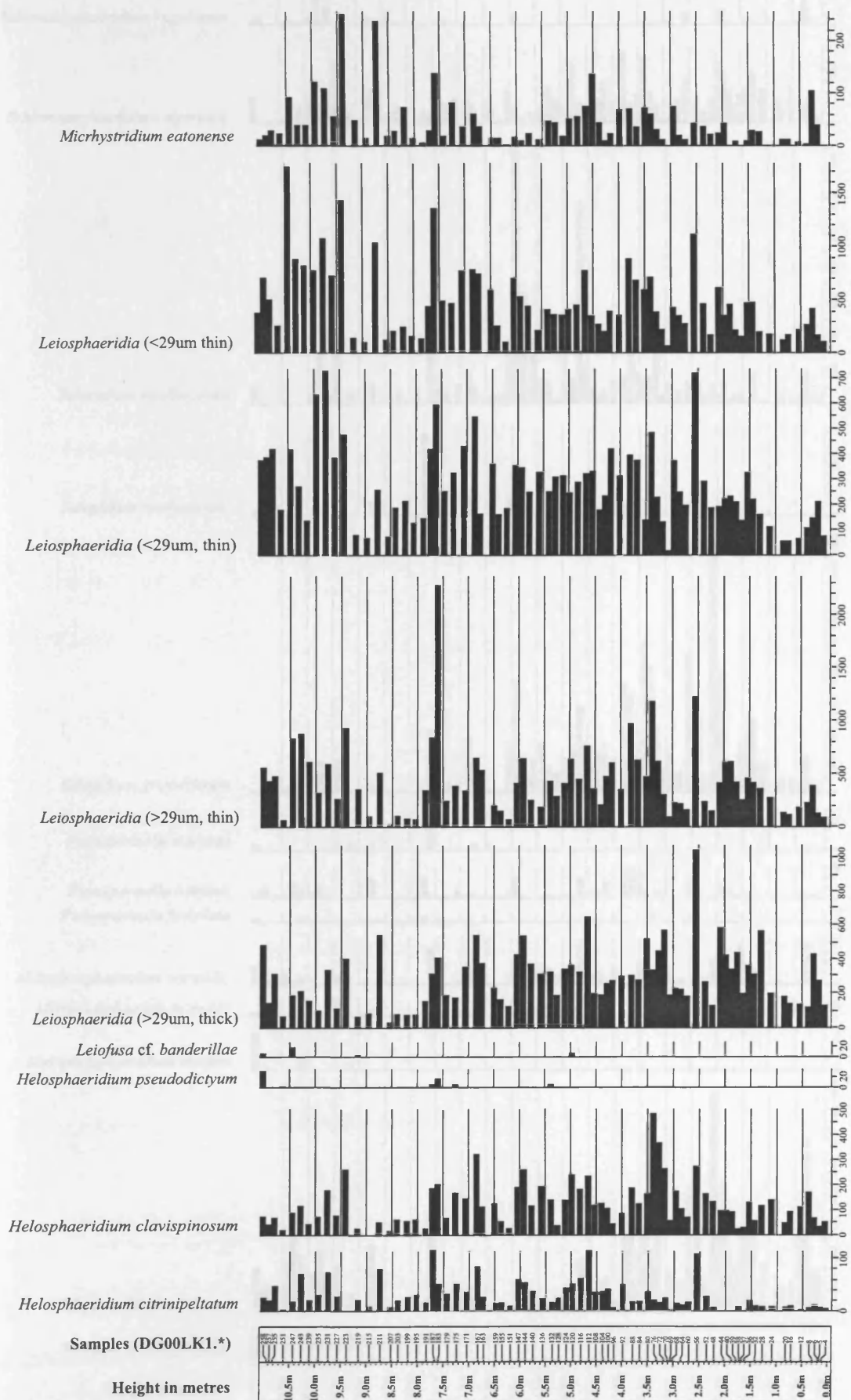
## **Appendix 5**

### **ABSOLUTE ABUNDANCE PLOTS FOR LUSKLINT 1**

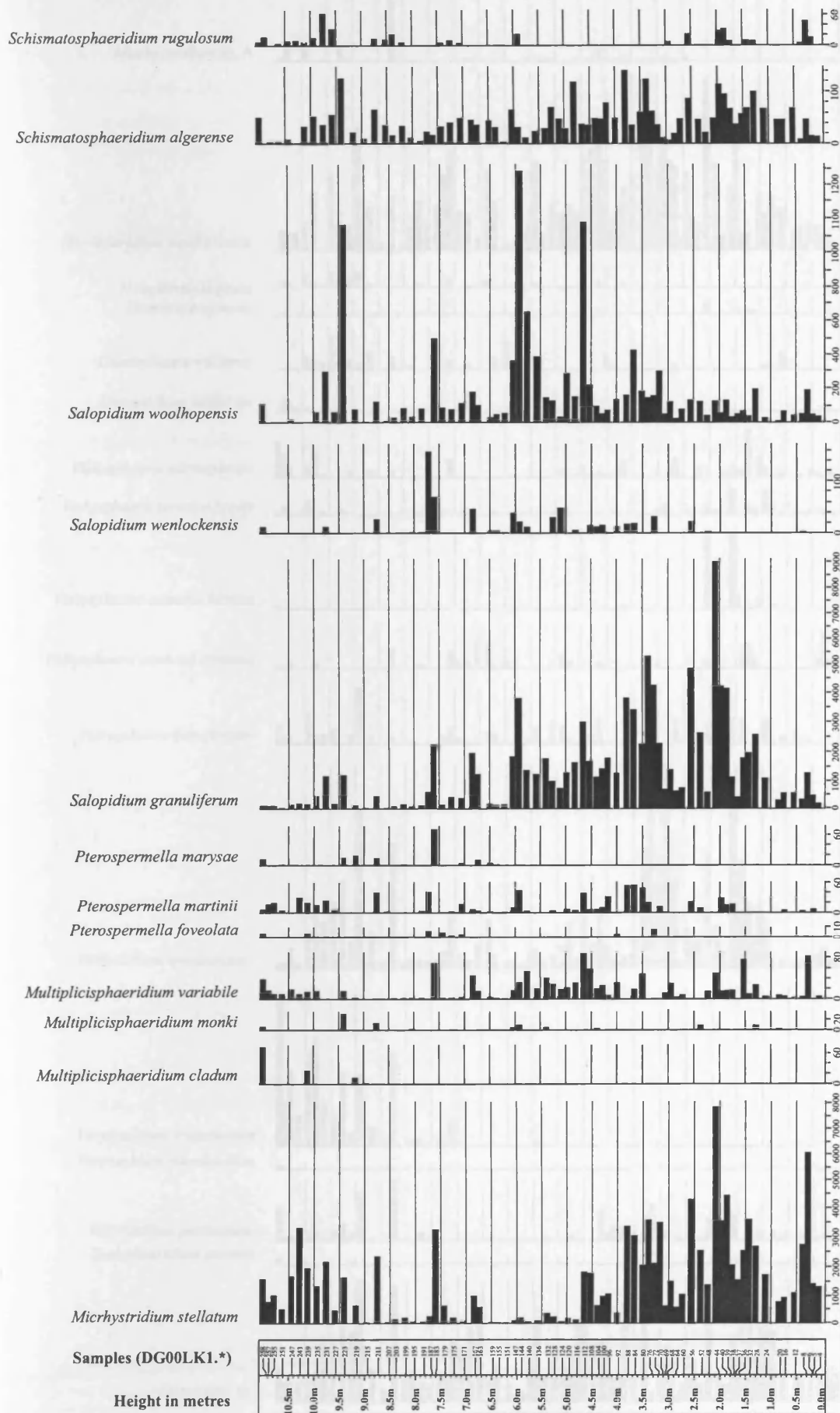


Appendix 5. Absolute abundance of palynomorphs, Luskint 1.

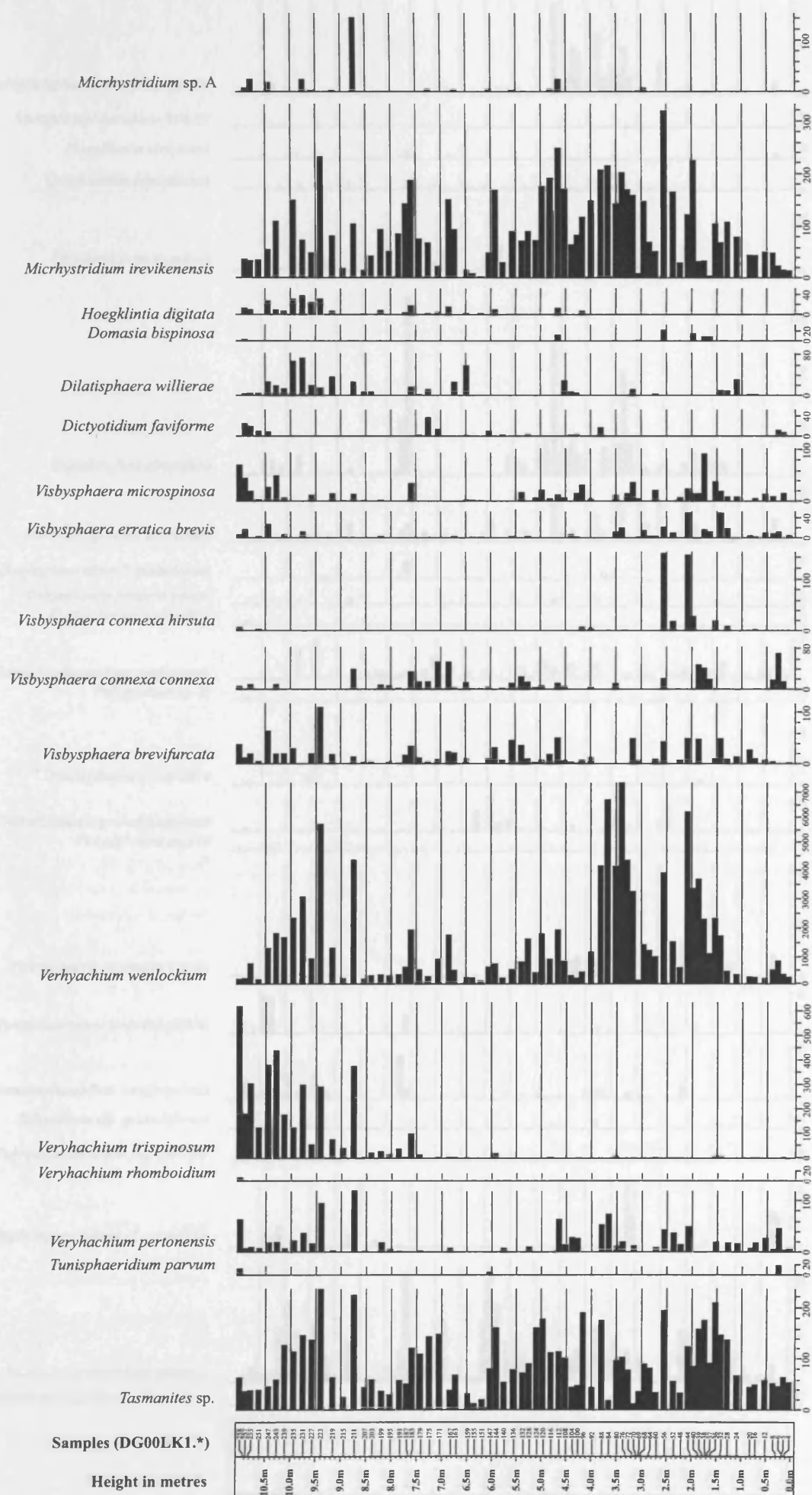




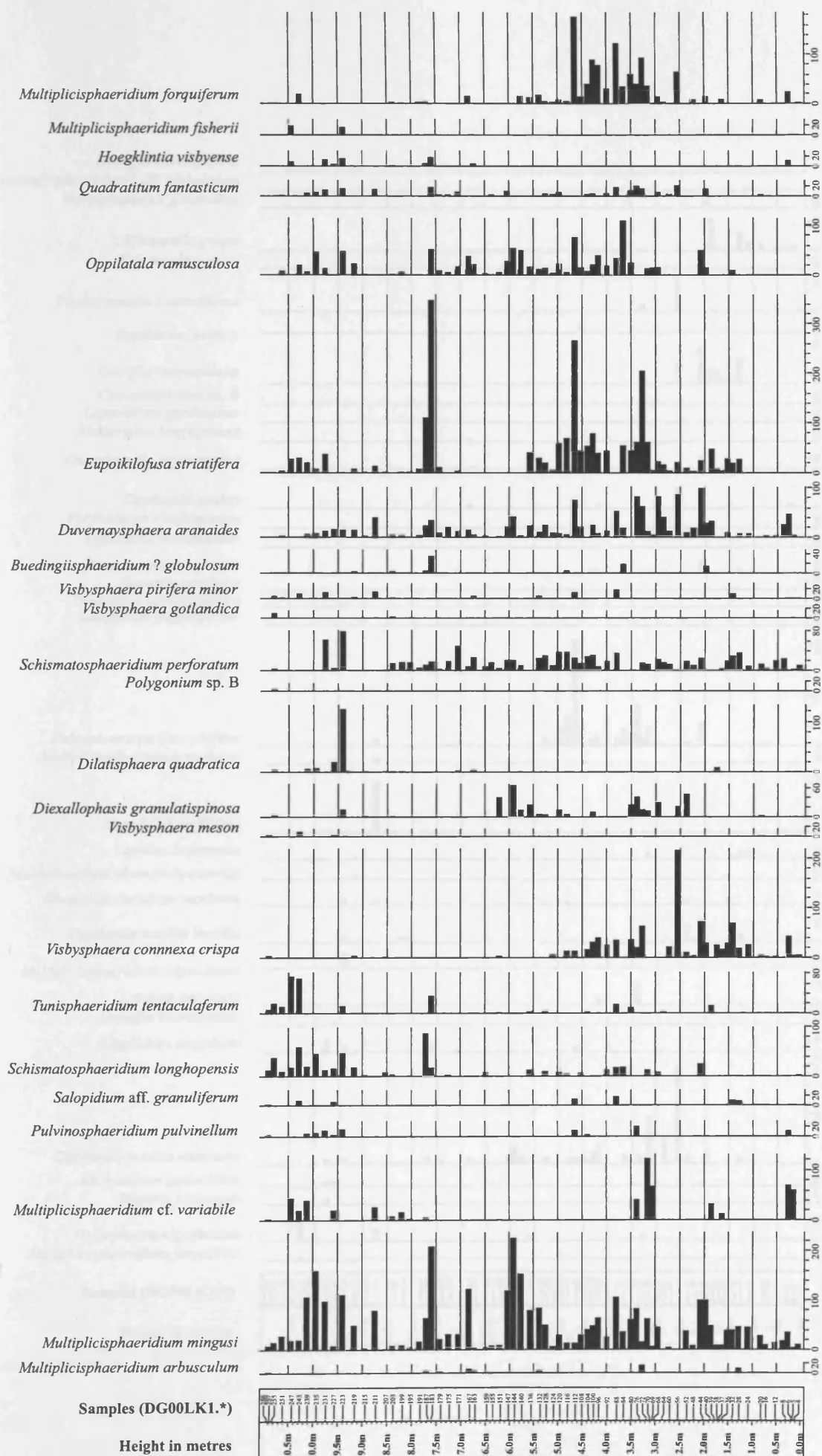
Appendix 5. Absolute abundance of palynomorphs, Luskint 1.



