PALYNOLOGY OF THE LOWER AND MIDDLE ELTON FORMATIONS (LUDLOW SERIES, SILURIAN) IN THE LUDLOW TYPE AREA, SHROPSHIRE.

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

by

Gary Lee Mullins BSc (Portsmouth) MSc (Southampton)
Department of Geology
University of Leicester

April 1996

ABSTRACT

This thesis documents and analyses the distribution of acritarchs, prasinophyte algae and palynofacies at the basal stratotype of the Ludlow Series (Silurian) at Pitch Coppice Quarry, Ludlow, Shropshire, and the nearby Goggin Road section.

Ten new species are erected; *Cymatiosphaera lawsonii*, *Cymatiosphaera multicrista*, *Cymatiosphaera paucimembrana*, *Cymatiosphaera triangula*, *Baltisphaeridium ? spinatum*, *Buedingiisphaeridium reticulum*, *Glyptosphaera heltaskelta*, *Gorgonisphaeridium ? listeri*, *Leptobrachion digitatum* and *Pulvinosphaeridium dorningii*; 31 new species are described in open nomenclature. The diagnoses of *Psenotopus*, *Psenotopus chondrocheus*, *Cymatiosphaera octoplana*, *Dorsennidium europaeum*, *Dorsennidium rhomboidium*, *Eupoikilofusa filifera*, *Evittia robustispinosa*, *Pulvinosphaeridium oligoprojectum*, *Schismatosphaeridium rugulosum* and *Veryhachium trisphaeridium* are emended. Six new combinations are proposed; *Comasphaeridium brevispinosum*, *Dorsennidium polygonale*, *Dorsennidium wenlockianum*, *Evittia aculeata*, *Evittia almarada*, *Gorgonisphaeridium citrinum*.

The ranges of *Buedingiisphaeridium pyramidale* and *Neoveryhachium mayhillense* are extended, producing an overlap between biozones W3 and L1 of Dorning (1981a). Biozone L2 may, possibly, be recognised by *G. ? listeri* 78.4m above the series boundary (Middle Elton Formation). Zone 6 (Gorstian-Ludfordian stages) of Martin (1989) is identified by *Percultisphaera stiphrospinata* (+83.5m, Middle Elton Formation). Potentially important taxa for future biostratigraphic research are highlighted and these may be used to refine the existing biostratigraphic schemes.

The palynofacies analysis undertaken identifies a Wenlock-Ludlow series boundary event correlating with the $\partial^{13}C$ event of Corfield *et al.* (1992). Transgression induced reworking, concentrating ^{12}C rich organic matter, is proposed as the cause. Between Pitch Coppice and Goggin Road this event is diachronous. Individual taxa, which occur through the section in ≥80% of samples, are grouped by cluster analysis. These groups, and the distribution of rarer taxa, are related to the palynofacies analysis, and a series of events are proposed (fluctuations in sea-level, marine/terrestrial productivity, sedimentation rates, palaeoenvironment, palaeoceanography) These events are compared to eustatic and climatic/oceanic models.

CONTENTS

CONTENTS

LIST OF FIGURES

ACKNOWLEDGEMENTS

This research was completed under the tenure of a NERC studentship.

Many thanks to my supervisors Drs Dick Aldridge and David Siveter for all their help throughout my period of research at Leicester. Special thanks must also go to Ken Dorning (Sheffield) and Dr. Stewart Molyneux (British Geological Survey) for sharing their opinions on my material. I would also like to thank Dr. Pete Harvey (Leicester) for his help with statistics and also Dr. Jan Zalasiewicz (Leicester) and Dr. Jim Riding (British Geological Survey) for their helpful comments.

Thanks to the staff at the Forestry Commission (Marches Forest District) for providing easy access to localities. I would also like to express my gratitude to the Forestry Commission, English Nature and the University of Leicester for providing the finance that allowed the Goggin Road locality to be cleaned.

I am also grateful to Bill Teasdale, Rod Branson, Andrew Swift and Dave York in the Geology Department for their help. Many postgrads/postdocs past and new have added their comments and I would like to thank Drs Giles Miller, Stuart Sutherland, Ruth Elliot, Mat Wakefield, Angela Fielding, Mark Purnell and Mark Williams, and also Jane Evans, Phil Donoghue and Sarah Gabbott.

Finally I would like to thank my parents, for a constant stream of financial rescue packages and moral support, and Louise for holding the ladder.

INTRODUCTION

RESEARCH AIMS

1). To collect high density samples across the Wenlock-Ludlow series boundary and through the earliest Ludlow Series in the type area and to process these samples for the recovery of palynomorphs.

2). To evaluate the application of previous biostratigraphic schemes, based on acritarchs and prasinophyte algae, in the type area.

3). To examine whether higher resolution biostratigraphy is possible using acritarchs and prasinophyte algae.

4). To examine the distribution of palynodebris, acritarchs and prasinophyte algae. To use this data to infer aspects of the latest Wenlock-earliest Ludlow palaeoenvironment and to examine the applicability of the eustatic (e.g. Johnson *et al.* 1991) and climatic/oceanic (P & S of Jeppsson 1990) models in explaining patterns of palaeoenvironmental change.

THESIS STRUCTURE

CHAPTER 1. Introduction. This chapter includes general information on the geology of the type area, a brief history of research, the stratigraphy and list of localities. It also includes information on the extraction technique used for recovery of palynomorphs, a brief résumé of important and recent developments in acritarch classification, and information on the terminology and general morphology of acritarchs and prasinophyte algae.

CHAPTER 2. Systematics. In accordance with generally accepted principles the acritarchs and prasinophyte algae are listed alphabetically (prasinophytes first). This chapter is written in the style of the Palaeontographical Society Monographs.

CHAPTER 3. Biostratigraphy. This chapter examines the fossil groups that have been used in biostratigraphy in the late Wenlock-early Ludlow series, listing details of their occurrences and applicability in the type area. More importantly this chapter deals with the recognition of previously erected local and global acritarch and prasinophyte biostratigraphic schemes and the implications for such schemes of new research, which includes this study. The chapter also details the stratigraphic distribution of acritarch and prasinophyte algal taxa in the present study, highlighting those that are considered to be of potential future importance in local and global biostratigraphy. This chapter is written in the style of the Palaeontographical Society Monographs.

CHAPTER 4. Palynofacies analysis. A combination of a detailed palynofacies analysis and a detailed analysis of the distribution of individual acritarch and prasinophyte algal taxa has been used to infer aspects of the palaeoenvironment over the Wenlock-Ludlow series boundary and through the earliest Ludlow Series. Results have been compared to models that have been proposed to explain the changes observed in facies, flora and fauna (eustatic - Johnson *et al.* 1991, climatic/oceanic (P & S) - Jeppsson 1990). This chapter is written in the style of the Journal of Geological Society, London.

GEOLOGICAL SETTING

The Ludlow area, Shropshire, forms part of a continuous NE-SW outcrop of Silurian rocks which extends from Much Wenlock, Shropshire, to the Marloes Peninsula, Pembrokeshire (Text-fig. 1.1). Around Ludlow, sediments from the Coalbrookdale Formation (Wenlock Series) to Ledbury Formation (Přídolí Series) are folded into an asymmetrical anticline, plunging ENE (Text-fig. 1.2).

CHRONOSTRATIGRAPHY

The Wenlock and Ludlow series are the second and third series of the Silurian, with the international stratotype for the base of the Ludlow Series being defined at Pitch Coppice Quarry (SO 4723 7298, Text-fig. 1.2), Mortimer Forest, Ludlow, Shropshire (Holland *et al.* 1963, Holland 1980).

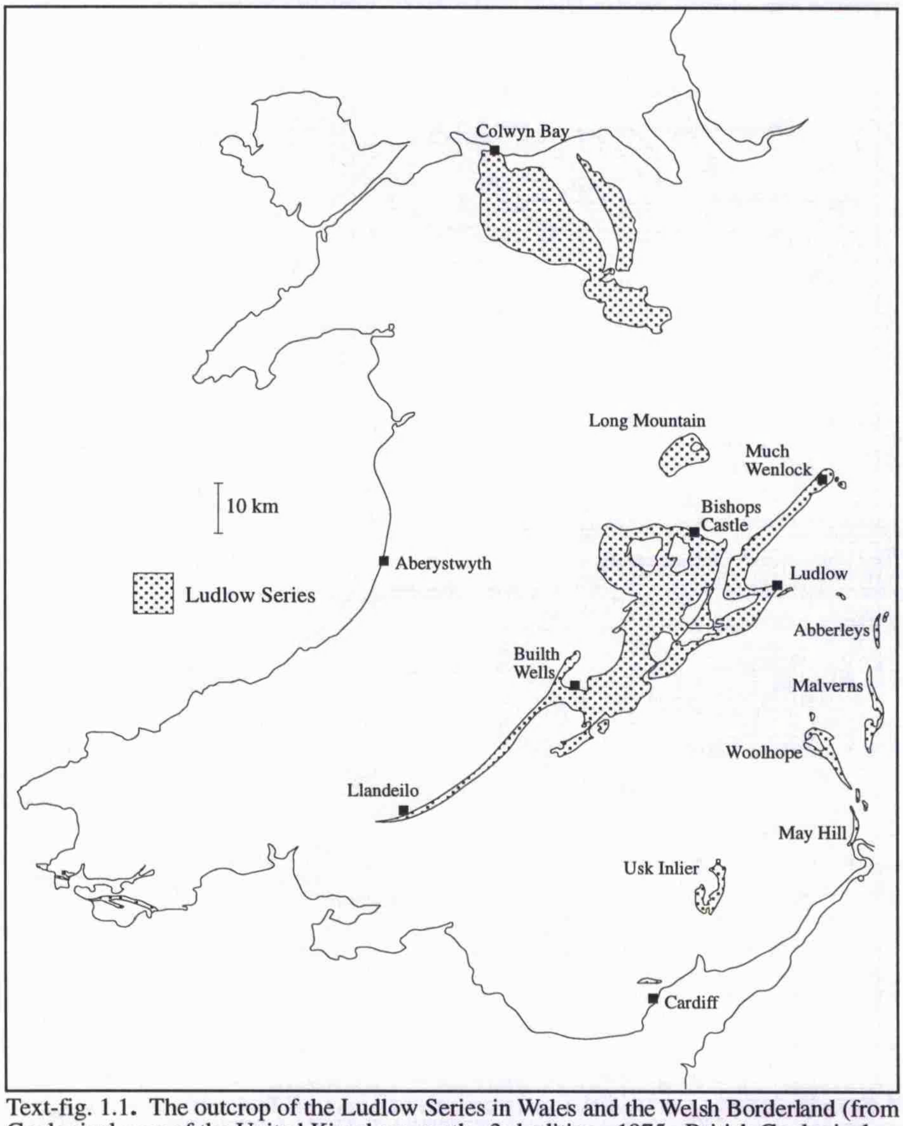
The Wenlock Series is divided into the Sheinwoodian and Homerian stages. At Ludlow the latest Sheinwoodian and earliest Homerian stages are represented by the Coalbrookdale Formation, the base of which is not observed. The latest Homerian Stage is represented by the Much Wenlock Limestone Formation.

The Ludlow Series is divided into the Gorstian and Ludfordian stages. The base of the Gorstian Stage is coincident with that of the Ludlow Series, and the stage is represented at Ludlow by the Lower, Middle and Upper Elton formations and the Lower and Upper Bringewood formations (Holland 1980, Holland *et al.* 1980). The Ludfordian Stage has its base defined at Sunnyhill Quarry (SO 4950 7255, Text-fig. 1.2), Mortimer Forest, Ludlow, and is represented there by the Lower and Upper Leintwardine formations and the Lower and Upper Whitcliffe formations (Holland 1980, Holland *et al.* 1980).

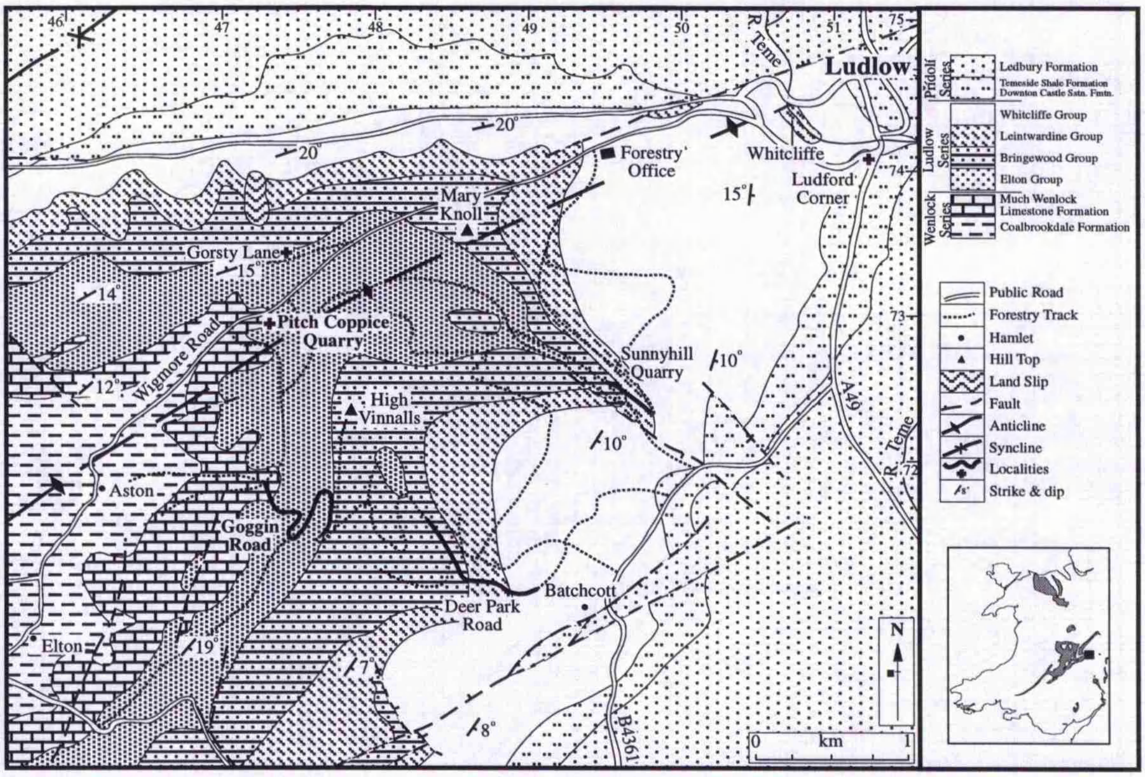
The top of the Ludfordian stage, and the Ludlow Series, is defined at the base of the Přídolí Series in the Barrandian area, Czech Republic (Kříz 1989, p. 69). Work on ostracods and conodonts indicates that the base of the Přídolí Series in the Welsh Borderland occurs at the base of the Downton Castle Sandstone Formation, Downton Group (Siveter 1978, 1989; Miller 1995). The stratotype section for the base of the Downton Group is located at Ludford Corner, Ludlow (SO 5124 7413, Text-fig. 1.2).

LITHOSTRATIGRAPHY

A description of the typical lithologies of the Ludlow Area is given below (after Holland *et al.* 1963, White & Lawson 1989).



Text-fig. 1.1. The outcrop of the Ludlow Series in Wales and the Welsh Borderland (from Geological map of the United Kingdom, south. 3rd edition. 1975. British Geological Survey).



Text-fig. 1.2. Geology of the Ludlow area, Shropshire (after Lawson & White 1989).

The poorly exposed Coalbrookdale Formation comprises soft, olive grey, calcareous silty mudstones and shales, with rare nodular limestone bands. Limestone bands gradually become more common upwards, and the Coalbrookdale Formation passes into the Much Wenlock Limestone Formation.

Above the Wenlock-Ludlow series boundary the limestone bands become less common, with the Lower Elton Formation being dominated by soft, olive, calcareous silty mudstones. At the Lower/Middle Elton formation boundary there is a rapid transition to light grey, conchoidally fractured siltstones, and a change from a brachiopod to graptolite/orthocone dominated fauna. Higher in this formation, calcareous siltstones occur and these dominate in the Upper Elton Formation. The development of shell and limestone bands and thick, irregularly bedded, calcareous siltstones marks the base of the Lower Bringewood Formation. Nodular limestones give way abruptly to olive grey, calcareous siltstones and shelly limestones at the base of the Lower Leintwardine Formation. The Upper Leintwardine Formation represents a transitional unit between the Lower Leintwardine and Lower Whitcliffe formations. It comprises irregularly bedded, light olive grey, calcareous siltstones with decalcified shelly layers. Massive calcareous siltstones with conchoidal or blocky fracturing identify the base of the Lower Whitcliffe Formation and these pass transitionally into the well bedded, olive siltstones with common shell and rare slump bands of the Upper Whitcliffe Formation.

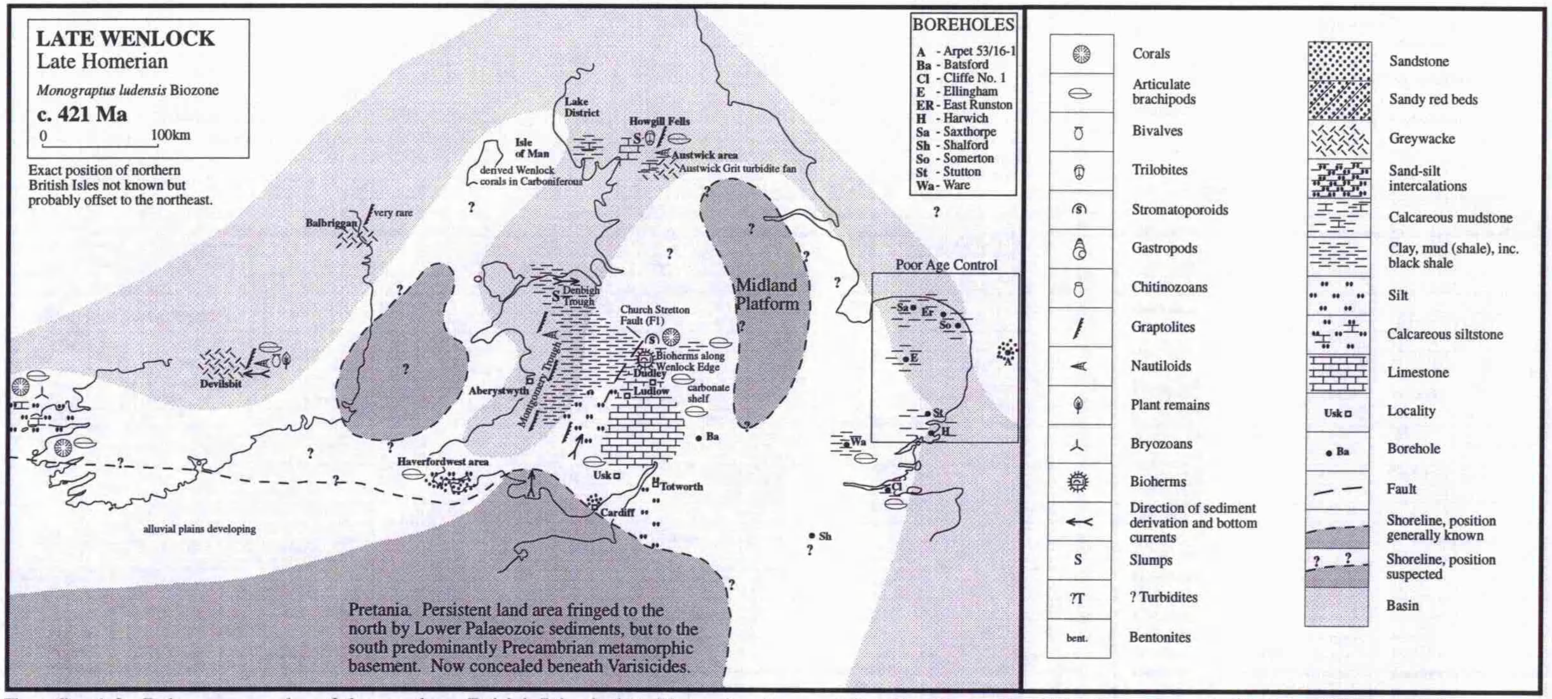
The base of the Prídolí Series, and Downton Castle Sandstone Formation, is identified by the Ludlow Bone Bed Member (ripple laminated and lenticular siltstones, interbedded with sands containing vertebrate fragments). The <2 m intertidal, laminated, olive mudstones and siltstones with vertebrate sands of the overlying Platychisma Shale Member are succeeded by the Sandstone Member, a yellow, fine grained, cross bedded, channelled, well sorted sandstone. The Ledbury Formation comprises red mudstones and siltstones with pedogenic carbonates, cross bedded sandstones and rare intraformational conglomerates and tuffs.