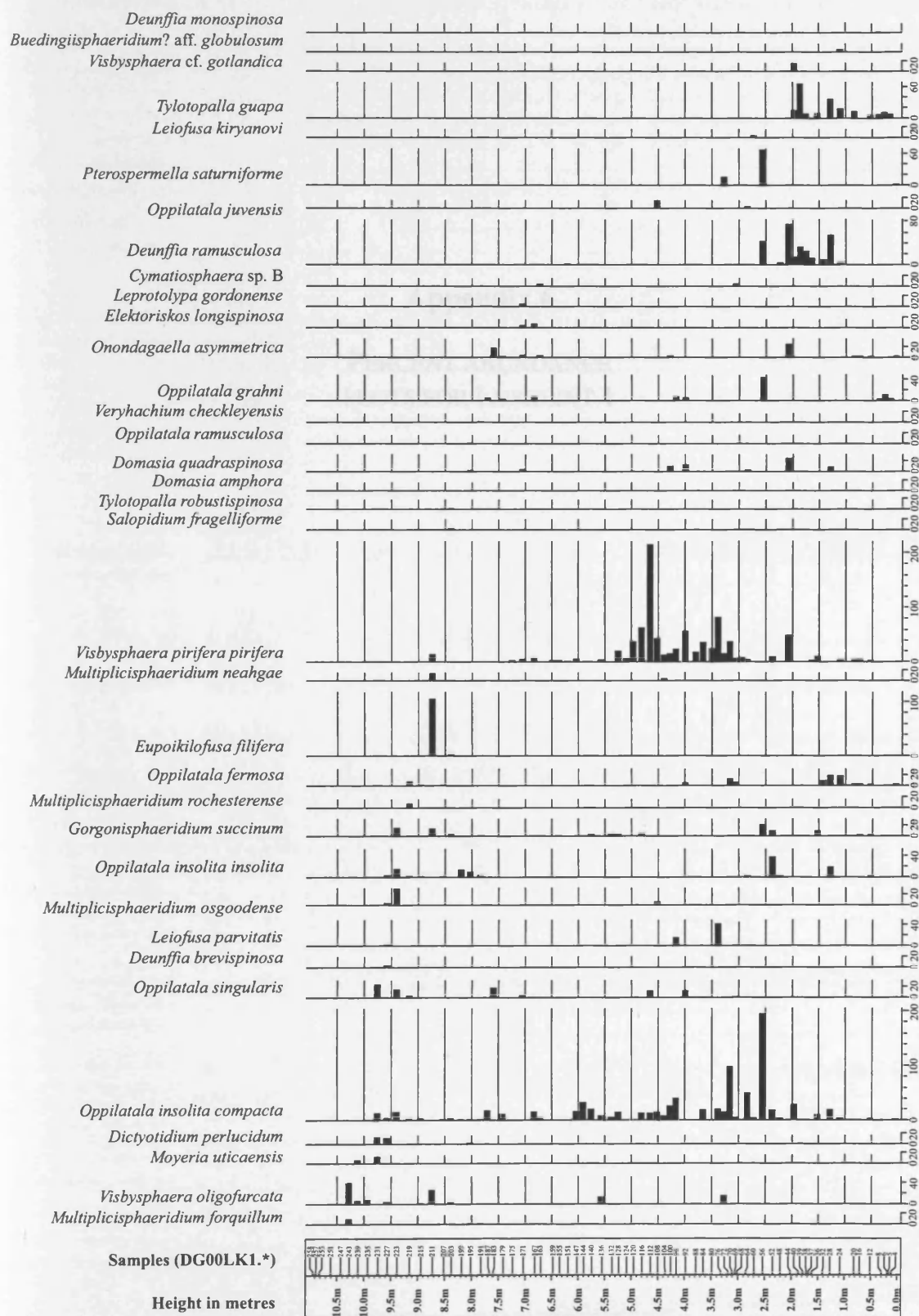
Appendix 5. Absolute abundance of palynomorphs, Luskint 1.



Appendix 5. Absolute abundance of palynomorphs, Luskint 1.



Appendix 5. Absolute abundance of palynomorphs, Luskint 1.



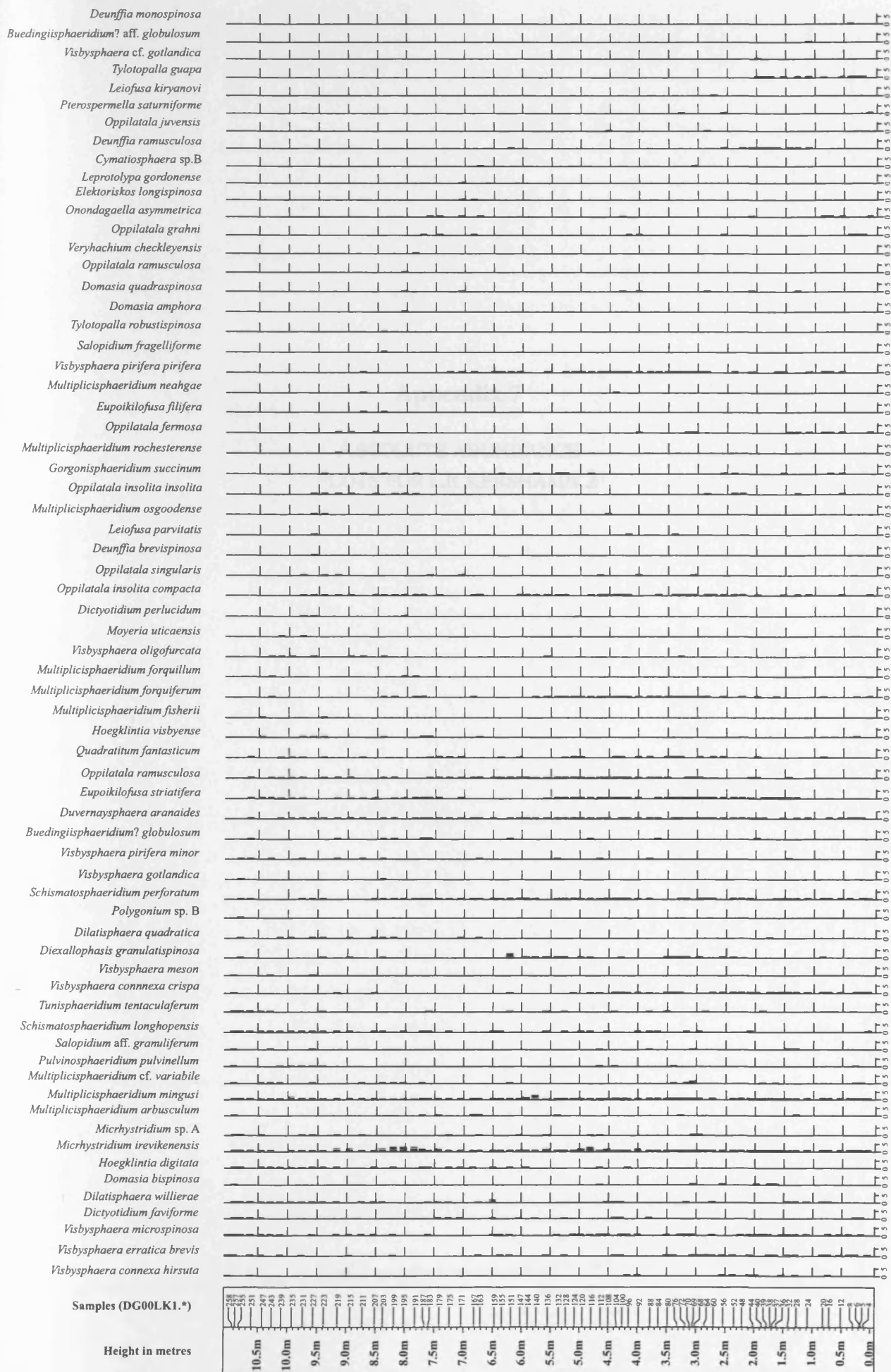
Appendix 5. Absolute abundance of palynomorphs, Luskint 1.

## **Appendix 6**

### **PERCENT ABUNDANCE PLOTS FOR LUSKLINT 1**







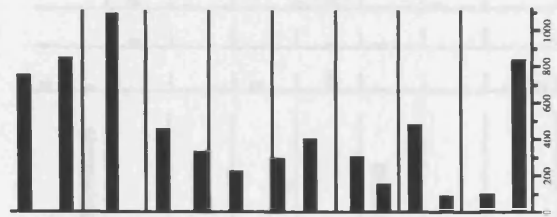
Appendix 6. Percentage abundance of palynomorphs, Luskint 1.



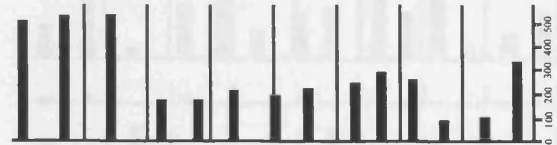
## **Appendix 7**

### **ABSOLUTE ABUNDANCE PLOTS FOR LICKERSHAMN 2**

*Leiosphaeridia* (Lg Thn) >29um



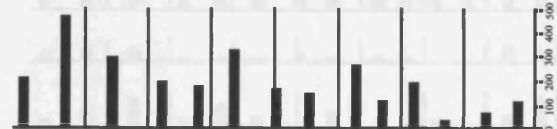
*Leiosphaeridia* (Lg Thk) >29um



*Hoegklintia digitata*



*Helosphaeridium clavispinosum*



*Helosphaeridium citrinipeltatum*



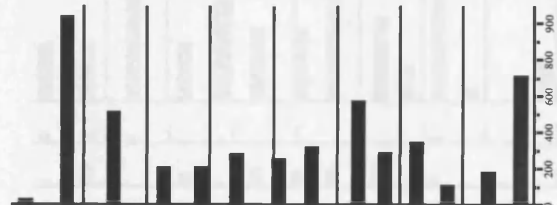
*Eupoikilofusa striatifera*



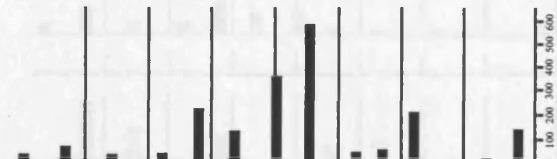
*Duvernaysphaera aranaides*



*Domasia trispinosa*



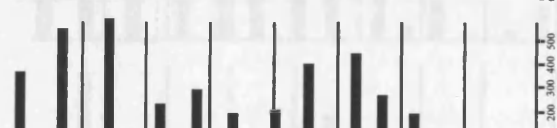
*Dilatisphaera willierae*



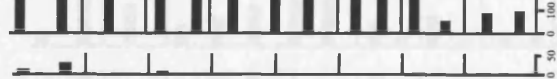
*Dilatisphaera laevigata*



*Diexallophasis gotlandica*



*Dictyotidium stenodictyum*



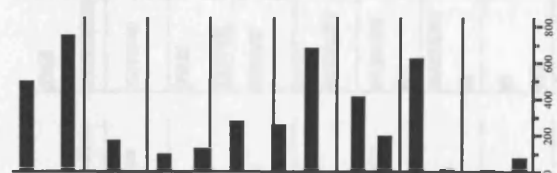
*Dictyotidium faviforme*



*Cymatiosphaera octoplana*

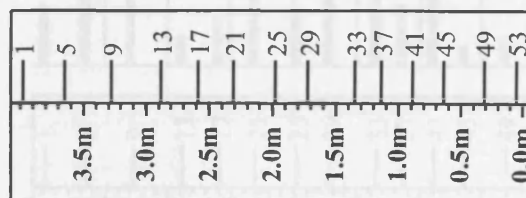


*Cymatiosphaera* aff. *ledburica*

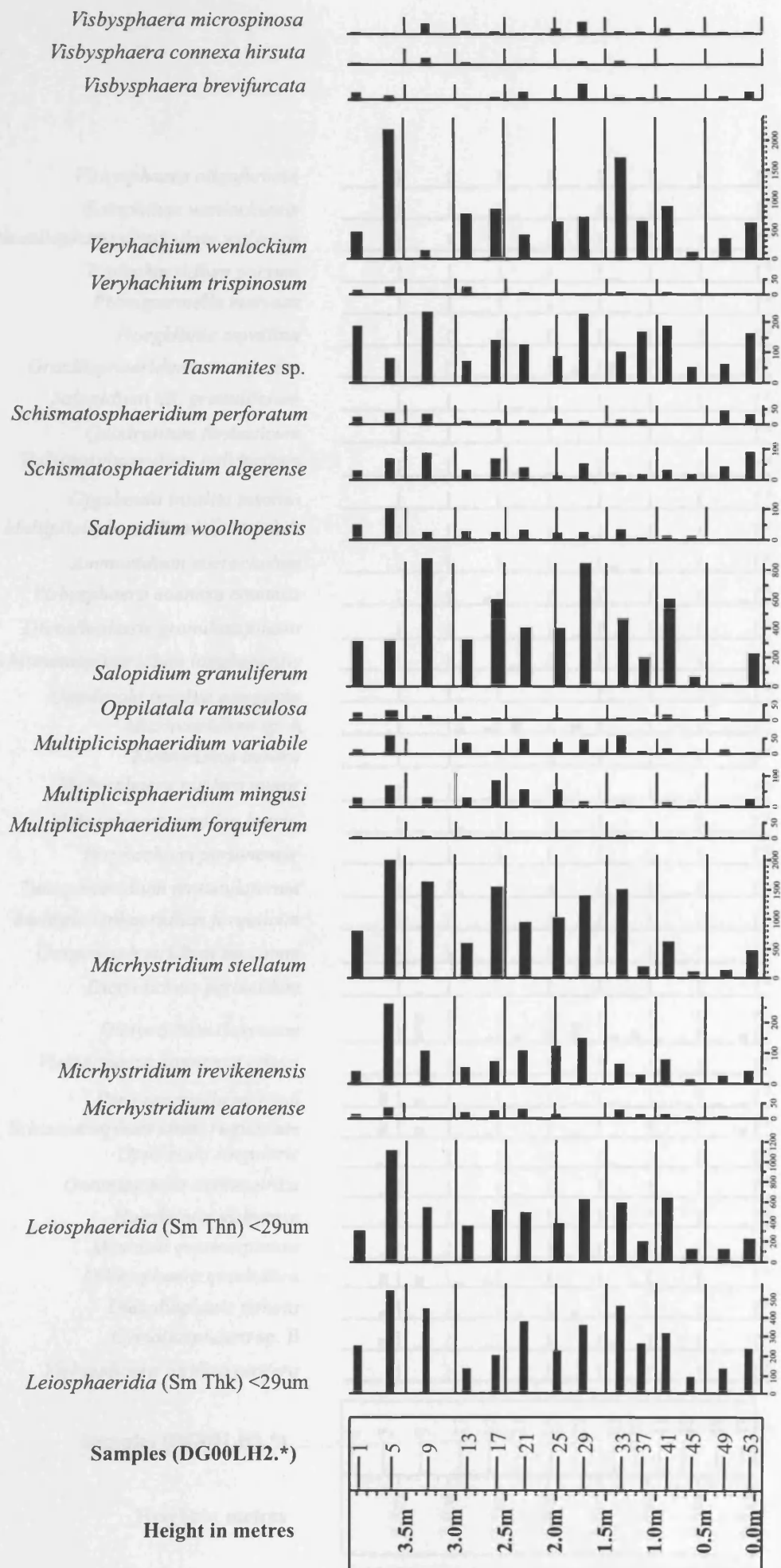


Samples (DG00LH2.\*)

Height in metres



Appendix 7. Absolute abundance of palynomorphs, Lickershamn 2.