The geology of the Ludlow Area is covered by the 1:25,000 Leintwardine-Ludlow special sheet (parts of SO 47 & 57) and the 1:50,000 Ordnance Survey Sheet 137, Ludlow and Wenlock Edge.

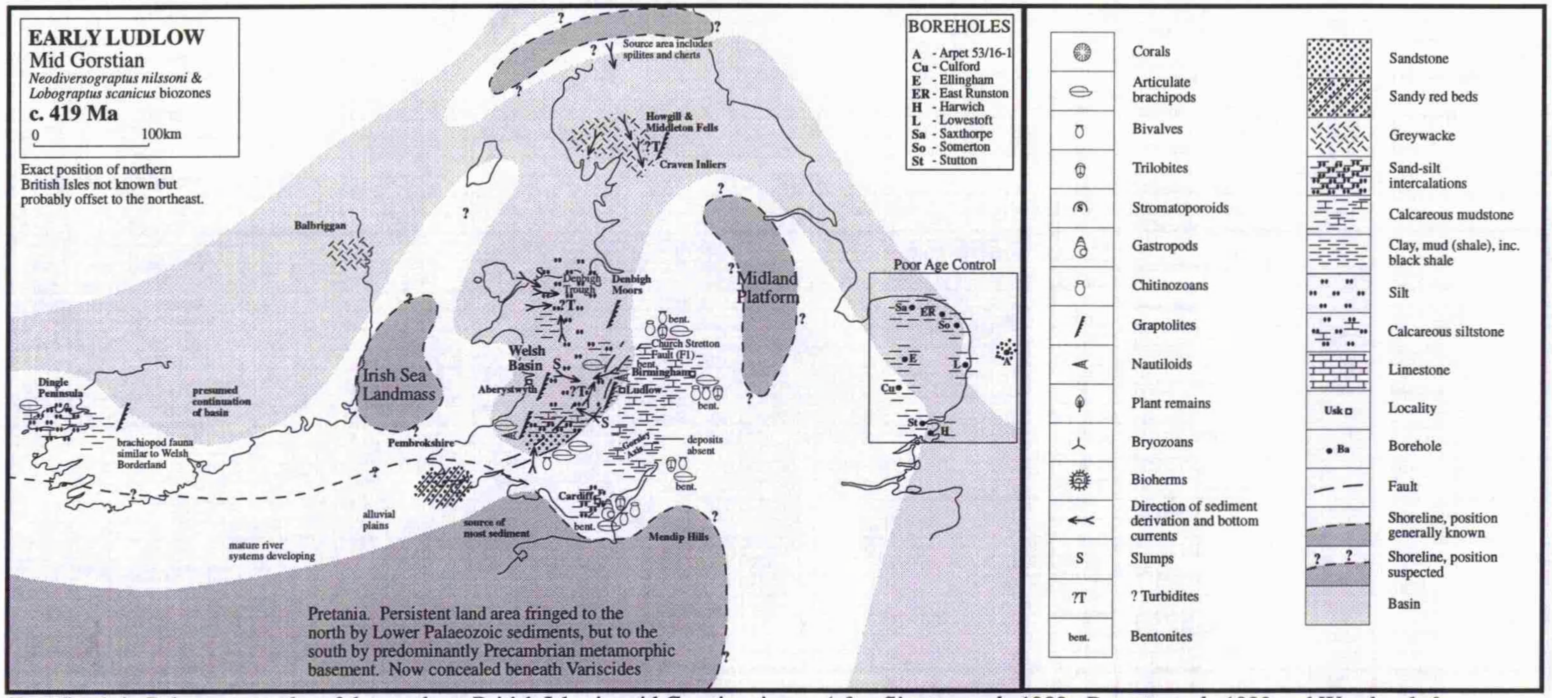
PREVIOUS RESEARCH

The first modern, detailed analysis of the Wenlock and Ludlow series of the Ludlow type area was completed by Holland *et al.* (1963), who also outlined a brief history of research in the Welsh Borderland back to 1832. The Ludlow rocks of the Ludlow District have been further described by Lawson (1973b), White & Lawson (1978), Siveter *et al.* (1989) and Lawson & White (1989). Other important areas, situated close to Ludlow, are the Leintwardine area, 11 kms W of Ludlow (Whitaker 1962, Siveter *et al.* 1989); the Wigmore Rolls area, 13 kms WSW of Ludlow (Whitaker 1994); the Aymestry area, 13 kms SSW of Ludlow (Lawson 1973a, Siveter *et al.* 1989); and the Craven Arms-Much Wenlock area, 11-27 kms NE-NNW of Ludlow (Shergold & Shirley 1968, Shergold & Bassett 1970, Siveter *et al.* 1989).

The standard Silurian series are fully described in Holland & Bassett (1989 and references therein), as are reviews of Silurian fauna and flora and aspects of global Silurian geology. Palaeogeographic maps for the Wenlock and Ludlow series (Text-figs. 1.3-1.4) have been produced by Siveter *et al.* (1989) and Bassett *et al.*



Text-fig. 1.3. Palaeogeography of the southern British Isles in late Homerian times. (after Siveter *et al.*, 1989; Bassett *et al.*, 1992 and Woodcock & Pharaoh, 1993).



Text-fig. 1.4. Palaeogeography of the southern British Isles in mid Gorstian times. (after Siveter *et al*., 1989; Bassett *et al*., 1992 and Woodcock & Pharaoh, 1993).

(1992). The sequence stratigraphy, plate tectonics and structural geology of Wales and the Welsh Borderland is outlined in Woodcock (1984, 1990), Woodcock & Gibbons (1988) and Soper & Woodcock (1990).

LOCALITIES

Two localities in the Ludlow type area have been sampled for the recovery of palynomorphs:

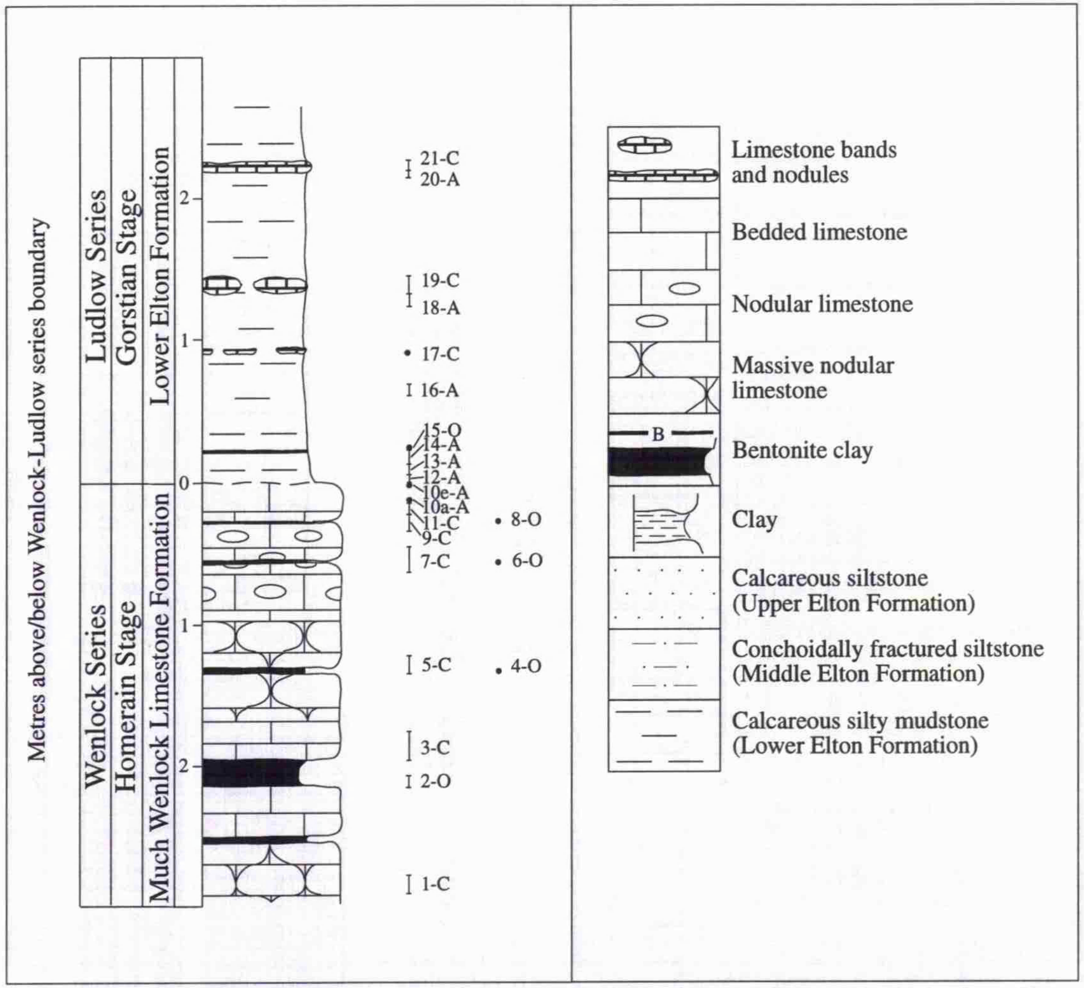
PITCH COPPICE QUARRY. (SO 4723 7298); Text-figs 1.2, 1.5; Holland *et al.* 1963, Lawson & White 1989, Siveter *et al.* 1989. A disused quarry approximately 4.5 km WSW of Ludlow. This section displays a transitional boundary between nodular and poorly bedded limestones (Much Wenlock Limestone Formation, Wenlock Series) and calcareous silty mudstones (Lower Elton Formation, Ludlow Series). This is the international stratotype, with the base of the Ludlow Series, Gorstian Stage and Lower Elton Formation being defined 0.23 m below a prominent bentonite horizon in the Lower Elton Formation (Holland *et al.* 1963, p. 139-141, fig. 11).

GOGGIN ROAD (SO 4720 7189-SO 4765 7170); Text-figs 1.2, 1.6, 1.7a-c; section A of White & Lawson 1978, Bassett *et al.* 1979, Siveter *et al.* 1989. A series of forestry track side exposures and temporary trenches in Mortimer Forest, approximately 1 km south of Pitch Coppice Quarry. The trenches were excavated, and the lower part of the section cleaned (GOG1-GOG7), in September-October 1992 for the purpose of this study. When sampled there was a near continuous exposure from the top of the Much Wenlock Limestone Formation to the base of the Lower Bringewood Formation.

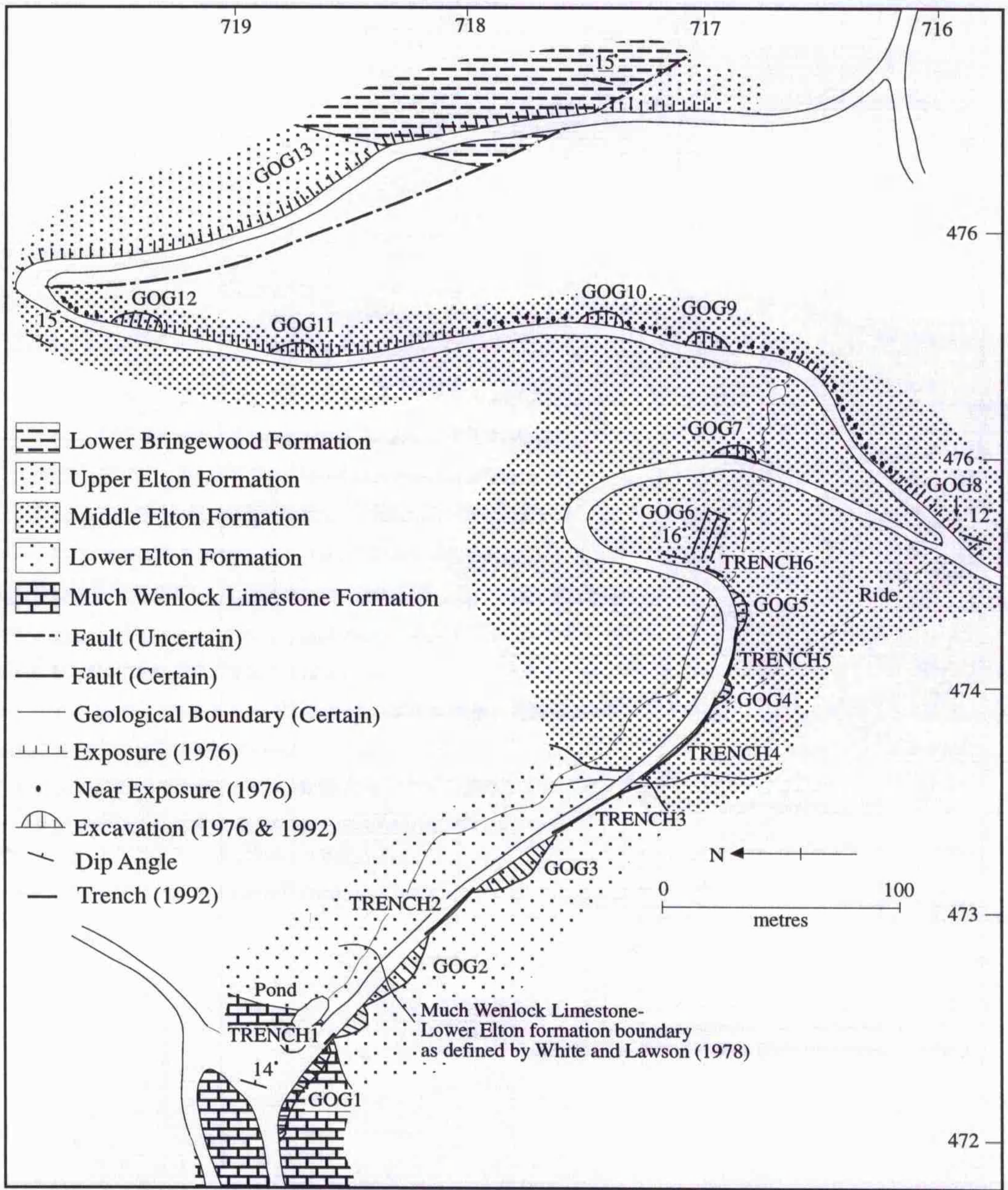
The succession across the Wenlock-Ludlow series boundary (Trench 1) is nearly identical to that at Pitch Coppice Quarry, but no longer exposed. There is a transitional boundary between nodular limestones (Much Wenlock Limestone Formation) and calcareous silty mudstones (Lower Elton Formation). Approximately 0.22m above the boundary a thin bentonite horizon occurs and for roughly 0.8m above the boundary no limestone bands or nodules are recorded (Text-fig. 1.7a); above this numerous limestone bands and nodules occur. White & Lawson (1978) identified this later level as part of the Much Wenlock Limestone Formation and originally placed the Much Wenlock Limestone-Lower Elton formation boundary above this very calcareous level, approximately 11m above the formation boundary identified herein (Text-fig. 1.6).

TECHNIQUES

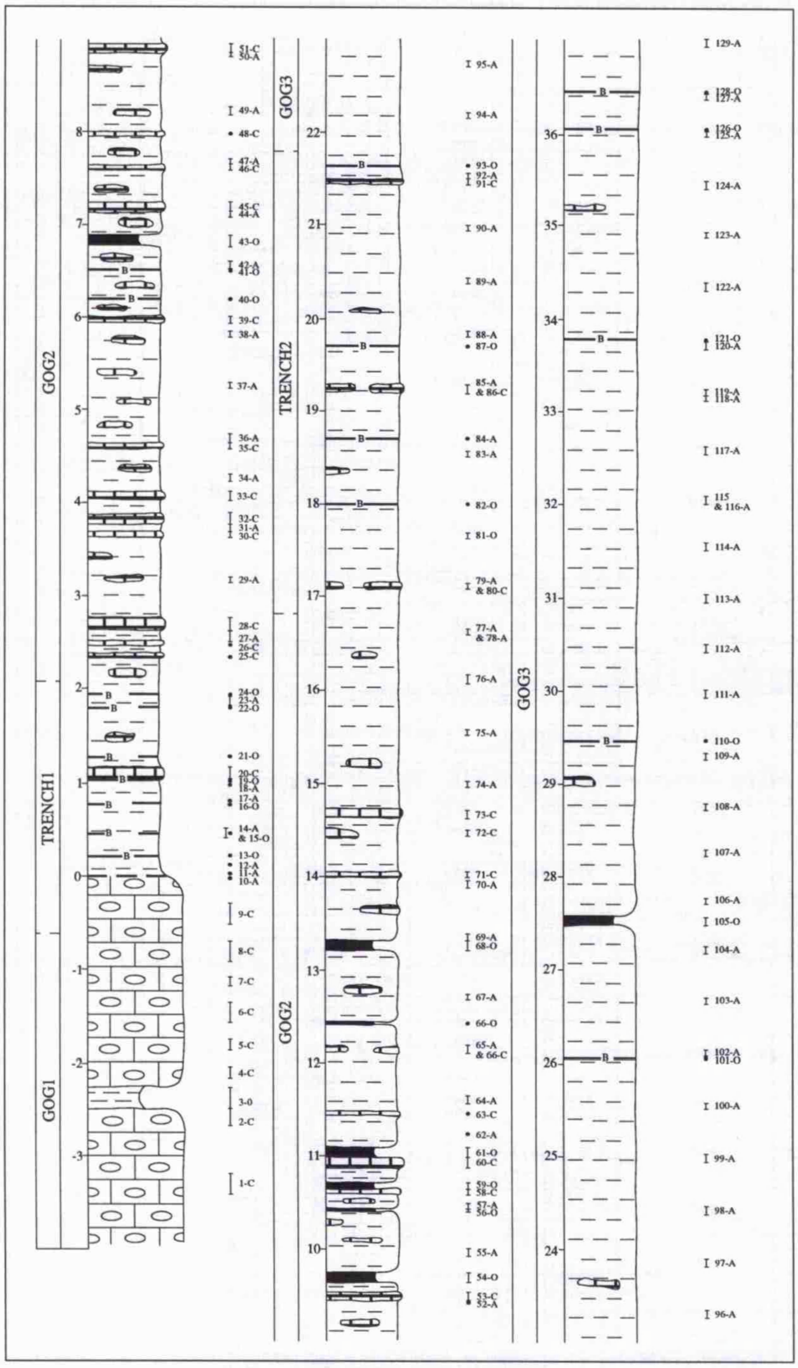
PALYNOLOGICAL PROCESSING. Approximately 50g of washed, crushed, dried sample was placed in a polypropylene beaker. Carbonates were dissolved using hydrochloric acid (c. 30%). Samples were washed three times. Hydrofluoric acid (c. 40%) was added to dissolve silicates, and samples were regularly stirred over several days. Samples were washed three times. Fluorides produced during this stage were dissolved using warm hydrochloric acid, and three tablets of *Lycopodium* spores, for quantitative analysis, were added at this time. After washing and neutralising, samples were removed from the fume cupboard and sieved at 10