Appendix 7. Absolute abundance of palynomorphs, Lickersham 2.



Appendix 7. Absolute abundance of palynomorphs, Lickersham 2.

## **Appendix 8**

### **PERCENT ABUNDANCE PLOTS FOR LICKERSHAMN 2**



Appendix 8. Percentage abundance of palynomorphs, Lickersham 2.



Appendix 8. Percentage abundance of palynomorphs, Lickersham 2.

## **Appendix 9**

### **CARBON AND OXYGEN ISOTOPE DATA FOR LUSKLINT 1**



Depth in metres above base of Lusklint 1	Stable C <sup>13</sup> value	Stable O <sup>18</sup> value
10.590	3.478	10.740
10.535	3.616	10.685
10.465	4.325	10.615
10.400	4.200	10.550
10.360	3.676	10.510
10.300	3.584	10.450
10.260	3.591	10.410
10.205	3.804	10.355
10.160	4.453	10.310
10.065	3.906	10.215
10.035	4.098	10.185
10.015	3.681	10.165
9.965	3.617	10.115
9.915	3.314	10.065
9.845	3.848	9.995
9.785	3.772	9.935
9.735	3.181	9.885
9.665	3.091	9.815
9.625	3.822	9.775
9.520	3.481	9.670
9.475	3.658	9.625
9.435	3.897	9.585
9.390	3.177	9.540
9.245	3.491	9.395
9.170	3.335	9.320
9.090	3.597	9.240
9.070	3.691	9.220
8.985	3.788	9.135
8.925	3.506	9.075
8.850	2.898	9.000
8.845	3.709	8.995
8.755	3.514	8.905
8.685	3.376	8.835
8.655	3.535	8.805
8.620	3.000	8.770
8.555	3.378	8.705
8.495	2.627	8.645
8.440	3.250	8.590
8.375	3.015	8.525
8.345	3.013	8.495
8.240	3.357	8.390
8.190	3.754	8.340
8.160	3.111	8.310
8.140	3.136	8.290
8.110	3.031	8.260
8.070	3.376	8.220
7.930	3.718	8.080
7.930	3.996	8.080
7.820	3.342	7.970
7.715	3.584	7.865
7.700	3.457	7.850
7.680	3.154	7.830
7.600	2.587	7.750
7.550	3.264	7.700
7.465	2.686	7.615
7.415	2.729	7.565
7.340	3.043	7.490
7.300	2.794	7.450
7.235	2.944	7.385
7.215	3.590	7.365
7.180	2.803	7.330
7.120	2.938	7.270
7.100	3.260	7.250
7.000	2.694	7.150
6.985	2.865	7.135
6.930	2.300	7.080
6.815	3.167	6.965
6.760	2.890	6.910
6.615	2.738	6.765
6.560	3.260	6.710
6.500	1.969	6.650
6.475	2.756	6.625
6.435	3.247	6.585
6.425	2.292	6.575
6.410	3.214	6.560

Depth in metres above base of Lusklint 1	Stable C <sup>13</sup> value	Stable O <sup>18</sup> value
6.330	2.678	6.480
6.330	3.206	6.480
6.280	2.755	6.430
6.250	2.350	6.400
6.230	2.736	6.380
6.210	2.879	6.360
6.190	2.846	6.340
6.140	3.027	6.290
6.105	2.307	6.255
6.080	2.144	6.230
6.030	1.970	6.180
5.970	1.997	6.120
5.780	2.501	5.930
5.740	2.243	5.890
5.700	2.639	5.850
5.700	2.035	5.850
5.700	2.311	5.850
5.700	2.337	5.850
5.665	2.547	5.815
5.630	1.893	5.780
5.605	2.303	5.755
5.575	2.776	5.725
5.500	2.200	5.650
5.500	2.276	5.650
5.500	2.381	5.650
5.500	2.168	5.650
5.500	2.192	5.650
5.465	2.193	5.615
5.410	2.091	5.560
5.390	2.023	5.540
5.390	1.853	5.540
5.355	1.770	5.505
5.330	2.180	5.480
5.300	2.010	5.450
5.273	2.077	5.423
5.195	1.657	5.345
5.175	1.642	5.325
5.155	1.943	5.305
5.140	1.901	5.290
5.060	1.623	5.210
4.930	1.719	5.080
4.900	1.962	5.050
4.845	1.644	4.995
4.830	1.653	4.980
4.815	1.921	4.965
4.815	1.923	4.965
4.815	1.855	4.965
4.815	1.870	4.965
4.815	2.607	4.965
4.790	2.365	4.940
4.790	1.244	4.940
4.790	1.268	4.940
4.790	0.424	4.940
4.790	0.915	4.940
4.765	1.494	4.915
4.765	1.798	4.915
4.765	1.482	4.915
4.765	2.386	4.915
4.765	1.538	4.915
4.740	1.678	4.890
4.735	1.720	4.885
4.735	2.078	4.885
4.735	2.406	4.885
4.735	2.247	4.885
4.735	1.927	4.885
4.645	1.674	4.795
4.510	1.616	4.660
4.510	1.644	4.660
4.440	1.752	4.590
4.400	1.584	4.550
4.400	1.885	4.550
4.330	1.637	4.480
4.305	2.359	4.455
4.265	1.841	4.415
4.260	2.090	4.410

Appendix 9. Carbon and Oxygen isotope data for Lusklint 1, provided by Corfield and Siveter

Depth in metres above base of Luskint 1	Stable C <sup>13</sup> value	Stable O <sup>18</sup> value
4.215	0.936	4.365
4.190	1.964	4.340
4.175	1.996	4.325
4.150	1.035	4.300
4.060	1.575	4.210
3.980	1.829	4.130
3.860	1.677	4.010
3.760	1.758	3.910
3.660	1.688	3.810
3.440	1.231	3.590
3.380	1.696	3.530
3.330	1.585	3.480
3.265	1.347	3.415
3.225	1.425	3.375
3.085	1.953	3.235
3.010	2.036	3.160
2.930	1.961	3.080
2.900	1.086	3.050
2.850	1.458	3.000
2.820	1.127	2.970
2.743	1.574	2.893
2.673	1.781	2.823
2.673	1.498	2.823
2.628	1.711	2.778
2.583	1.768	2.733
2.545	1.606	2.695
2.515	1.738	2.665
2.435	1.264	2.585
2.345	1.590	2.495
2.250	1.217	2.400
2.145	1.793	2.295
2.030	1.284	2.180
1.970	1.539	2.120
1.910	1.366	2.060
1.870	1.549	2.020
1.810	1.247	1.960
1.730	1.195	1.880
1.730	1.190	1.880
1.670	1.184	1.820
1.645	1.538	1.795
1.635	1.457	1.785
1.595	1.575	1.745
1.555	1.606	1.705
1.555	1.631	1.705
1.555	1.440	1.705
1.555	1.445	1.705
1.555	1.467	1.705
1.555	1.603	1.705
1.525	1.287	1.675
1.505	1.486	1.655
1.480	1.043	1.630
1.475	1.516	1.625
1.430	1.640	1.580
1.385	1.535	1.535
1.340	1.545	1.490
1.340	1.564	1.490
1.230	1.056	1.380
1.180	1.626	1.330
1.105	1.504	1.255
1.070	1.518	1.220
1.050	1.499	1.200
1.030	1.590	1.180
1.030	1.504	1.180
1.005	1.467	1.155
0.965	1.516	1.115
0.960	1.583	1.110
0.895	1.557	1.045
0.870	1.487	1.020
0.845	1.582	0.995
0.845	1.757	0.995
0.800	1.535	0.950
0.780	1.401	0.930
0.775	1.450	0.925
0.775	1.517	0.925
0.760	1.493	0.910

Depth in metres above base of Luskint 1	Stable C <sup>13</sup> value	Stable O <sup>18</sup> value
0.738	1.481	0.888
0.738	1.136	0.888
0.695	1.416	0.845
0.655	1.313	0.805
0.655	1.542	0.805
0.620	1.577	0.770
0.580	0.751	0.730
0.560	1.415	0.710
0.520	1.335	0.670
0.490	1.339	0.640
0.445	1.604	0.595
0.400	1.268	0.550
0.350	1.309	0.500
0.300	1.436	0.450
0.295	1.347	0.445
0.240	1.593	0.390
0.240	1.625	0.390
0.180	1.179	0.330
0.115	1.550	0.265
0.070	1.221	0.220
0.010	1.264	0.160
0.005	1.278	0.155
0.005	1.234	0.155
-0.020	1.607	0.130
-0.060	1.587	0.090
-0.105	1.513	0.045
-0.150	1.347	0.000
-0.250	1.483	-0.100
-0.350	1.503	-0.200
-0.450	1.514	-0.300
-0.550	1.462	-0.400
-0.650	1.287	-0.500
-0.750	1.508	-0.600
-0.850	1.517	-0.700
-0.950	1.534	-0.800
-1.050	1.534	-0.900
-1.150	1.489	-1.000
-1.250	1.525	-1.100
-1.350	1.519	-1.200
-1.450	1.622	-1.300
-1.550	1.544	-1.400
-1.650	1.600	-1.500
-1.750	1.562	-1.600
-1.850	1.664	-1.700
-1.950	1.720	-1.800
-2.050	1.628	-1.900
-2.150	1.518	-2.000
-2.250	1.529	-2.100
-2.350	1.549	-2.200
-2.385	1.379	-2.235
-2.385	1.509	-2.235
-2.450	1.511	-2.300
-2.550	1.402	-2.400
-2.570	1.453	-2.420
-2.630	1.540	-2.480
-2.650	1.330	-2.500
-2.670	1.585	-2.520
-2.740	1.459	-2.590
-2.750	1.451	-2.600
-2.790	1.528	-2.640
-2.850	1.391	-2.700
-2.950	1.583	-2.800
-3.050	1.524	-2.900
-3.150	1.558	-3.000
-3.250	1.577	-3.100
-3.350	1.586	-3.200
-3.450	1.575	-3.300
-3.550	1.531	-3.400
-3.650	1.708	-3.500
-3.750	1.557	-3.600
-3.850	1.645	-3.700
-3.950	1.698	-3.800
-4.050	1.499	-3.900
-4.150	1.623	-4.000
-4.150	1.170	-4.000

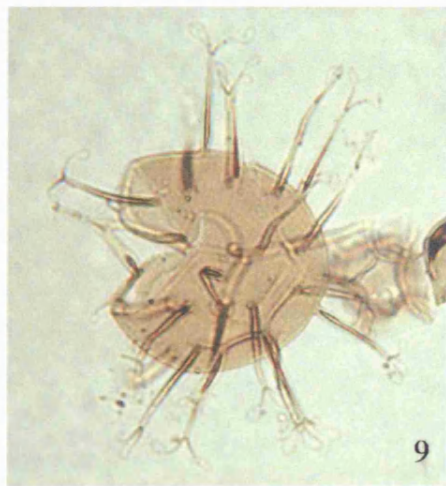
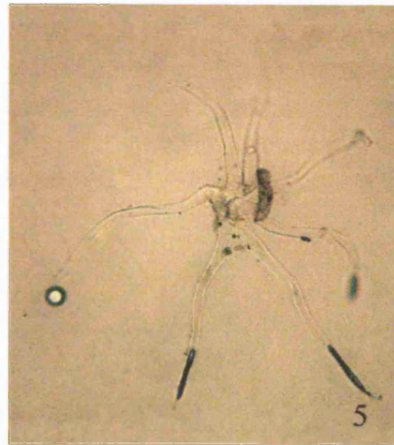
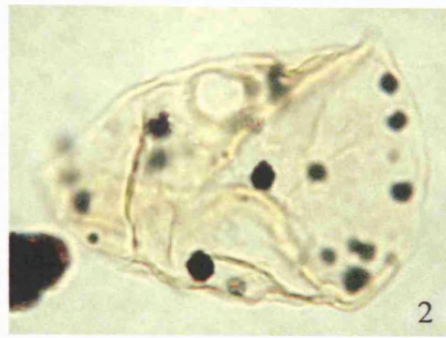
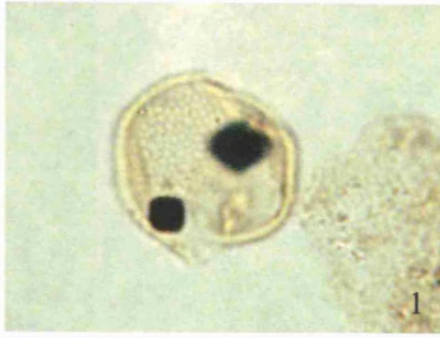
Appendix 9. Carbon and Oxygen isotope data for Luskint 1, provided by Corfield and Siveter

Depth in metres above base of Lusklint 1	Stable C <sup>13</sup> value	Stable O <sup>18</sup> value
-4.250	1.520	-4.100
-4.350	1.522	-4.200
-4.450	1.391	-4.300
-4.550	1.404	-4.400
-4.650	1.364	-4.500
-4.750	1.565	-4.600
-4.850	1.444	-4.700
-4.950	1.510	-4.800
-5.050	1.579	-4.900
-5.150	1.496	-5.000
-5.250	1.311	-5.100
-5.350	1.489	-5.200
-5.450	1.543	-5.300
-5.550	1.621	-5.400
-5.650	1.905	-5.500
-5.850	1.296	-5.700
-5.950	1.621	-5.800
-5.950	1.529	-5.800
-6.050	1.434	-5.900
-6.150	1.534	-6.000
-6.250	1.529	-6.100
-6.350	1.574	-6.200
-6.450	1.541	-6.300
-6.550	1.836	-6.400
-6.650	1.628	-6.500
-6.750	1.704	-6.600
-6.850	1.616	-6.700
-6.950	2.069	-6.800
-7.050	1.655	-6.900
-7.150	1.621	-7.000
-7.250	1.524	-7.100
-7.350	1.658	-7.200
-7.450	1.560	-7.300
-7.550	1.816	-7.400
-7.650	1.595	-7.500
-7.750	1.826	-7.600
-7.850	1.647	-7.700
-7.950	1.671	-7.800
-8.050	1.677	-7.900
-8.150	1.920	-8.000
-8.710	1.872	-8.560
-8.978	1.808	-8.828
-9.055	1.836	-8.905