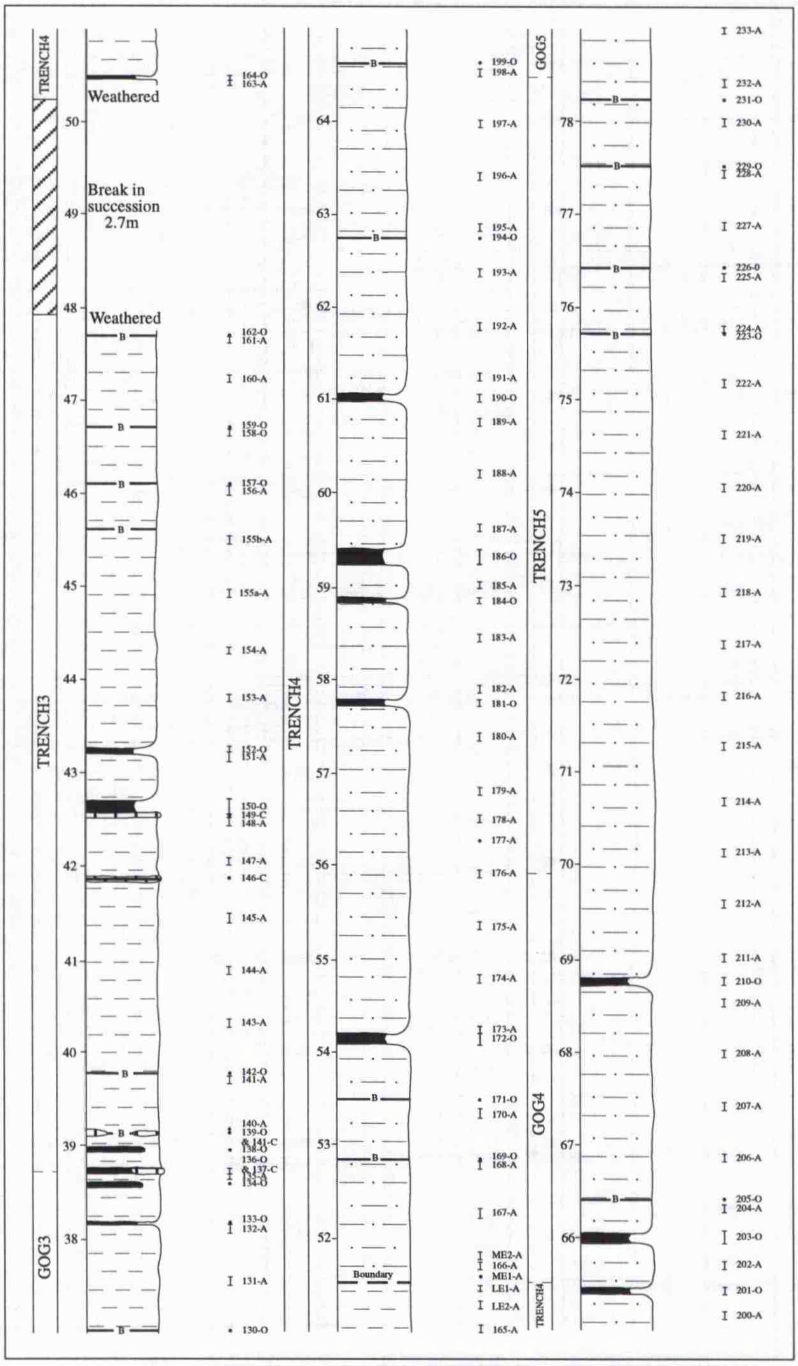
Text-fig. 1.5. Stratigraphic log of the section at Pitch Coppice Quarry, Mortimer Forest, Ludlow. The positions of samples are also shown. Key also for Text-figs 1.7a-c.



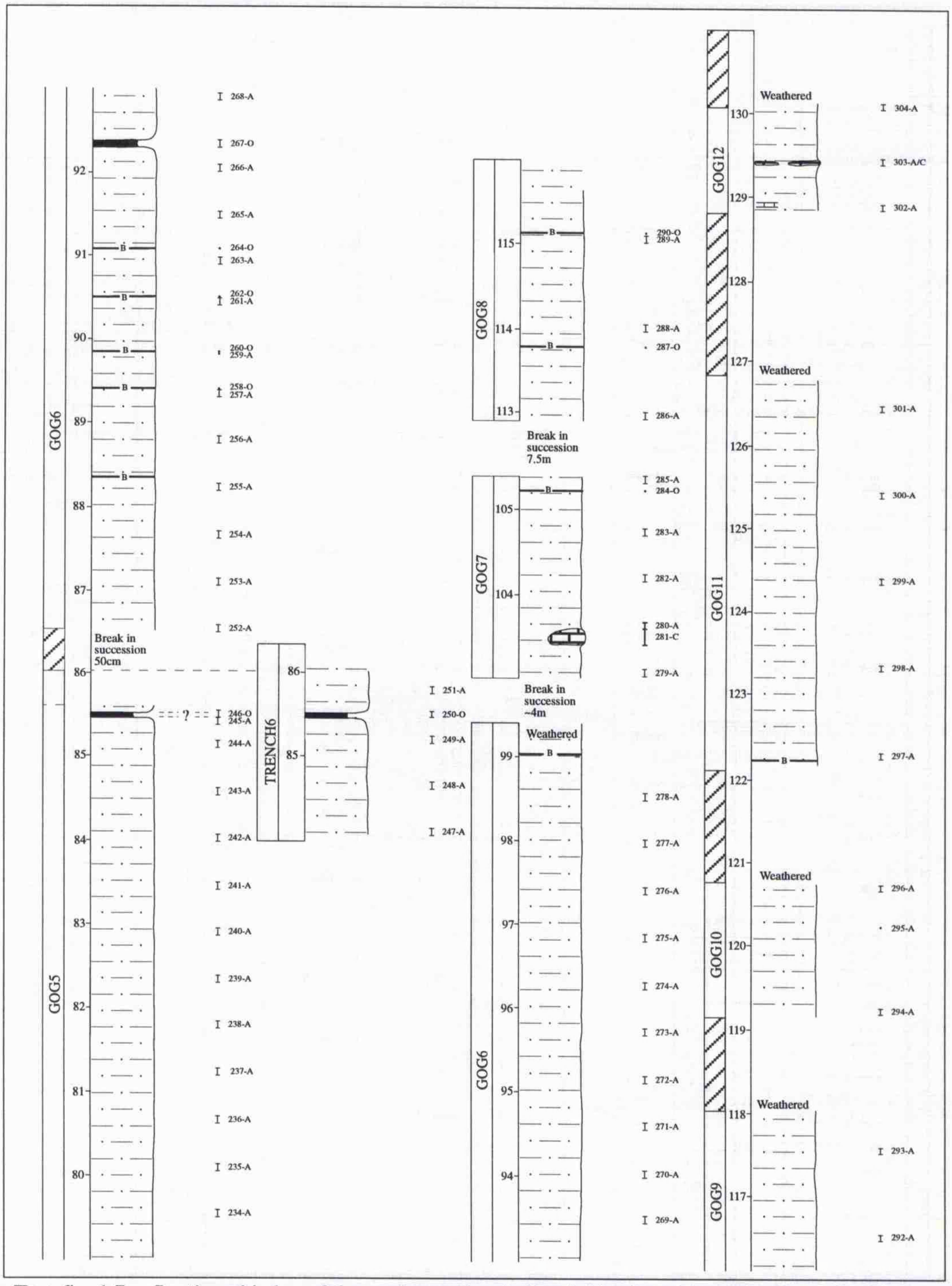
Text-fig. 1.6. The geology of the Goggin Road section, Mortimer Forest, Ludlow (after White & Lawson (1978) and Siveter *et al.* (1989).