## **PLATES**

# EXPLANATION OF PLATE 1

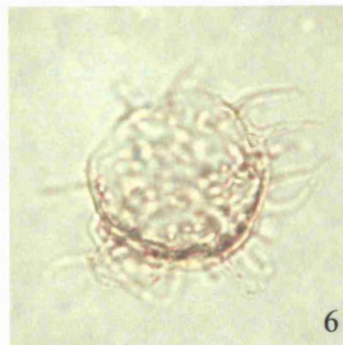
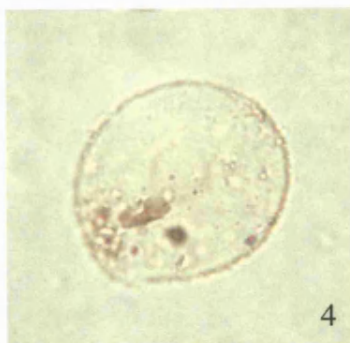
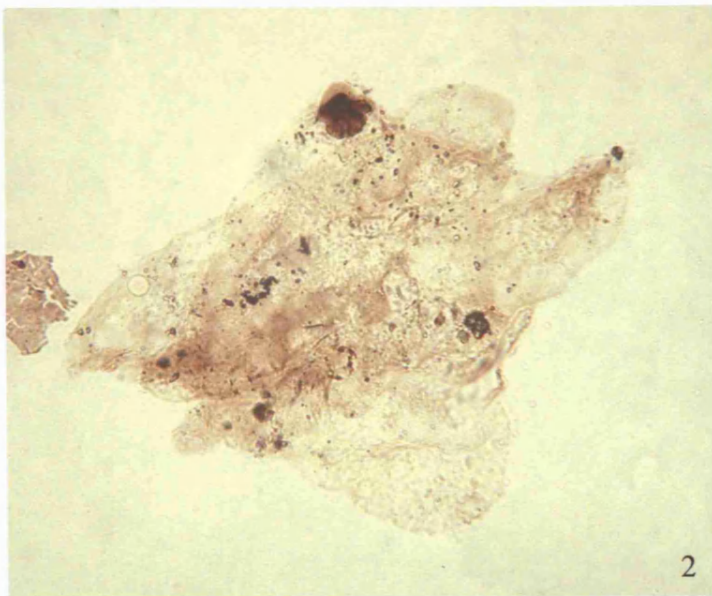
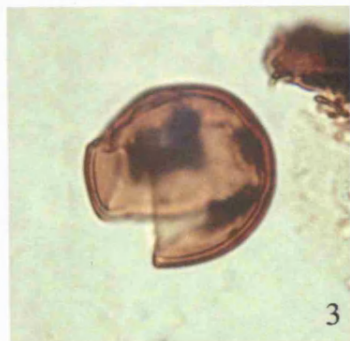
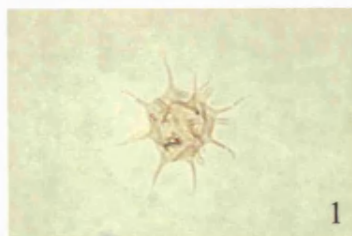
Fig.		Page
	<b><i>Dictyotidium alveolatum</i> (Kiryanov, 1978) Le Hérissé, 1989</b>	35
1	DG00LK1.259npg1–S29, 3, Upper Visby Beds, x 750. Specimen showing typical extent of pyritization prior to nitric acid treatment.	
	<b><i>Schismatosphaeridium algerense</i> Cramer &amp; Díez, 1976a</b>	42
2	DG00LK1.259npg1–P28, Upper Visby Beds, x 750. Specimen showing typical extent of pyritization prior to nitric acid treatment.	
	<b>Recent organic debris</b>	
3	Deionised water slide 3–J 52, 2, x 400.	
4	Deionised water slide 3–D48, 1, x 400. Debris showing a cell structure	
5	Deionised water slide 2–V 47, 1, x 400. Debris showing pseudo-processes radiating from a central body.	
	<b><i>Pterospermella martinii</i> Cramer, 1966a</b>	36
6	DG00LK1.187npg1–S38, Upper Visby Beds, x 750. Photograph showing a pale unheated specimen.	
7	DG00LK1.187ckd1–N39, 1, Upper Visby Beds, x 750. Photograph showing a dark specimen, which has undergone heating.	
	<b><i>Gracilisphaeridium encantador</i> (Cramer, 1970) <i>ex</i> Eisenack <i>et al.</i>, 1973</b>	38
8	DG00LK1.187ckd1–K34, 1, Upper Visby Beds, x 750. Photograph showing a pale unheated specimen.	
9	DG00LK1.187ckd1–U41, 3, Upper Visby Beds, x 750. Photograph showing a dark specimen, which has undergone heating.	



## EXPLANATION OF PLATE 2

Fig.		Page
	<b><i>Micrhystridium stellatum</i> Deflandre, 1945</b>	39
1	DG00LK1.21npg1– T47, Lower Visby Beds, x 1000.	
	<b><i>Pulvinosphaeridium pulvinellum</i> Eisenack, 1954</b>	42
2	DG00LH2.25npg1–H46, 4, Lower Visby Beds, x 600.	
	<b><i>Tasmanites</i> sp.</b>	36
3	DG00LK1.258ckd 1–K34, 1, Upper Visby Beds, x 1000.	
	<b><i>Schismatosphaeridium rugulosum</i> Dorning, 1981</b>	43
4	DG00LH2.9npg1–F34, 2, Upper Visby Beds, x 1000. Specimen showing coarse globular ornament on the vesicle surface.	
	<b><i>Pterospermella marysae</i> Le Hérissé, 1989</b>	36
5	DG00LK1.258ckd 1–Q35, Upper Visby Beds, x 1000. Specimen showing wide equatorial flange.	
	<b><i>Salopidium granuliferum</i> (Downie 1959) Dorning, 1981</b>	42
6	DG00LK1.100npg1–R34, 2, Lower Visby Beds, x 1000. Specimen showing simple process form and a granulate vesicle.	
	<b><i>Oppilatala insolita insolita</i> Cramer &amp; Diez 1972</b>	41
7	DG00LK1.219npg1–R45, Upper Visby Beds, x 1000. Specimen showing complex branching pattern.	
	<b><i>Eupoikilofusa striatifera</i> Cramer, 1964a</b>	38
8	DG00LK1.100npg1–N40, Lower Visby Beds, x 1000. Specimen showing fusiform vesicle shape.	
	<b><i>Veryhachium wenlockium</i> (Downie, 1959) Stockmans &amp; Willière, 1962b</b>	43
9	DG00LK1.258 ckd 1, R34/4, Upper Visby Beds, x 1000. Specimen showing triangular vesicle.	







# EXPLANATION OF PLATE 3

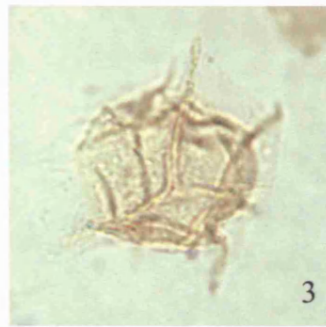
Fig.		Page
	<b><i>Cymatiosphaera aff. ledburica</i> Dorning, 1981</b>	34
1	DG00LK1.258ckd1–O43, 1, Upper Visby Beds. x 750.	
2	DG00LK1.258ckd1–S32, Upper Visby Beds, x 750.	
12	DG00LK1.120–J6, (SEM), Lower Visby Beds, x 750.	
13	DG00LK1.112–J12, (SEM), Lower Visby Beds. x 750.	
	<b><i>Cymatiosphaera octoplana</i> Downie, 1959</b>	35
3	DG00LK1.24npg1–L41, 1, Lower Visby Beds, x 750.	
4	DG00LK1.48npg3–Q36, Lower Visby Beds, x 750.	
5	DG00LK1.20npg1–N39, 4, Lower Visby Beds x 750.	
6	DG00LK1.207npg1–T35, 1, Lower Visby Beds x 750. Specimen showing characters that closely follow the description of “ <i>C. prismatica</i> ” (Le Hérisse 1989 pp. 76), which is now combined with <i>C. octoplana</i> .	
9	DG00LK1.120–L5, (SEM) Lower Visby Beds, x 750.	
	<b><i>Cymatiosphaera</i> sp. B Le Hérisse, 1989</b>	35
7	DG00LK2.9npg1–T45, 2, Upper Visby Beds, x 750.	
8	DG00LK1.258npg1ckd–N42, 4, Upper Visby Beds x 750.	
	<b><i>Cymatiosphaera heloderma</i> Cramer &amp; Díez, 1972</b>	34
10	DG00LK1.257–T10, (SEM) Upper Visby Beds, x 750. Specimen showing an unopened thickened linear excystment structure. This specimen shows some similarities to the structures in the fields of <i>C. mariae</i> Le Hérisse, 1989, but here these are only an over–development of the foveolate structure.	
11	DG00LK1.255–M3, (SEM), Upper Visby Beds, x 750. Specimen similar to <i>C. octoplana</i> , but with a foveolate, not granulate, vesicle.	
	<b><i>Duvernaysphaera aranaides</i> (Cramer, 1964b) Cramer &amp; Díez, 1972</b>	35
14	DG00LK1.128npg1–O41, 1, Lower Visby Beds, x 750.	
15	DG00LK1.144npg1–L41, Upper Visby Beds, x 750.	



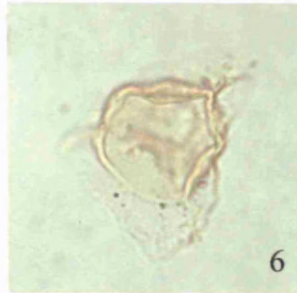
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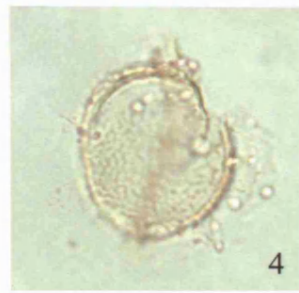
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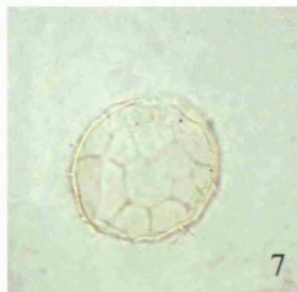
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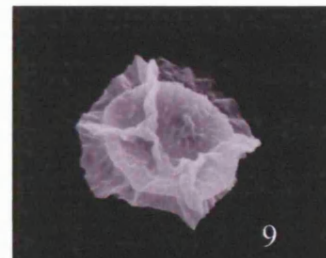
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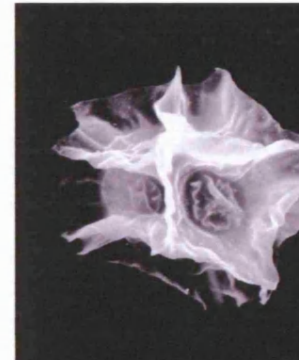
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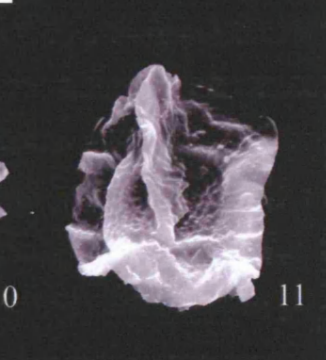
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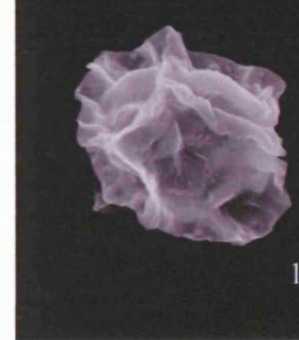
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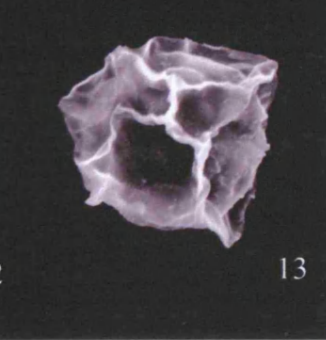
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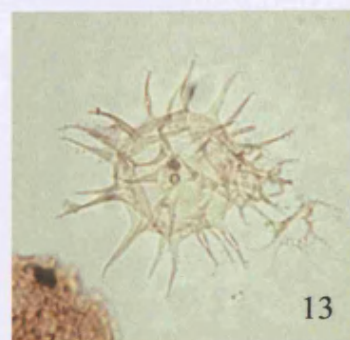
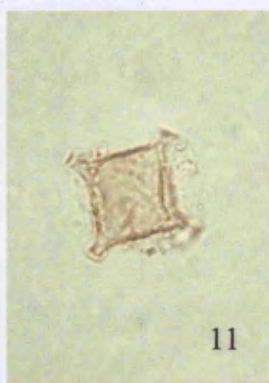
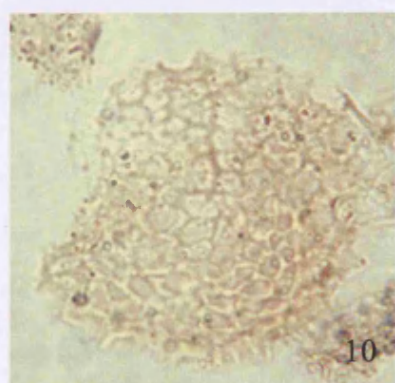
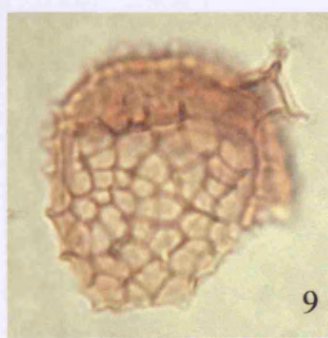
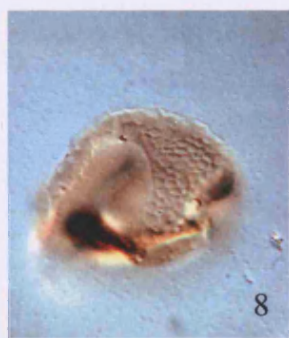
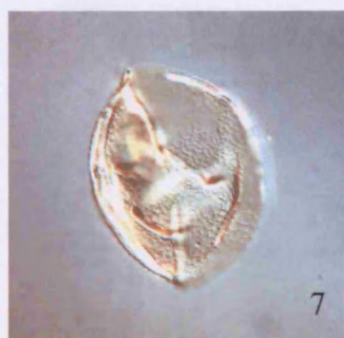
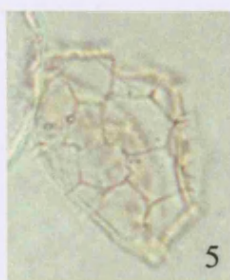
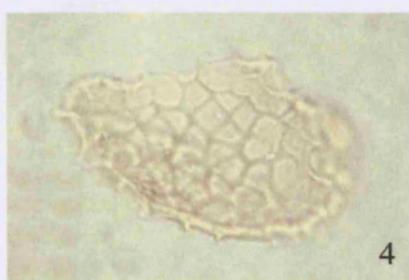
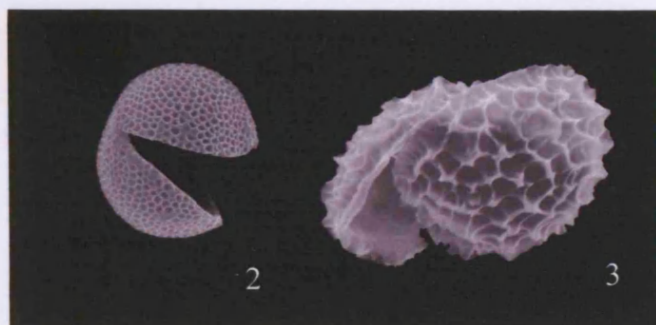
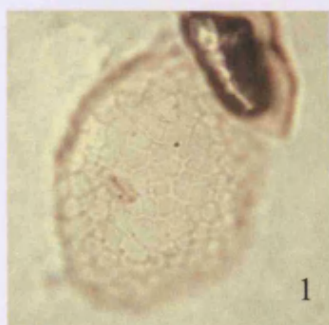
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13

# EXPLANATION OF PLATE 4

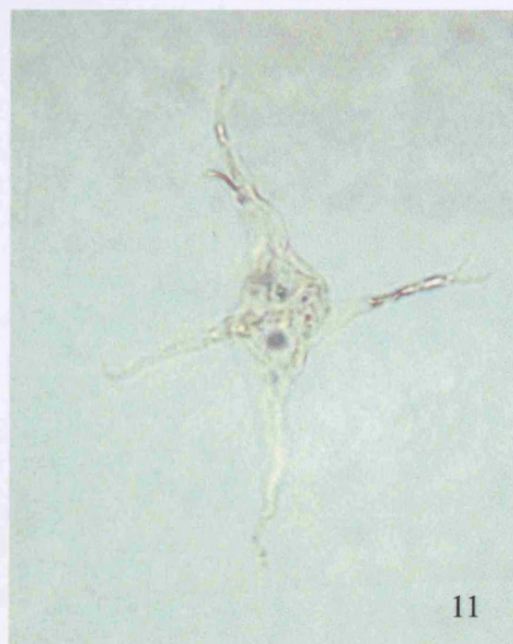
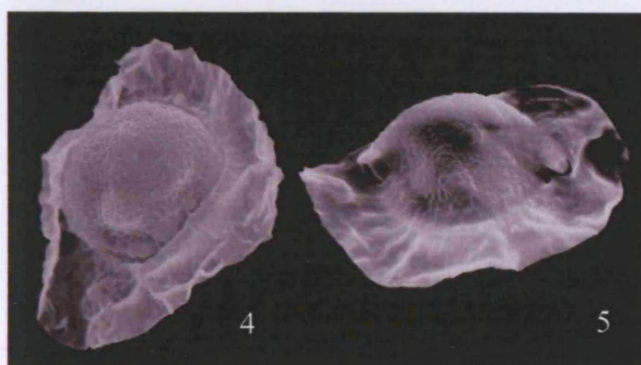
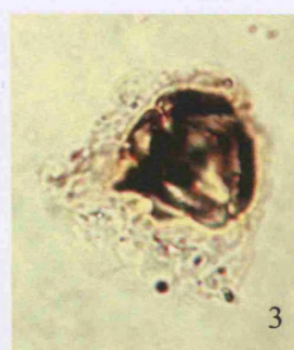
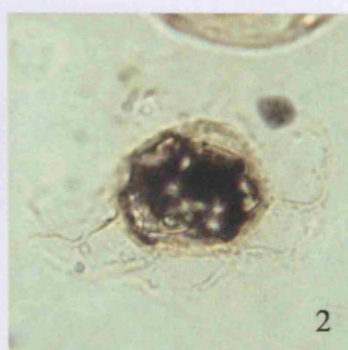
Fig.		Page
	<b><i>Dictyotidium alveolatum</i> (Kiryanov, 1978) Le Hérisse, 1989</b>	35
1	DG00LK1.171npg1–Q41, Upper Visby Beds, x 750. This specimen is similar to <i>D. dictyotum</i> (fig. 4), but possesses smaller and more numerous fields (about twice as many as seen in fig. 4).	
	<b><i>Dictyotidium dictyotum</i> Eisenack, 1938</b>	35
4	DG00LK1.100npg1–N36, Lower Visby Beds, x 750.	
5	DG00LK1.199npg1–P38, Lower Visby Beds, x 750.	
9	DG00LK1.258ckd1–H48, Upper Visby Beds, x 750.	
10	DG00LK1.56npg1–L35, 3, Lower Visby Beds, x 750.	
	<b><i>Dictyotidium perlucidum</i> Le Hérisse, 1989</b>	35
6	DG00LK1.211npg1–E38, Upper Visby Beds, x 750.	
	<b><i>Dictyotidium faviforme</i> Schulz, 1967</b>	35
2	DG00LK1.257–J10, (SEM), Upper Visby Beds, x 750. Specimen showing lateral split.	
7	DG00LH2.49npg1–P45, 1, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
8	DG00LH2.33npg1–M39, 4, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Dictyotidium stenodictyum</i> Eisenack, 1965</b>	35
3	DG00LK1.120–P12, (SEM), Lower Visby Beds, x 750. Specimen showing lateral split.	
	<b><i>Quadraticum fantasticum</i> Cramer, 1964b</b>	36
11	DG00LK1.235npg3–S37, 3, Upper Visby Beds, x 750.	
12	DG00LK1.251npg1–N45, 2, Upper Visby Beds, x 750.	
	<b><i>Ammonidium microcladum</i> (Downie, 1963) Lister, 1970</b>	36
13	DG00LK1.258ckd1–J29, Upper Visby Beds, x 750.	
14	DG00LK1.112–D5, (SEM) Upper Visby Beds, x 750.	
	<b><i>Tasmanites</i> sp.</b>	36
15	DG00LK1.39npg1–P38, Lower Visby Beds, x 750.	



# EXPLANATION OF PLATE 5

Fig.		Page
	<b><i>Pterospermella foveolata</i> Dorning, 1981</b>	35
1	DG00LK1.171ckd1-J39, 2, Upper Visby Beds, x 750. Specimen showing characteristic granulate vesicle.	
2	DG00LK1.72npg1-M36, Lower Visby Beds, x 750.	
3	DG00LK1.215npg1-J34, 3, Upper Visby Beds, x 750.	
	<b><i>Pterospermella martinii</i> Cramer, 1966a</b>	36
4	DG00LK1.120-G5, (SEM), Lower Visby Beds, x 750. Specimen showing characteristic smooth vesicle.	
5	DG00LK1.100-I14, (SEM), Lower Visby Beds, x 750.	
6	DG00LH2.9ckd1-L33, Upper Visby Beds, x 750.	
	<b><i>Pterospermella marysae</i> Le Hérissé, 1989</b>	36
7	DG00LH2.9ckd1-M49, 1, Upper Visby Beds, x 750. Specimen showing characteristic narrow flange (less than half the width of the vesicle).	
8	DG00LK.171ckd1-G41, 3, Upper Visby Beds, x 750.	
	<b><i>Deunffia brevifurcata</i> Hill, 1974</b>	36
9	DG00LK.227npg1-G1, 1, Upper Visby Beds, 750.	
	<b><i>Diexallophasis remota</i> (Deunff, 1955) emend. Playford, 1977</b>	37
10	DG00LK1.96npg1-M37, 3, Lower Visby Beds, x 750.	
11	DG00LK1.171ckd1-L35, 4, Lower Visby Beds, x 750.	
	<b><i>Deunffia monospinosa</i> Downie, 1960</b>	36
12	DG00LK.8npg1-H40, 3, Lower Visby Beds, x 750.	

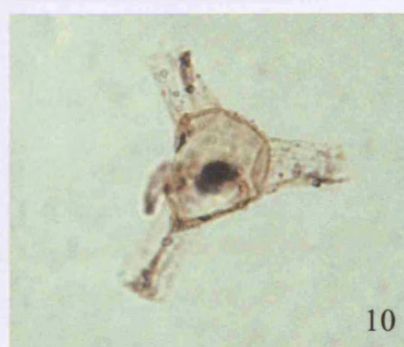
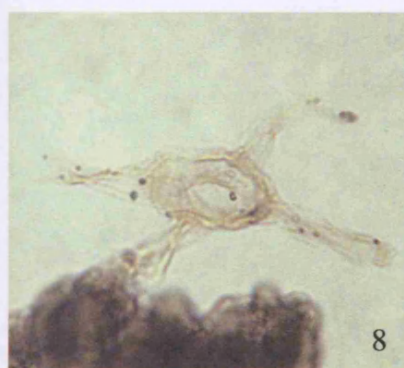
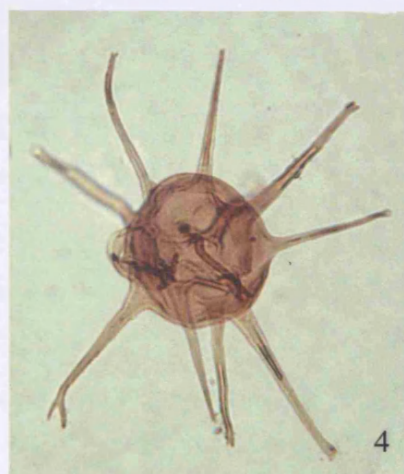




## EXPLANATION OF PLATE 6

Fig.		Page
	<b><i>Deunffia ramusculosa</i> Downie, 1960</b>	36
1	DG00LK1.28npg1-N31, 4, Lower Visby Beds, x 750.	
2	DG00LK1.28npg1-H34, 4, Lower Visby Beds, x 750.	
	<b><i>Diexallophasis gotlandica</i> Cramer, 1970</b>	37
3	DG00LK1.258ckd1-L30, 2, Upper Visby Beds, x 750.	
4	DG00LH2.9ckd1-S32, 2, Upper Visby Beds, x 750.	
	<b><i>Diexallophasis denticulata wolynica</i> Kriyanov, 1978</b>	37
5	DG00LH2.41npg1-V39, Upper Visby Beds, x 750.	
	<b><i>Diexallophasis granulatispinosa</i> (Downie, 1963) Hill, 1974</b>	37
6	DG00LK1.223npg1-K43, 1, Upper Visby Beds, x 750.	
7	DG00LK1.255npg1-G5, (SEM), Upper Visby Beds, x 750.	
	<b><i>Dilatisphaera laevigata</i> Lister, 1970</b>	37
8	DG00LH2.9ckd1-K31, 1, Upper Visby Beds, x 750.	
9	DG00LK1.255npg1-I12, (SEM), Upper Visby Beds, x 750.	
10	DG00LH2.33ckd1-F40, 4, Upper Visby Beds, x 750.	

PLATE 6

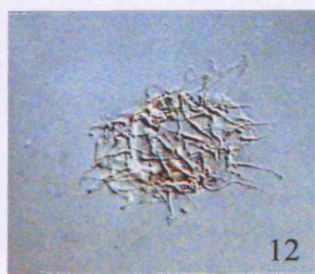
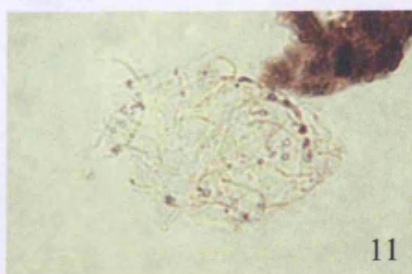
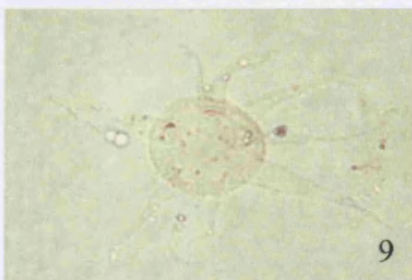
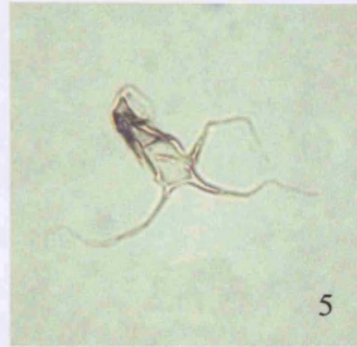
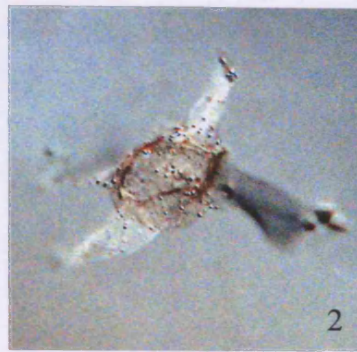
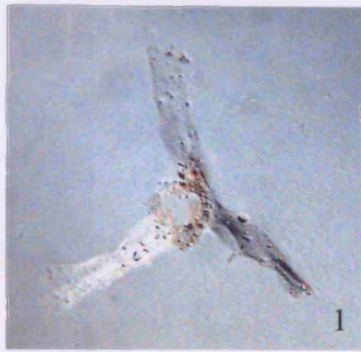




# EXPLANATION OF PLATE 7

Fig.		Page
	<b><i>Dilatisphaera williereae</i> (Martin, 1966) Lister, 1970</b>	37
1	DG00LK1.24ckd1-K35, 1, Lower Visby Beds, x 750. Specimen photographed under differential interference contrast.	
2	DG00LH2.49npg1-V47, 1, Lower Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Domasia amphora</i> (Martin, 1969) emend. Hill, 1974</b>	37
3	DG00LK1.219npg1-H43, Upper Visby Beds, x 750.	
	<b><i>Domasia bispinosa</i> Downie, 1960</b>	37
4	DG00LK1.40npg1-L39, 1, Lower Visby Beds, x 750.	
	<b><i>Domasia quadrispinosa</i> Hill, 1974</b>	37
5	DG00LK1.28npg1-Q42, 2, Lower Visby Beds, x 750.	
6	DG00LK1.195npg1-P45, Upper Visby Beds, x 750.	
	<b><i>Domasia trispinosa</i> (Downie, 1960) emend. Hill, 1974</b>	37
7	DG00LH2.33ckd1-L33, Upper Visby Beds, x 750.	
8	DG00LH2.33ckd1-D39, 1, Upper Visby Beds, x 750.	
	<b><i>Eisenackidium ranaemanum</i> Le Hérissé, 1989</b>	38
9	DG00LK1.239npg1-G34, Upper Visby Beds, x 750.	
	<b><i>Moyeria uticaensis</i> Thusu, 1973</b>	40
10	DG00LK1.239npg1-P36, 1, Upper Visby Beds, x 750.	
	<b><i>Elektoriskos aurora</i> Loeblich, 1970a</b>	38
11	DG00LH2.17npg1-O33, Upper Visby Beds, x 750.	
12	DG00LH2.41npg1-Q40, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Eupoikilofusa filifera</i> (Downie, 1959) Dorning, 1981 emend</b>	38
13	DG00LK1.211npg1-N38, Upper Visby Beds, x 750.	

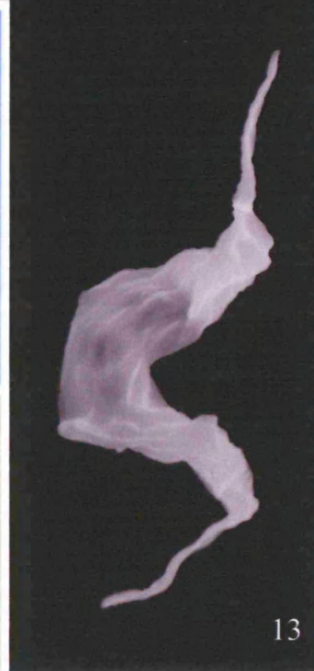
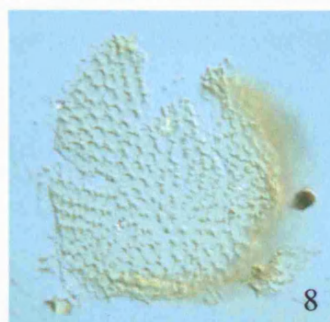
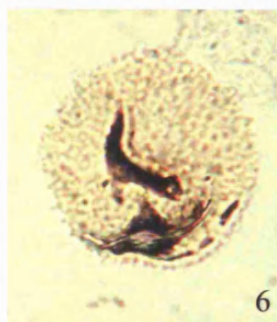
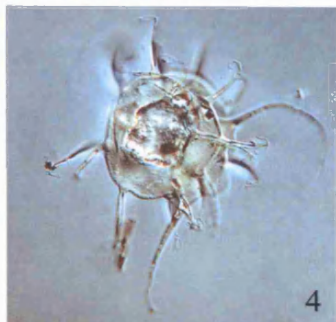
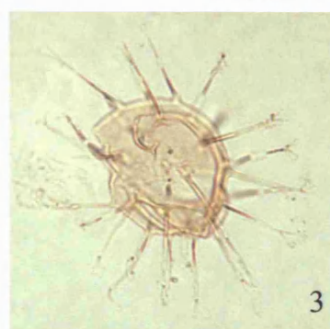
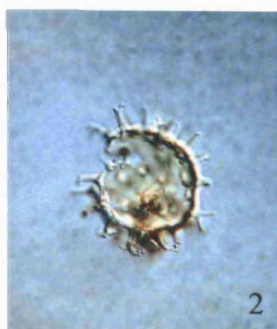
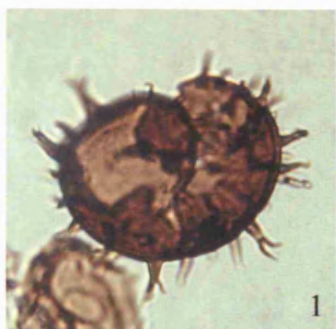
PLATE 7