Text-fig. 1.7a. Stratigraphic log of the Goggin Road section, Mortimer Forest, Ludlow. The positions of samples are also shown. Figures refer to height in metres above/below Wenlock-Ludlow series boundary. Key as for Text-fig. 2.



Text-fig. 1.7b. Stratigraphic log of the Goggin Road section, Mortimer Forest, Ludlow. The positions of samples are also shown. Figures refer to height in metres above the Wenlock-Ludlow series boundary. Key as for Text-fig. 2.



Text-fig. 1.7c. Stratigraphic log of the section at Goggin Road, Mortimer Forest, Ludlow. Positions of samples are also shown. Figures refer to height in metres above Wenlock-Ludlow series boundary. Key as for Text-fig. 2.

μm. Undigested fragments of rock were dried, weighed and the result subtracted from the original weight. The organic fraction was concentrated by centrifuging the residue at 2400 rpm in sodium polytungstate (SG=2.0). Residue was added to a centrifuge tube and excess water tipped off after settling. Sodium polytungstate was added and the sample mixed slowly to avoid damaging the palynomorphs. After centrifuging, the organic fraction was tipped off and washed in a 10 μm sieve with deionised water. The organic residue was then pipetted into a vial for mounting.

Well mixed sample was pipetted into a drop of cellosize dispersant on a coverslip (22 x 22mm). The residue was mixed with the dispersant, spread evenly over the coverslip and dried slowly to avoid particle clumping. Four coverslips were made for each sample and attached to glass slides with petropoxy adhesive.

For scanning electron microscope (SEM) work, nickel grids, to enable specimen relocation, were attached to circular coverslips (x16mm) with petropoxy. Well mixed palynological residue was pipetted into a small amount of cellosize dispersant, spread to cover the grids and dried slowly. Coverslips were attached, using dental wax, to 12.5 mm Cambridge SEM stubs. A sputter coater (30-90 seconds) added a thin layer of gold and, to avoid charging, graphite paint was applied to join the metal stub and gold coated surface. After use in the SEM coverslips were mounted on glass slides with petropoxy and the stub removed. Specimens could then be re-examined under transmitted light.

PHOTOGRAPHY. Light microphotographs were taken on either a Zeiss photomicroscope (under normal transmitted light) or Leitz Aristoplan photomicroscope (using Differential Interference Contrast - DIC). In the plate descriptions those photomicrographs taken with the Leitz Aristoplan are indicated by (DIC) after the magnification. Photomicrographs were taken on Ilford 35mm Pan F (ISO 50, din 18). Scanning electron microphotographs were taken on a Hitachi S-520, at 15-20 kv, using Ilford 120 HP5 (ISO 400, din 27).

ACRITARCH AND PRASINOPHYTE ALGAL CLASSIFICATION

The informal group Acritarcha Evitt (1963) is a polyphyletic group of generally Palaeozoic, eukaryotic, unicellular, organic walled microfossils of uncertain affinities. Most are probably algal (?phytoplanktonic) cysts (Martin 1993, Colbath & Grenfell 1995) and recent molecular studies have strongly indicated that some acritarchs are the phylogenetic precursors of dinoflagellates (Moldowan *et al.* 1996).

Some acritarchs have been related to oomycete fungi (Pirozynski 1976). Colbath & Grenfell (1995, p. 303) also considered a fungal origin for some acritarchs a possibility; they stated, however, that current morphological and chemical evidence suggested that the majority of acritarchs were not fungal. The claim that some acritarchs (e.g. *Hoegklintia* Dorning 1981a) were cysts of possibly benthic thallose macroalgae (Dorning 1981a) was regarded as unproven by Colbath & Grenfell (1995), who stated that these taxa had little resemblance to the modern disseminules of macroalgae. The genus *Moyeria* Thusu (considered a junior synonym of *Eupoikilofusa* herein) has been suggested to be a euglenid pellicle (Gray & Boucot 1989). The identification of triaromatic dinosteroids in samples from the Precambrian to Triassic indicates that some acritarchs were the evolutionary precursors of dinoflagellates (Moldowan *et al.* 1996). Triaromatic dinosteroids are derived from dinosterols, compounds that are known in modern organisms to be almost exclusive to dinoflagellates, and their frequency through time approximately correlates with the relative frequency of acritarch and dinoflagellate species (Moldowan *et al.* 1996, fig. 2c).

Acritarchs are treated under the Botanical Code of Nomenclature (Deflandre 1936b, Downie *et al.* 1961, 1963) and a more complete historical classification was outlined by Martin (1993). Morphological characteristics are used to classify the acritarchs (see Tappan 1980), but the value attached to each character varies from author to author. Acritarch genera are listed alphabetically herein (e.g. Cramer & Diez 1972; Loeblich 1970), a scheme that has general acceptance over artificial classifications (e.g. Downie *et al.* 1963, Eisenack 1969, Downie 1973).

The definition of a series of clades was considered prefatory to the introduction of a natural, Linnaean classification by Colbath & Grenfell (1995, p. 308). They proposed three clades (*Baltisphaeridium* Eisenack, *Peteinosphaeridium* Staplin *et al.* and *Cymbosphaeridium* Lister), concentrating on those taxa that can be obviously grouped together by their wall structure and excystment mechanisms. The *Cymbosphaeridium* clade was likened very strongly to dinocysts, but the lack of a demonstrated paracingulum or paratabulation maintains their exclusion (Colbath & Grenfell 1995, p. 310).

TERMINOLOGY

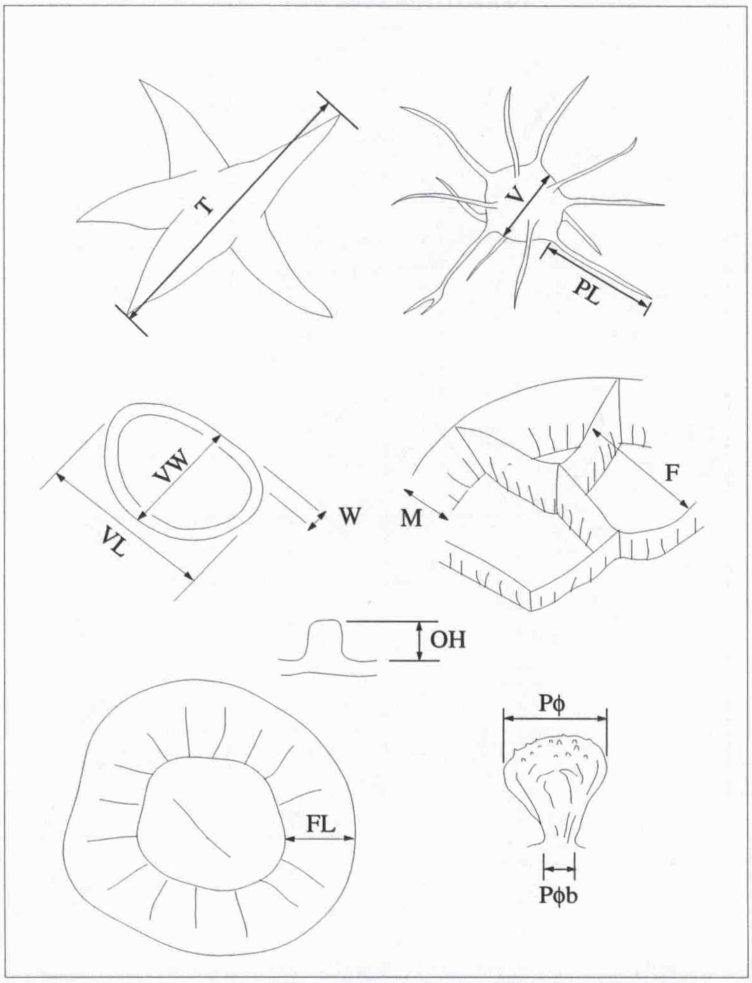
Details of the position of the measurements that are referred to in the systematics section are given in Text-fig. (1.8); glossaries of terms may be found in Lister (1970, p. 24-26), Eisenack *et al.* (1973, p. 9-18, figs 2a, b, 3 or 1976, p. XV-XXIV, figs2a, b, 3). Colbath & Grenfell (1995, p. 306, pl. 8) have listed and illustrated the types of excystment openings present in Palaeozoic acritarchs.

SYNONYMY LISTS

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

REPOSITORIES

Specimens illustrated herein are temporarily deposited in the Department of Geology, University of Leicester, UK.



Text-fig. 1.8. Examples of the positions of measurements referred to in Chapter 2 (systematics section). T = Total length/diameter; VL = Vesicle length; VW = Vesicle width; V = Vesicle diamter; PL = Process length; PØb = Process diameter base; PØ = Process diameter; PN = Process number; M = Membrane height; F = Field width; FL = Flange width; W = Wall thickness; OH = Ornament height.

SYSTEMATIC PALAEONTOLOGY

Class PRASINOPHYCEAE Christensen 1962
Order Chlorodendrales Fritsch 1917
Family Halosphaeraceae Haekel 1894

Genus **Cymatiosphaera** O.Wetzel 1933b ex Deflandre 1954

1933b *Cymatiosphaera* n. gen.; O.Wetzel, p. 24, pl. 4, fig. 8 (invalid under I.C.Z.N. article 13b according to Playford 1977, p. 16)

1954 *Cymatiosphaera* O.Wetzel emend.; Deflandre 1954, p. 257.

1963 *Cymatiosphaeropsis*; Mädler, p. 355. (according to Playford 1977, p. 16).

Type Species. By subsequent designation, *Cymatiosphaera radiata* O.Wetzel 1933b, p. 27, pl. 4, fig. 8; from the Baltic, Cretaceous-Paleocene.

Diagnosis. (Translated from Deflandre 1954, p. 257.). "Vesicle of organic matter, often brownish, globular (spherical-ellipsoidal) with the external surface divided into polygonal fields by membranes perpendicular to the surface; points of junction of membranes (corner of polygons) generally thickened and give, in lateral view, the impression of rods or small columns; no system of equatorial differentiation of fields; no horns or spines; margin of membranes often sharp and parallel to the surface of the vesicle, sometimes a little concave, possibly serrated or corroded; surface of the vesicle smooth, punctate, or with granulations; dimensions variable between a few μ and a few tens of μ, sometimes over 100μ crests included."

Remarks. The genera *Dictyotidium*, *Melikeriopalla*, *Muraticavea* Wicander 1974, *Polyedrixium* and *Pterosphaeridia* Mädler 1963 are all similar to *Cymatiosphaera.* Fields generally formed by low ridges, not membranes, distinguish *Dictyotidium*; *Melikeriopalla* (as applied herein) has fields formed by low ridges, which possess a small node or pore in their centre; *Muraticavea* has fields formed by folding of the vesicle wall; *Fimbriaglomerella* (a possible junior synonym) has a complete rupture type of excystment opening; *Polyedrixium* has an indistinct vesicle-membrane contact and crenulate membranes which can extend into processes. Although morphologically akin to *Cymatiosphaera*, the vesicle wall of *Pterosphaeridia* possesses pore canals (Playford 1977, p. 16).

Cymatiosphaeropsis was originally separated from *Cymatiosphaera* by the presence of sculptural elements on the vesicle surface; this was considered to be of interspecific importance only by Playford (1977, p. 16), who transferred the type species to *Cymatiosphaera.* Other species of *Cymatiosphaeropsis* have been transferred to *Cymatiosphaera*, though from a cursory examination some of these transfers must be questioned as the morphology of several taxa do not appear typical of cymatiosphaerids.

Cymatiosphaera aff. **cornifera** Deunff 1955 Pl. 1, figs 1-2; Pl. 9, figs 1-2.

aff	1955	*Cymatiosphaera cornifera* n. sp.; Deunff, p. 147, fig. 23.
aff	1977	*Cymatiosphaera cornifera* Deunff 1955; Playford, p. 17, pl. 4, figs 4-14.
	1989	*Cymatiosphaera cornifera* Deunff; Le Hérissé, p. 73, pl. 1, figs 11-13, 18-20.
aff	1990	*Cymatiosphaera cornifera* Deunff 1955a; Fensome *et al.*, p. 169 (no fig.).

Holotype. Deunff 1955, fig. 23; from the Middle Devonian, Canada.

Diagnosis. (Translated from Deunff 1955, p. 147.). "Vesicle spherical with diameter of 15μ. Surface divided into polygonal fields partitioned by membranes of 5μ in height. Each polygonal field possesses, in the centre, a short spine of height 2μ."

Description. Vesicle spherical, finely reticulate, with low membranes giving an overall polygonal, rarely subcircular, outline. Membranes define rectangular and polygonal fields, at the centre of which, short projections can occur; these projections are generally simple spines, though linear ridges and groups of numerous projections can occur. The number of projections varies between individuals; on some specimens they are completely lacking, whilst others may only possess a few in some of the fields. Excystment by rupture of vesicle wall; specimens with thickened lips and unornamented ruptures have been found.

Dimensions. V=13-18μm, M=3-7μm, F=4.5-10μm, W=0.25-1μm (13 specimens measured).

Remarks. Specimens recovered in the present study have been referred to *C.* aff. *cornifera* as they differ from those forms recovered from the Devonian (e.g. Deunff 1955, Playford 1977), raising the possibility that Silurian forms assigned to *C. cornifera* belong in a separate species. The diagnosis of Deunff (1955, p. 147) was based on a single specimen, illustrated by a line drawing. This specimen lies within the size range of forms recovered herein, but appears to possess a laevigate vesicle and larger projections. A comprehensive description, based on a larger number of specimens, was given by Playford (1977, p. 17), in which the excystment mechanism was cited as a simple split. Examples recovered herein excyst via a rupture; specimens with unornamented ruptures (Pl. 9, fig. 1) and examples with thickened lips (Pl. 9, fig. 2) have been found. Those examples described by Playford (1977) also differ from specimens described herein in having generally larger, laevigate vesicles and higher membranes (V = 14-(21)-29μm, M = 5-11μm).

Forms recovered in the present study have similarities with specimens recovered from the Llandovery-Wenlock series boundary of Gotland by Le Hérissé (1989, pl. 1, figs 11-13, 18-20, as *C. cornifera*). These examples also possess reticulate vesicles and projections which may be completely absent, or present in the centre of some, or all, fields. One specimen (Le Hérissé 1989, pl. 1, fig. 18) possesses an unopened rupture with thickened lips.

The presence of projections in the centre of the fields in some specimens of *C.* aff. *cornifera* separates them from similar species, which may be further distinguished by their overall size, shape and number of fields. *Cymatiosphaera* aff. *multisepta* differs in having numerous, smaller, laevigate fields; *Cymatiosphaera* aff. *pavimenta* is generally larger, subcircular in outline, with shorter membranes.

Occurrence (*C. cornifera*). Middle Devonian, Canada (Deunff 1955, 1966, 1967a & b); Devonian of Europe and North Africa (Deunff 1966); Famennian Stage, Belgium (Stockmans & Willière 1969); Lower-Middle Devonian, Moose River Basin, Ontario, Canada (Playford 1977); Silica Formation, Givetian Stage, Ohio (Wicander & Wood 1981); Columbus and Delaware formations, Eifelian-lower Givetian stages, Ohio (Wicander & Wright 1983); topmost Givetian-lower Frasnian stages, France (Le Hérissé & Deunff 1988);

Occurrence (forms which can be assigned to *C.* aff. *cornifera*). Upper and Lower Visby formations, Llandovery-Wenlock series boundary, Gotland (Le Hérissé 1989); Much Wenlock Limestone-lower Middle Elton formation, rare in the upper Middle Elton Formation, Pitch Coppice Quarry and Goggin Road. Known range (*C.* aff. *cornifera*): upper Llandovery-lower Ludlow series.

Cymatiosphaera ? cf. **imperfecta** Le Hérissé 1989 Pl. 1, figs 6-8.

cf 1989 ? *Cymatiosphaera imperfecta* n. sp.; Le Hérissé, p. 74, pl. 1, figs 2-4.

Holotype. Le Hérissé 1989, pl. 1, fig 3,4; sample G445.P5.1, slide SGU 7259 (U46.1); from the lowermost Eke Formation, upper Ludlow Series, Hummelbosholm 1, Gotland.

Diagnosis. (Translated from Le Hérissé 1989, p. 74). "Species placed with doubt into the genus *Cymatiosphaera*; vesicle with spherical outline, a thick wall, surface divided into polygonal or rounded areas of variable diameters, interconnected or independent; the fields are limited by the lower part of membranous crests, often flexuous, 14 to 20 fields visible. The surface of the vesicle is smooth or with a light ornament, appearing granulate. The opening was not observed."

Description. Vesicle spherical, laevigate under transmitted light, thick walled, divided into irregular, rounded or polygonal fields by low membranes; fields joined or isolated. Vesicle flattened or crumpled, rarely preserved in three dimensions. Excystment mechanism not observed.

Dimensions. V=25-42μm, M=0.5-1.75μm, F=3.5-10μm, W=1-3μm (11 specimens measured).

Remarks. This species, provisionally placed in *Cymatiosphaera* because of the irregular nature of its fields, was compared to the Australian, Eocene-Miocene gonyaulacoid dinoflagellate cyst *Shematophora* Deflandre & Cookson 1955 by Le Hérissé (1989, p. 74). Specimens recovered herein have been assigned to *C.* ? cf. *imperfecta* as the majority have membranes that are too poorly preserved for their exact nature and distribution to be ascertained. Only from three dimensionally preserved specimens recovered from around the Wenlock-Ludlow series boundary is it clearly possible to see the irregular nature of the membranes; even these specimens appear to have fields which are generally joined and not isolated to the same degree as those recovered by Le Hérissé (1989).

Occurrence. Slite, Mulde, Klinteberg and Eke formations, Wenlock-Ludlow series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock-Ludlow series.

Cymatiosphaera lawsonii sp. nov. Pl. 2, fig. 6; Pl. 9, figs 6-8.

Name. Species name *lawsonii*, after J. D. Lawson who first described the forestry track exposures of Mortimer Forest, Ludlow.

Holotype. Pl. 2, fig. 6; TRENCH3/151-A (1)-Q36; from the Lower Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle spherical, commonly ellipsoidal, laevigate under transmitted light, faintly reticulate with a SEM; vesicle of equal thickness to, or slightly thicker than membranes. Membranes thin, delineating large polygonal fields; excystment by large, unornamented rupture of the vesicle wall.

Dimensions. V=26-43μm, M=4-8.5μm, F=10-15μm (9 specimens measured).

Remarks. This species resembles *Cymatiosphaera gorstia* Dorning 1981a, which is larger, with shorter membranes and smaller fields.