# EXPLANATION OF PLATE 8

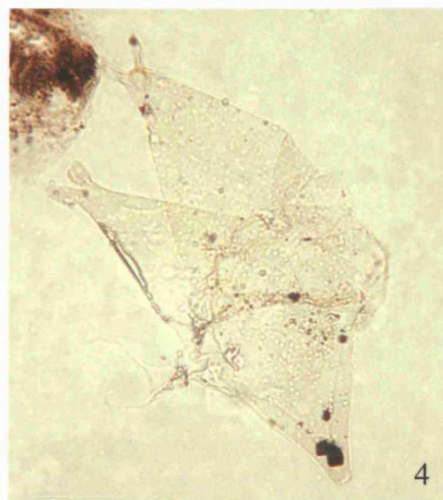
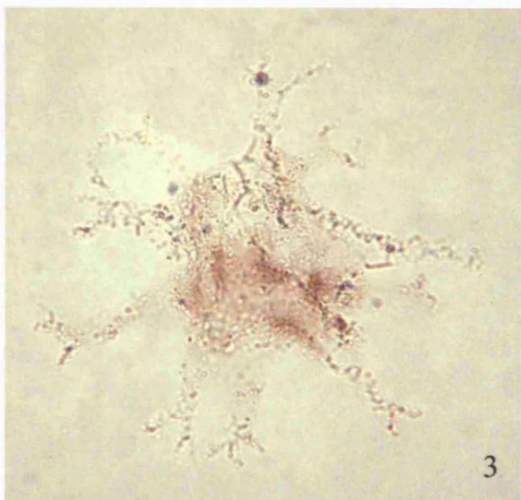
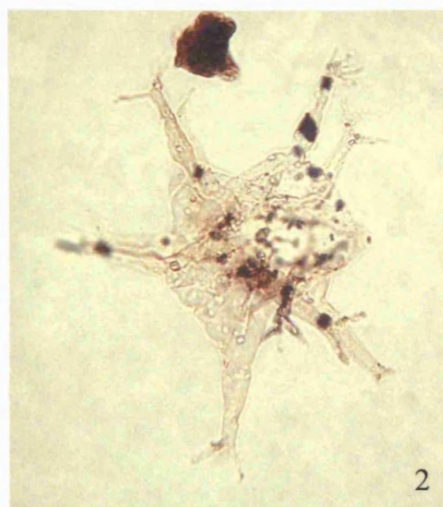
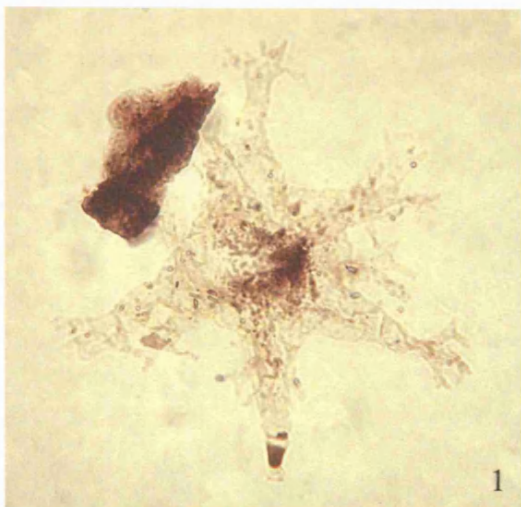
Fig.		Page
	<b><i>Gorgonisphaeridium succinum</i> Lister, 1970</b>	38
1	DG00LH2.9ckd1–Y48, Upper Visby Beds, x 750.	
2	DG00LH2.45npg2–U38, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Gracilisphaeridium encantador</i> (Cramer, 1970) ex Eisenack <i>et al.</i>, 1973</b>	38
3	DG00LH2.33ckd1–G39, Upper Visby Beds, x 750.	
4	DG00LH2.49npg1–H45, 2, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
5	DG00LK1.255–J3, (SEM), Upper Visby Beds, x 750.	
	<b><i>Helosphaeridium clavispinulosum</i> Lister, 1970</b>	38
6	DG00LK1.6npg1–N38, 4, Lower Visby Beds, 750.	
7	DG00LK1.112–Q9, (SEM), Lower Visby Beds, x 750.	
	<b><i>Helosphaeridium citrinipeltatum</i> (Cramer &amp; Diez, 1972) Dorning, 1981</b>	38
8	DG00LK1.258ckd1–O35, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
9	DG00LK1.255–O10, (SEM), Upper Visby Beds, x 750.	
	<b><i>Helosphaeridium pseudodictyum</i> Lister, 1970</b>	38
10	DG00LK1.132npg1–K38, Lower Visby Beds, x 750. Specimen photographed under differential interference contrast.	
11	DG00LK1.183npg1–T34, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Eupiokilofusa striatifera</i> Cramer, 1964a</b>	38
12	DG00LH2.33ckd1–G30, 4, Upper Visby Beds, x 750.	
13	DG00LK1.112–N9, (SEM), Lower Visby Beds, x 750.	





# EXPLANATION OF PLATE 9

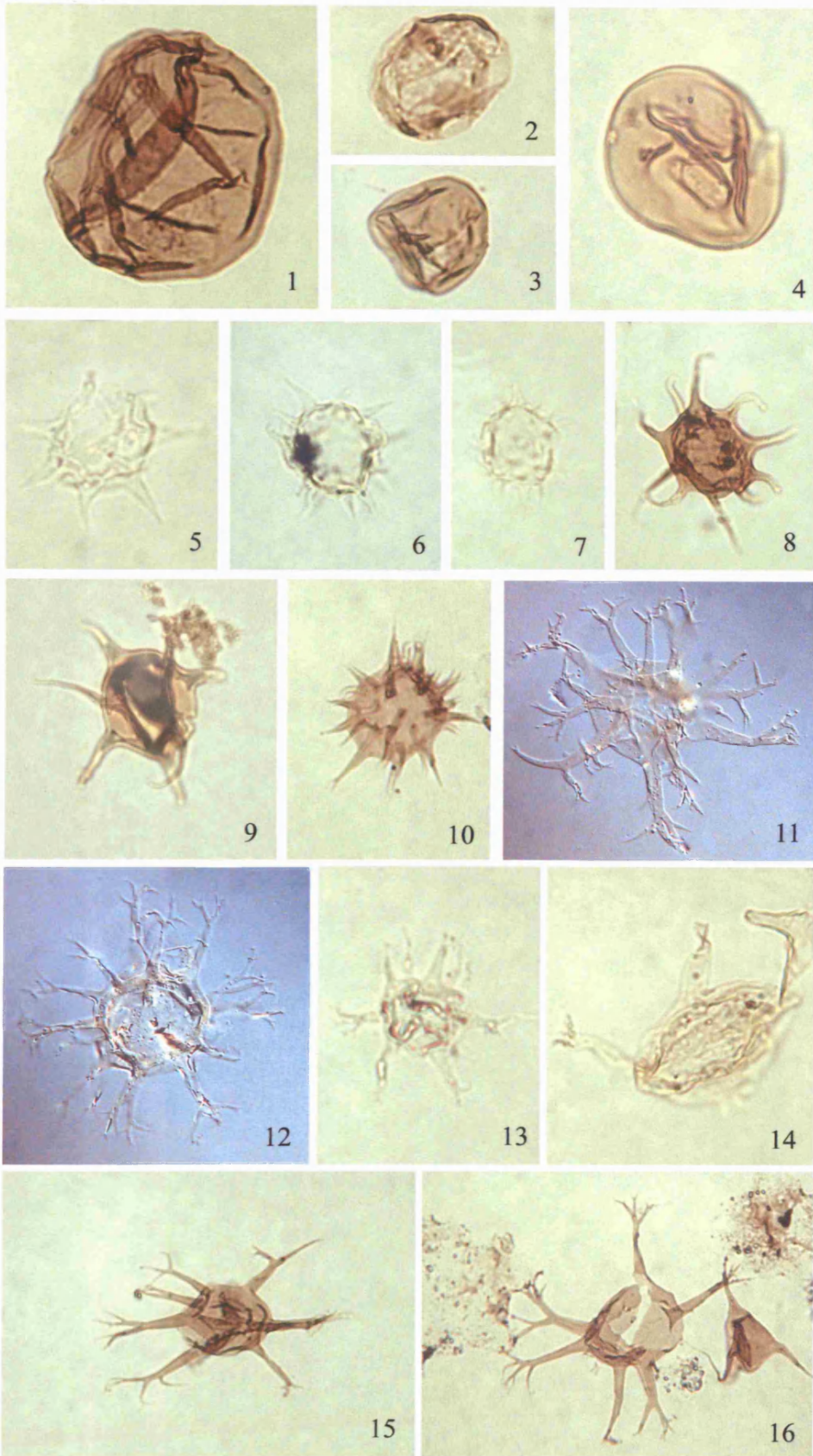
Fig.		Page
	<b><i>Hoegklintia corallina</i> Eisenack, 1959</b>	38
1	DG00LH2.33npg1–X38, 2, Upper Visby Beds, x 500.	
	<b><i>Hoegklintia digitata</i> (Eisenack, 1938) Dorning, 1981</b>	39
2	DG00LH2.33npg1–N40, 3, Upper Visby Beds, x 500.	
3	DG00LK1.187npg1–K45, 4, Upper Visby Beds, x 500.	
	<b><i>Hoegklintia visbyensis</i> (Eisenack, 1959) Dorning, 1981</b>	39
4	DG00LH2.41npg1–L41, 3, Upper Visby Beds, x 500.	
	<b><i>Leiofusa parvitatis</i> Loeblich, 1970</b>	39
5	DG00LK1.227npg1–M34, Upper Visby Beds, x 750.	
6	DG00LK1.96npg1–G37, Lower Visby Beds, x 750.	
	<b><i>Leiofusa</i> cf. <i>banderillae</i> Cramer, 1964b</b>	39
7	DG00LK1.247npg1–P38, Upper Visby Beds, x 750.	
8	DG00LK1.219npg1–T45, Upper Visby Beds, x 750.	



# EXPLANATION OF PLATE 10

Fig.		Page
	<b><i>Leiosphaeridia</i> (Eisenack, 1958b) emend. Downie &amp; Sarjeant, 1963, emend. Turner, 1984</b>	39
1	DG00LK1.80ckd1-M33, 4, Lower Visby Beds, x 750. Large thin walled specimen.	
2	DG00LK1.80ckd1-F29, 3, Lower Visby Beds, x 750. Small thin walled specimen.	
3	DG00LK1.80ckd1-R30, 2, Lower Visby Beds, x 750. Small thick walled specimen.	
4	DG00LK1.258ckd1-N45, 4, Upper Visby Beds, x 750. Large thick walled specimen.	
	<b><i>Leprotolypa gordonense</i> Cramer, 1963</b>	39
5	DG00LK1.171npg1-N49, 4, Upper Visby Beds, x 750.	
	<b><i>Micrhystridium eatonense</i> Downie, 1959</b>	39
6	DG00LK1.187npg1-L35, 4, Upper Visby Beds, x 750.	
7	DG00LH2.5npg1-H38, Upper Visby Beds, x 750.	
	<b><i>Micrhystridium irevikensis</i> Le Hérissé, 1989</b>	39
8	DG00LK1.80ckd1-O40, Lower Visby Beds, x 750. Specimen showing some coarse granulation to micro barbs on the distal parts of the processes.	
9	DG00LK1.258ckd1-J29, Upper Visby Beds, x 750.	
	<b><i>Micrhystridium stellatum</i> Deflandre, 1945</b>	39
10	DG00LK1.144ckd1-Q46, 1, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium arbusculum</i> Dorning, 1981</b>	40
11	DG00LK1.187npg1-O42, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
12	DG00LK1.28npg1-K30, 4, Lower Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Multiplicisphaeridium cladum</i> (Downie, 1963) Eisenack, 1969</b>	40
13	DG00LK1.219npg1-G51, Upper Visby Beds, x 750.	
14	DG00LK1.215npg1-H43, 3, Upper Visby Beds, x 750. Broken specimen, but distal palmate branching can be seen.	
	<b><i>Multiplicisphaeridium forquiferum</i> (Cramer &amp; Díez, 1972b) Eisenack et al., 1973</b>	40
15	DG00LK1.144ckd1-K33, 1, Upper Visby Beds, x 750.	
16	DG00LH2.9ckd1-M49, 1, Upper Visby Beds, x 750.	

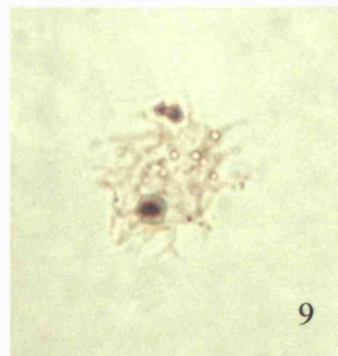
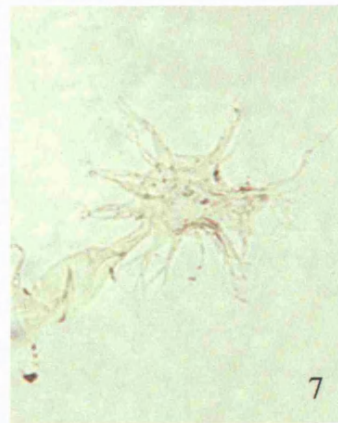
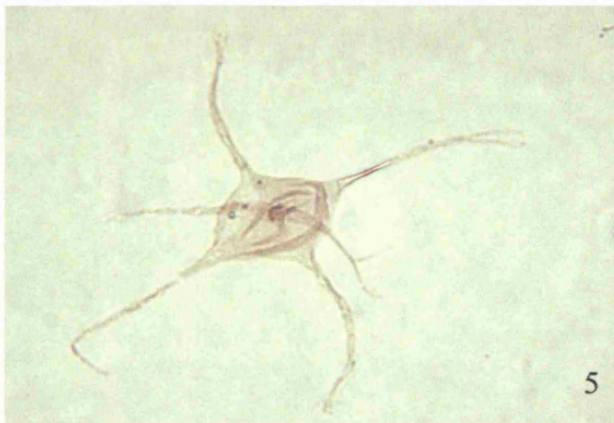
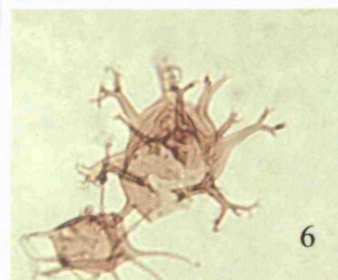
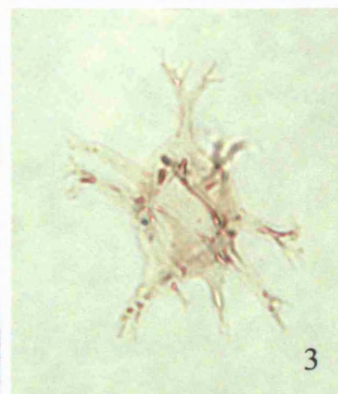
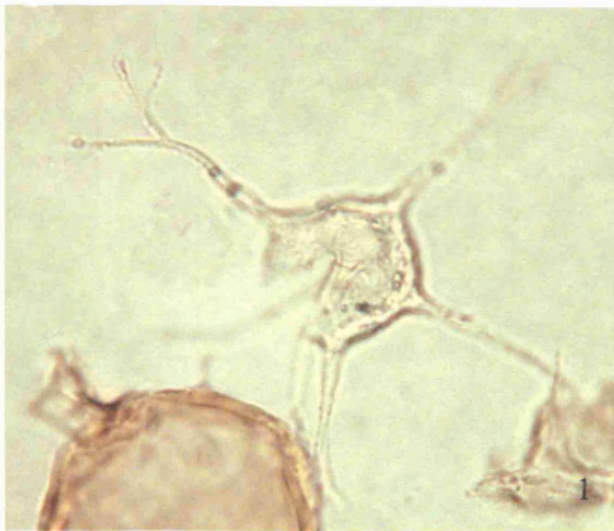






# EXPLANATION OF PLATE 11

Fig.		Page
	<b><i>Multiplicisphaeridium fisheri</i> (Cramer, 1968) Lister, 1970</b>	40
1	DG00LK1.223npg1–O40, Upper Visby Beds, x 750. Specimen showing lateral split.	
	<b><i>Multiplicisphaeridium minguisi</i> Le Hérissé, 1989</b>	40
2	DG00LK1.144ckd1–P36, Upper Visby Beds, x 750.	
3	DG00LH2.33ckd1–P45, 3, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium forquillum</i> (Cramer &amp; Díez, 1972b) Eisenack <i>et al.</i>, 1973</b>	40
4	DG00LH2.9ckd1–M48, 1, Upper Visby Beds, x 750.	
5	DG00LH2.9ckd1–R50, 3, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium monki</i> Le Hérissé, 1989</b>	40
6	DG00LK1.144ckd1–L36, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium neaghae</i> Cramer, 1970 ex Eisenack <i>et al.</i>, 1973</b>	40
7	DG00LK1.211npg1–F40, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium osgoodense</i> (Cramer &amp; Díez 1972b) Eisenack <i>et al.</i> 1973</b>	40
8	DG00LK1.223npg1–M40, 2, Upper Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium rochesterense</i> (Cramer and Díez, 1972b) Eisenack <i>et al.</i>, 1973</b>	41
9	DG00LK1.219npg1–J36, Upper Visby Beds, x 750.	



# EXPLANATION OF PLATE 12

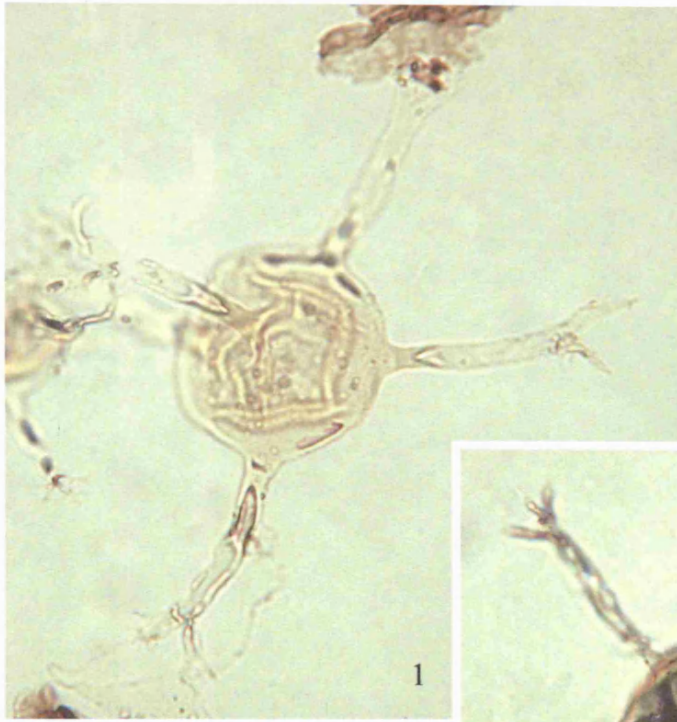
Fig.		Page
	<b><i>Multiplicisphaeridium variabile</i> (Lister, 1970) Dorning, 1981</b>	41
1	DG00LH2.39npg1–L32, 3, Upper Visby Beds, x 750.	
2	DG00LK1.80ckd1–Q39, 1, Lower Visby Beds, x 750.	
	<b><i>Multiplicisphaeridium cf. variabile</i> (Lister, 1970) Dorning, 1981</b>	41
3	DG00LH2.39npg1–U42, Upper Visby Beds, x 750.	
	<b><i>Onondagella asymmetrica</i> (Deunff, 1954 ex Deunff, 1961) Cramer, 1966b, emend. Playford, 1977</b>	41
4	DG00LK1.4npg1–F43, 3, Lower Visby Beds, x 750.	
	<b><i>Oppilatala ferrosa</i> (Cramer, 1970) Le Hérissé, 1989</b>	41
5	DG00LK1.80ckd1–G39, Lower Visby Beds, x 750.	
6	DG00LK1.12npg1–L41, 4, Lower Visby Beds, x 750.	
	<b><i>Oppilatala insolita compacta</i> Le Hérissé, 1989</b>	41
7	DG00LK1.56npg1–R36, 1, Lower Visby Beds, x 750.	
8	DG00LK1.179npg1–E43, Upper Visby Beds, x 750.	



# EXPLANATION OF PLATE 13

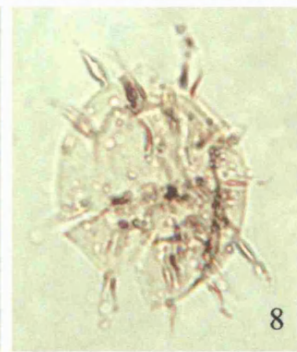
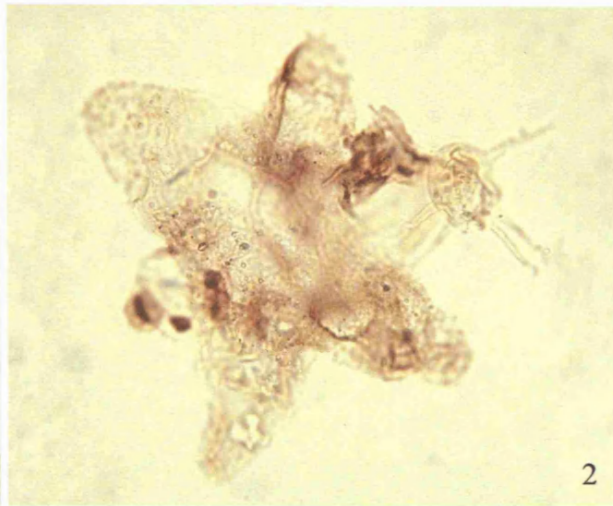
Fig.		Page
	<b><i>Oppilatala grahni</i> Le Hérissé, 1989</b>	41
1	DG00LK1.56npg1–N37, 3, Lower Visby Beds, x 750.	
	<b><i>Oppilatala juvenis</i> Le Hérissé, 1989</b>	41
2	DG00LK1.108npg1–L36, Upper Visby Beds, x 750.	
	<b><i>Oppilatala insolita insolita</i> Cramer &amp; Díez, 1972</b>	41
3	DG00LK1.52npg1–L31, Lower Visby Beds, x 750.	
4	DG00LK1.12npg1–Q48, 3, Lower Visby Beds, x 750.	
	<b><i>Oppilatala ramusculosa</i> (Deflandre, 1945) Dorning, 1981</b>	41
5	DG00LK1.144ckd1–S38, Upper Visby Beds, x 750.	
6	DG00LK1.171ckd1–L39, Upper Visby Beds, x 750.	
	<b><i>Oppilatala singularis</i> Le Hérissé, 1989</b>	42
7	DG00LK1.171ckd1–T41, 3, Upper Visby Beds, x 750.	





# EXPLANATION OF PLATE 14

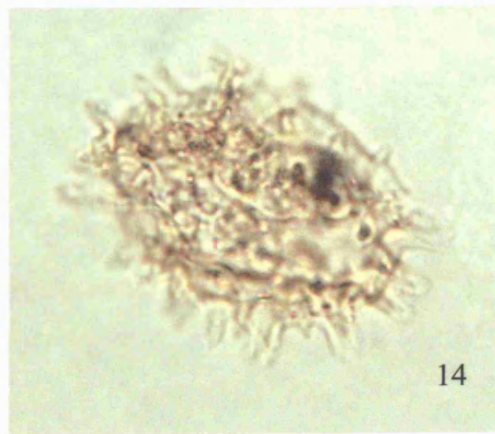
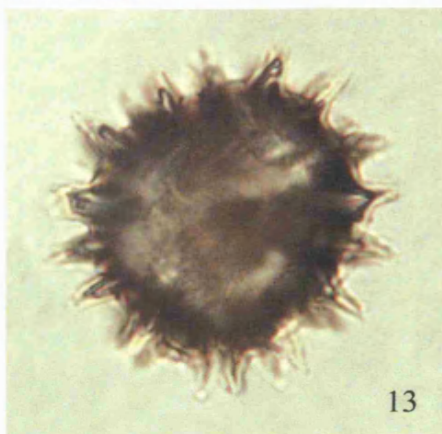
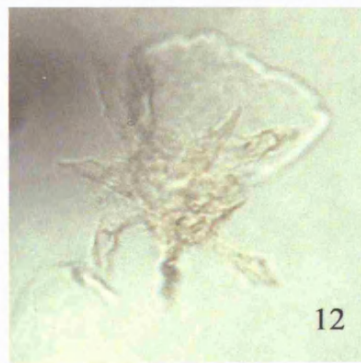
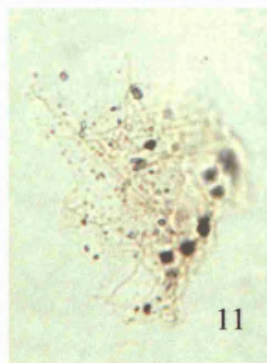
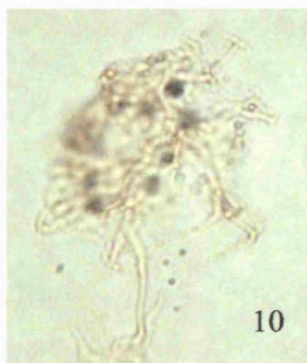
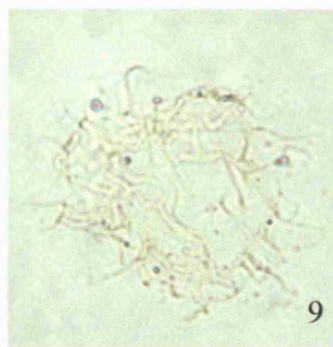
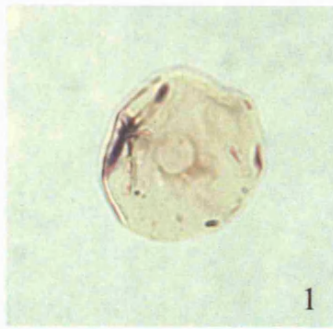
Fig.		Page
	<b><i>Polygonium</i> sp. B Le Hérissé, 1989</b>	42
1	DG00LK1.155npg1–E33, 2, Upper Visby Beds, x 750.	
	<b><i>Pulvinosphaeridium pulvinellum</i> Eisenack, 1954</b>	42
2	DG00LK1.76npg1–S42, 3, Lower Visby Beds, x 500.	
	<b><i>Salopidium fragelliforme</i> Le Hérissé, 1989</b>	42
3	DG00LK1.203npg1–T34, Upper Visby Beds, x 750.	
	<b><i>Salopidium granuliferum</i> (Downie, 1959) Dorning, 1981</b>	42
4	DG00LK1.144ckd1–J45, 2, Upper Visby Beds, x 750.	
5	DG00LK1.80ckd1–T31, Lower Visby Beds, x 750.	
	<b><i>Salopidium wenlockense</i> (Downie, 1959) Dorning, 1981</b>	42
6	DG00LK1.84npg1–R45, 3, Lower Visby Beds, x 750.	
7	DG00LK1.8npg1–O42, Lower Visby Beds, x 750.	
	<b><i>Salopidium</i> aff. <i>granuliferum</i> (Downie, 1959) Dorning, 1981</b>	42
8	DG00LK1.257npg1–R35, 1, Upper Visby Beds, x 750.	
9	DG00LK1.24npg1–G34, Lower Visby Beds, x 750.	
	<b><i>Salopidium woolhopense</i> Dorning, 1981</b>	42
10	DG00LK1.80ckd1–F39, 4, Lower Visby Beds, x 750.	
11	DG00LK1.80ckd1–J34, 4, Lower Visby Beds, x 750.	





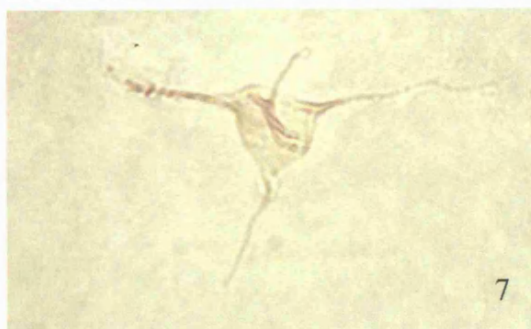
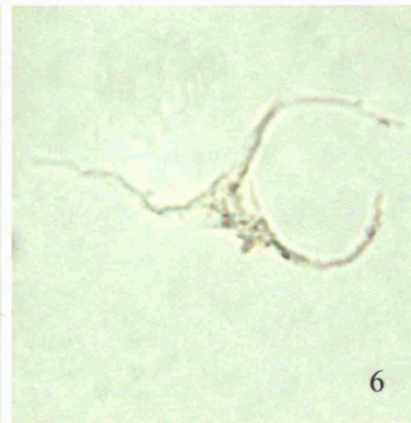
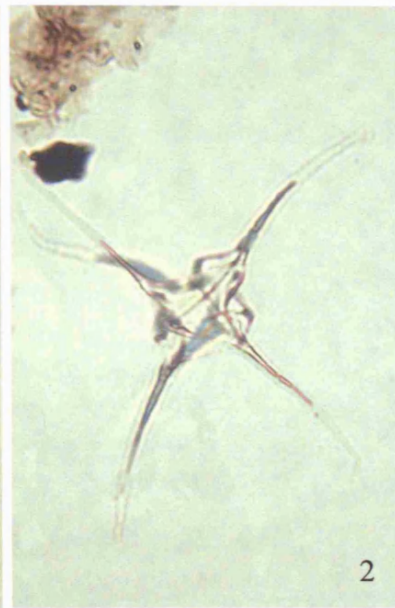
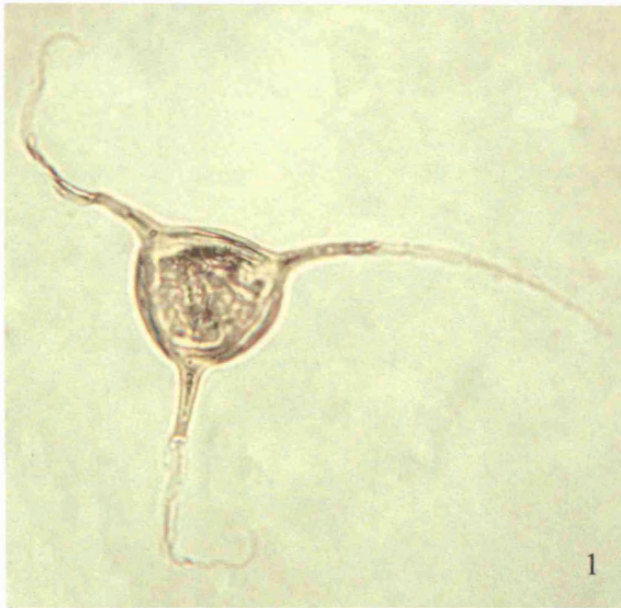
# EXPLANATION OF PLATE 15

Fig.		Page
	<b><i>Schismatosphaeridium algerense</i> Cramer &amp; Díez, 1976</b>	42
1	DG00LH2.33ckd1–F41, 4, Upper Visby Beds, x750.	
2	DG00LH2.9ckd1–K31, Upper Visby Beds, x 750.	
	<b><i>Schismatosphaeridium longhopense</i> Dorning, 1981</b>	42
3	DG00LK1.44npg1–P35, Lower Visby Beds, x 750.	
4	DG00LK1.68npg1–P35, Lower Visby Beds, x 750.	
	<b><i>Schismatosphaeridium rugulosum</i> Dorning, 1981 emend</b>	43
5	DG00LK1.44npg1–S38, Upper Visby Beds, x 750.	
6	DG00LH2.9npg1–L34, 3, Upper Visby Beds, x 750.	
	<b><i>Schismatosphaeridium perforatum</i> Staplin <i>et al.</i>, 1965</b>	42
7	DG00LK1.8npg1–O45, 3, Lower Visby Beds, x 750.	
8	DG00LK1.8npg1–K38, 1, Lower Visby Beds, x 750.	
	<b><i>Tunisphaeridium parvum</i> Deunff &amp; Evitt, 1968</b>	43
9	DG00LK1.147npg1–N34, Upper Visby Beds, x 750.	
	<b><i>Tunisphaeridium tentaculaferum</i> (Martin, 1967) Cramer, 1970</b>	43
10	DG00LK1.88npg1–U38, Lower Visby Beds, x 750.	
11	DG00LK1.128npg1–Q39, Lower Visby Beds, x 750.	
	<b><i>Tylotopalla robustispinosa</i> (Downie, 1959) Eisenack <i>et al.</i>, 1973</b>	43
12	DG00LK1.203npg1–N42, Upper Visby Beds, x 750.	
	<b><i>Tylotopalla gaupa</i> (Cramer, 1964b) Eisenack <i>et al.</i>, 1973</b>	43
13	DG00LK1.8npg1–G39, 4, Lower Visby Beds, x 750.	
14	DG00LK1.12npg1–K45, 4, Lower Visby Beds, x 750.	



# EXPLANATION OF PLATE 16

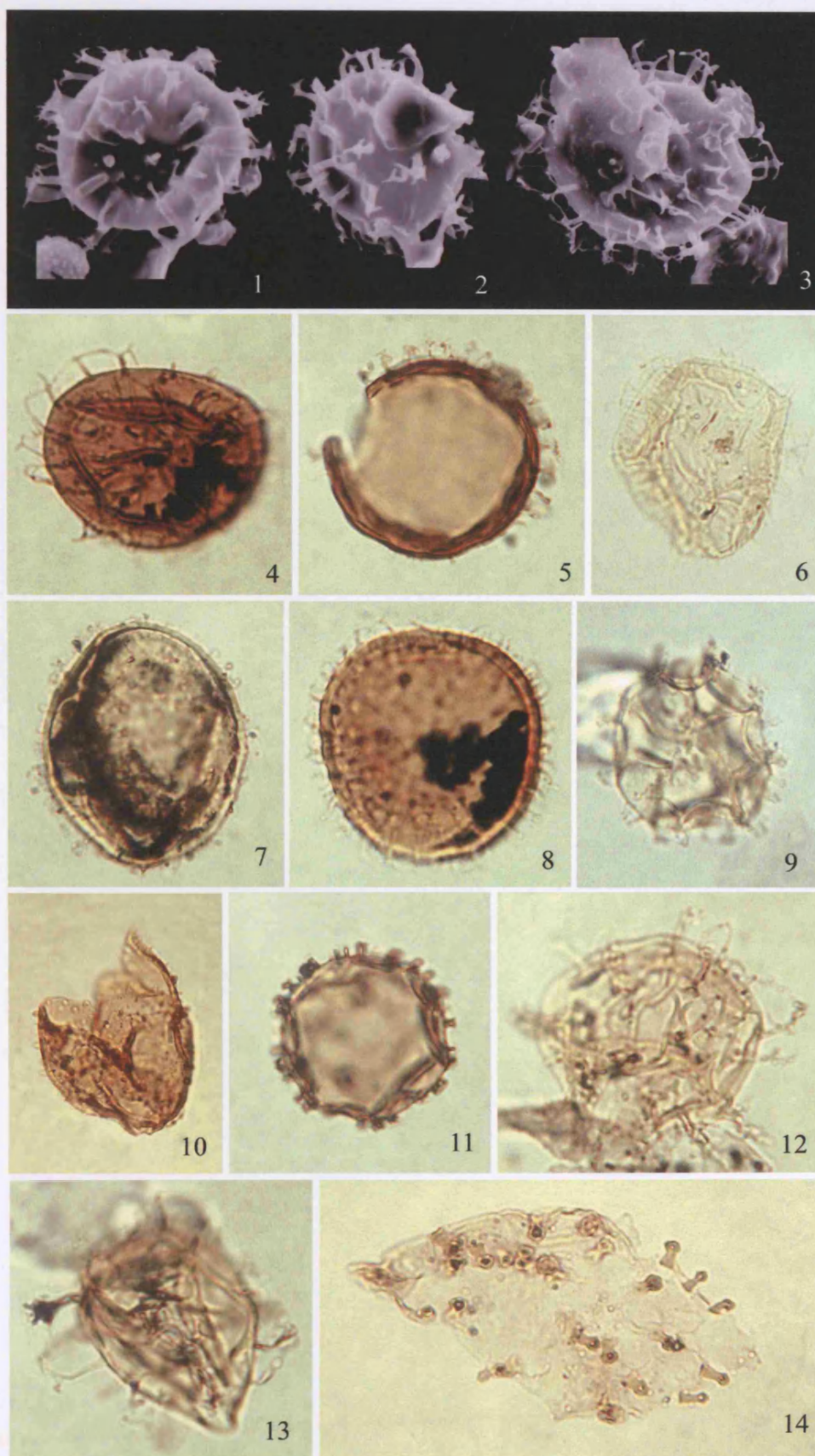
Fig.		Page
	<b><i>Veryhachium checkleyense</i> Dorning, 1981</b>	43
1	DG00LK1.191npg1–D36, 1, Upper Visby Beds x 750.	
	<b><i>Veryhachium pertonense</i> Dorning, 1981</b>	43
2	DG00LH2.33npg1–N37, 1, Upper Visby Beds x 750.	
3	DG00LH2.9ckd1–L33, 1, Upper Visby Beds x 750.	
	<b><i>Veryhachium rhomboidium</i> (Downie, 1959) emend. Turner, 1984</b>	43
4	DG00LK1.258npg1–T40, 4, Upper Visby Beds x 750.	
	<b><i>Veryhachium trispinosum</i> (Eisenack, 1938) Stockmans &amp; Willièrè, 1962</b>	43
5	DG00LK1.32npg1–K40, 4, Lower Visby Beds, x 750.	
6	DG00LK1.60npg1–H32, Lower Visby Beds, x 750.	
	<b><i>Veryhachium wenlockium</i> (Downie, 1959) Stockmans &amp; Willièrè, 1962</b>	43
7	DG00LK1.258ckd1–J38, Upper Visby Beds x 750.	
8	DG00LK1.258ckd1–H35, Upper Visby Beds x 750.	





# EXPLANATION OF PLATE 17

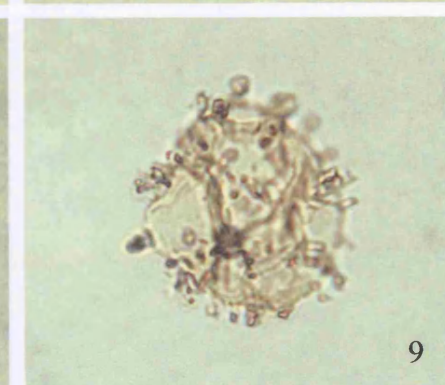
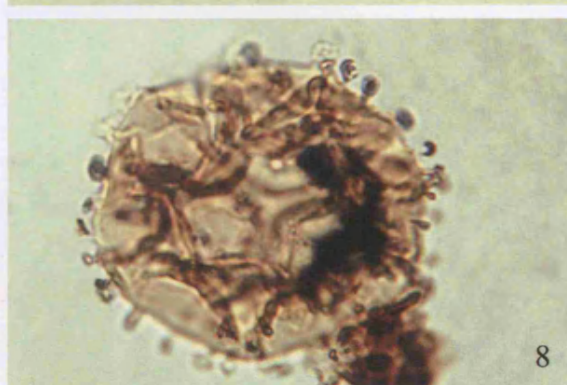
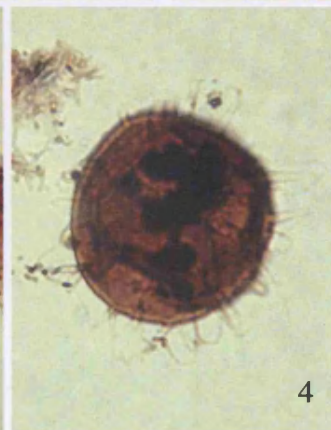
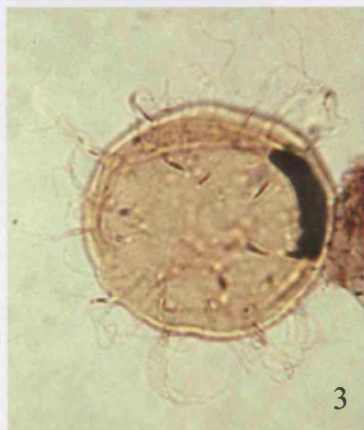
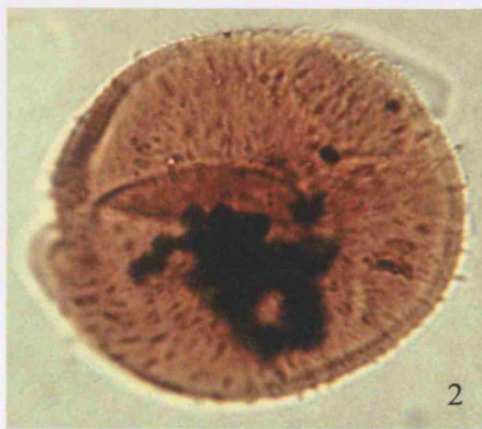
Fig.		Page
	<b><i>Visbysphaera brevifurcata</i> (Eisenack, 1954) Lister, 1970</b>	43
1	DG00LK1.211–L15, (SEM), Upper Visby Beds, x 750.	
2	DG00LK1.211–O12, (SEM), Upper Visby Beds, x 750.	
	<b><i>Visbysphaera connexa connexa</i> Le Hérissé, 1989</b>	44
3	DG00LK1.112–M7, (SEM), Lower Visby Beds, x 750.	
4	DG00LK1.80ckd1–J35, 1, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera connexa crispa</i> Le Hérissé, 1989</b>	44
5	DG00LK1.24npg1–L34, Lower Visby Beds, x 750.	
6	DG00LK1.4npg1–M43, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera connexa hirsuta</i> Le Hérissé, 1989</b>	44
7	DG00LK1.36npg1–U41, 1, Lower Visby Beds, x 750.	
8	DG00LK1.40npg1–L37, 1, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera gotlandica</i> Eisenack, 1954</b>	44
9	DG00LK1.203npg1–J39, 3, Upper Visby Beds, x 750.	
	<b><i>Visbysphaera erratica brevis</i> Le Hérissé, 1989</b>	44
10	DG00LK1.12npg1–J46, Lower Visby Beds, x 750.	
11	DG00LH2.33ckd1–P40, Upper Visby Beds, x 750.	
	<b><i>Visbysphaera meson</i> Eisenack 1955</b>	44
12	DG00LK1.257npg1–L35, 3, Upper Visby Beds, x 750.	
13	DG00LK1.234npg1–O34, Upper Visby Beds, x 750.	
	<b><i>Visbysphaera cf. gotlandica</i> (Downie, 1959) Dorning, 1981</b>	44
14	DG00LK1.40npg1–L47, 4, Lower Visby Beds, x 750.	



# EXPLANATION OF PLATE 18

Fig.		Page
	<b><i>Visbysphaera microspinosa</i> (Eisenack, 1954) Lister, 1970</b>	44
1	DG00LK1.28npg1–P34, Lower Visby Beds, x 750.	
2	DG00LK1.40npg1–L38, 3, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera oligofurcata</i> Eisenack, 1954</b>	44
3	DG00LK1.72npg1–S38, Lower Visby Beds, x 750.	
4	DG00LH2.9npg1–X32, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera pirifera pirifera</i> (Eisenack, 1954) Kiryanov, 1978</b>	44
5	DG00LK1.120–L4, (SEM), Lower Visby Beds, x 750.	
6	DG00LK1.211npg1–R43, 1, Upper Visby Beds, x 750.	
7	DG00LK1.112npg1–H33, Lower Visby Beds, x 750.	
	<b><i>Visbysphaera pirifera minor</i> Le Hérissé, 1989</b>	44
8	DG00LK1.112npg1–F38, Lower Visby Beds, x 750.	
9	DG00LK1.88npg1–U40, 1, Lower Visby Beds, x 750.	





## EXPLANATION OF PLATE 19

Fig.		Page
	<b><i>Dilatisphaera quadratica</i> sp. nov.</b>	48
1	DG00LK1.227npg1-U42, Upper Visby Beds, x 750. Holotype. Specimen photographed under differential interference contrast.	
2	DG00LK1.223npg1-R40, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
3	DG00LK1.179npg1-D15, (SEM), Upper Visby Beds, x 750. Specimen showing the inside of the vesicle where one of the processes has been broken off.	
	<b><i>Micrhystridium</i> sp. A</b>	51
4	DG00LH2.17npg1-J32, 1, Upper Visby Beds, x 750. Specimen shows lateral split (on the left). Specimen photographed under differential interference contrast.	
5	DG00LK1.112npg1-O36, Upper Visby Beds, x 750. Specimen photographed under differential interference contrast.	
	<b><i>Elektoriskos longispinosum</i> sp. nov.</b>	49
6	DG00LK1.171npg1-O42, Upper Visby Beds, x 1000. Holotype.	
7	DG00LK1.167npg1-M43, 3, Lower Visby Beds, x 750.	
	<b><i>Pterospermella saturniforme</i> sp. nov.</b>	45
8	DG00LK1.56npg1-N34, 4, Lower Visby Beds, x 750. Holotype.*	
9	DG00LK1.40npg1-M36, 4, Lower Visby Beds, x 750.	
	<b><i>Buedingiisphaeridium?</i> <i>globulosum</i> sp. nov.</b>	47
10	DG00LK1.183npg1-R38, Upper Visby Beds, x 750.	
11	DG00LK1.72npg1-J48, 3, Lower Visby Beds, x 750. Holotype.	
	<b><i>Buedingiisphaeridium?</i> <i>aff. globulosum</i> sp. nov.</b>	36
12	DG00LK1.24npg1-H43, 1, Lower Visby Beds, x 750.	
	<b>Abnormal acritarchs, probably mutations of</b>	45
	<b><i>Multiplicisphaeridium cladum</i> (Downie, 1963) Eisenack, 1969.</b>	
13	DG00LK1.12npg1-N42, 3, Lower Visby Beds, x 750. Specimen showing multiple primary branching on the right most process.	
14	DG00LK1.155npg1-S43, 2, Upper Visby Beds, x 750. Specimen showing very thick-walled, robust processes, with first order branching.	