Occurrence. Rare over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), absent from the lowermost Lower Elton Formation (Goggin Road), common in every sample from the middle Lower Elton-Middle Elton formation (Goggin Road).

Cymatiosphaera aff. **ledburica** Dorning 1981a Pl. 1, fig. 9; Pl. 9, figs 3-4.

aff v* 1981a *Cymatiosphaera ledburica* n. sp.; Dorning, p. 185, pl. 2, figs 13-14.
aff 1990 *Cymatiosphaera ledburica* Dorning 1981a; Fensome *et al.*, p. 171 (no fig.).

Holotype. Dorning 1981a, pl. 2, fig. 14; LE25K, M28/0, MPK 2925; from the Bringewood Group, Ludlow Series, Ledbury Hill, Herefordshire (SO 713 386).

Diagnosis. (Dorning 1981a, p. 185). "Vesicle spherical to subspherical, 25-30 μm in diameter, laevigate, divided into 8 fields by thin flanges 10-12 μm high; excystment by a straight split."

Description. Vesicle spherical to ellipsoidal, relatively thick walled; laevigate under transmitted light, finely reticulate with a SEM. Thin membranes define a subcircular outline and delineate a number of large polygonal fields. Excystment mechanism not observed.

Dimensions. V=17-28μm, M=4-10μm, F=8-15μm W=1-1.5μm (9 specimens measured).

Remarks. The morphology of *C.* aff. *ledburica* differs from the type material illustrated by Dorning (1981a) in two ways; the membranes are shorter and the fields lack the circular structures visible on the holotype. These structures, not mentioned in the original diagnosis, are not recorded on all specimens from the type material (e.g. Dorning 1981a, pl. 2, fig. 13). They are distinct, however, from the structures of *C. mariae*, having the shape of a single, thickened, hoop approximately 2μm in diameter.

Occurrence. Biozones L2 and L3, uppermost Elton to middle Leintwardine groups, Ludlow Series, Welsh Borderland (Dorning 1981a, as *C. ledburica*); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road (as *C.* aff. *ledburica*).

Cymatiosphaera mariae Cramer, Diez, Rodriguez & Fombella 1976 emend. Le Hérissé 1989 — Pl. 1, fig. 10; Pl. 9, fig. 5.

1976 *Cymatiosphaera mariae* n. sp.; Cramer, Diez, Rodriguez & Fombella, p. 446, pl. 2, figs 21-23.

1978 *Cymatiosphaera subrotunda* sp. nov.; Kiryanov, p. 31-32, pl. 5, figs 7, 8.

1989 *Cymatiosphaera mariae* Cramer *et al.*, emend.; Le Hérissé, p. 74-75, pl. 2, figs 1-6, text-fig. 4B.

1990 *Cymatiosphaera mariae* Cramer *et al.* 1976; Fensome *et al.*, p. 172 (no fig.).

Holotype. Cramer *et al.* 1976, pl. 2, fig. 21; from the San Pedro Formation, Ludlow Series-lower Gedinnian Stage, Cantabric Mountains, León, NW Spain.

Diagnosis. (Translated from Le Hérissé 1989, p. 75). "The vesicle is spherical, with circular outline, with one relatively thick wall (2-2.5μm); the surface is divided into polygonal or subcircular fields (between 6 and 14 fields) delineated by high, transparent, membranous crests (height 4.5 to 16μm); ratio total diameter/vesicle diameter = 1.7 to 1.9. The floor of each field has on $^2/_3$rds of the area a particular ornament composed of a double concentric circle in relief with radial crests; under SEM the ornament, slightly protruding from the surface of the fields, evokes a flower or rosette; around the ornament the vesicle surface is granulate. Some specimens, observed with light microscope, have permitted the location of the excystment structure which cuts cross-wise each of the polygonal fields and is of the slit type with fine lips on the borders."

Description. Vesicle spherical, moderately thick walled, with a polygonal outline produced by thin membranes that delineate polygonal fields. In the centre of each field a structure of concentric circles is evident. With a SEM these structures appear to stand proud of the surface and have an inner hub and outer rim; the vesicle surface around these structures is laevigate. Excystment mechanism not observed.

Dimensions. V=14-28μm, M=4.5-9μm, F=7-10μm, W=0.5-2.5μm, concentric structures 3-4.7μm diameter (9 specimens measured).

Remarks. The dimensions of the laevigate specimens found in this study compare well with those of the type material (V = 12-22μm, M = 3.5-9μm, F = 3-12μm), but are smaller than the granulate examples recovered by Le Hérissé (1989; V = 19-34μm, M = 4.5-16μm, F = 14-20μm).

The morphology of *C. mariae* was compared to the modern prasinophyte algal cyst *Pterosperma marginatum* Gaarder 1954, illustrated in Parke *et al.* (1978, pl. 1, fig. F), by Le Hérissé (1989, p. 75). Circular structures visible on *Cymatiosphaera numisma* Le Hérissé 1989 (p. 75-76, pl. 2, figs 7-8) differ from those of *C. mariae* in being composed of large reticulae, arranged in concentric circles, that extend to the base of the membranes.

Occurrence. San Pedro Formation, Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer *et al.* 1976); lower Ludlow Series, Podolia (Kiryanov 1978, as *C. subrotunda*); Slite, upper Mulde, upper Hemse (unit a, «marl top»), lower Eke and Hamra (units a-c) formations, Wenlock-Ludlow Series, Gotland (Le Hérissé 1989); rare over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), more common from the middle Lower Elton Formation and particularly common in the Middle Elton Formation, Goggin Road. Known range: Wenlock Series-lower Gedinnian Stage.

Cymatiosphaera multicrista sp. nov. Pl. 1, figs 4-5; Pl. 9, fig. 12.

Name. Species name *multicrista*, from the latin *multi* = many, *cresta* = crests, referring to the many numerous small crest-like membranes found on individuals of this taxon.

Holotype. Pl. 1, fig. 4; GOG1/7-C (1)-K42/4; from the Much Wenlock Limestone Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle spherical to ellipsoidal, thin or moderately thick walled, laevigate. Short membranes define numerous, small, polygonal fields; excystment by a large, simple, unornamented, rupture, which cuts across numerous fields.

Dimensions. V=11-22μm, M=0.3-1.5μm, F=0.3-3μm, W=0.3-2.5μm (9 specimens measured).

Remarks. This is a distinctive species of *Cymatiosphaera* and does not resemble any other taxa recovered in the present study; it is, however, almost identical to *Cymatiosphaera longhopica* Dorning 1981a, which differs in having a solid node in the centre of each field.

Occurrence. Rare over the Wenlock-Ludlow series boundary (Pitch Coppice Quarry and Goggin Road), with even scarcer occurrences in the Lower and Middle Elton formations, Goggin Road.

Cymatiosphaera aff. **multisepta** Deunff 1955 Pl. 1, fig. 3; Pl. 9, fig. 9.

aff 1955 *Cymatiosphaera multisepta* n. sp.; Deunff, p. 147, fig. 25.
aff 1977 *Cymatiosphaera multisepta* Deunff 1955; Playford, p. 17, pl. 4, fig. 3.
aff 1990 *Cymatiosphaera multisepta* Deunff 1955a; Fensome *et al.*, p. 172 (no fig.).

Holotype. Deunff 1955, fig. 25; from the Onondaga Formation, middle Devonian, Ontario, Canada.

Diagnosis. (Translated from Deunff 1955, p. 147.). "Vesicle spherical of 8μ in diameter, widened in optical section by formation of partitioning membranes of 2μ in height determining sufficiently regular, polygonal fields on the surface of the vesicle of approximately twenty in number in frontal view."

Description. Vesicle spherical, laevigate; thin, short membranes produce a circular outline and define numerous small, irregular or polygonal fields. Excystment mechanism not observed.

Dimensions. V=12-16μm, M=1.5-2.5μm, F=1.5-5μm, W=0.5μm (8 specimens measured).

Remarks. Specimens have been assigned to *C.* aff. *multisepta* as they have morphological similarities with the type material, but occur within the Silurian, not the Devonian. The smaller laevigate vesicle and more numerous fields differentiate *C.* aff. *multisepta* from *C. pavimenta*; *C.* aff. *cornifera* has an overall polygonal outline, larger membranes and fields, which may possess central projections.

Occurrence. (*C. multisepta*) Onondaga Formation, middle Devonian, Canada (Deunff 1955, 1967b); Devonian, North Africa and Europe (Deunff 1967b); Ordovician-Silurian, Belgium (Martin 1969); Devonian, Belgium (Stockmans & Willière 1969, 1974); Lower-Middle Devonian, Moose River Basin, Ontario, Canada (Playford 1977).

(*C.* aff. *multisepta*) very rare from the Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road.

Cymatiosphaera octoplana Downie 1959 emend. Pl. 1, figs 11-13.

v* 1959 *Cymatiosphaera octoplana* sp. nov.; Downie, p. 63, pl. 11, fig. 2.
v* 1959 *Cymatiosphaera wenlockia* sp. nov.; Downie, p. 63-64, pl. 11, fig. 4.
v. 1959 *Cymatiosphaera cubus* Deunff; Downie, pl. 11, fig. 3 (*nomen nudum*).
1989 *Cymatiosphaera wenlockia* (Downie); Le Hérissé, pl. 1, figs 9, 10.
.1989 *Cymatiosphaera* cf. *prismatica* Deunff 1954a; Le Hérissé, p. 76-77, pl. 1, figs 14-15.
1990 *Cymatiosphaera octoplana* Downie 1959; Fensome *et al.*, p. 173 (no fig.).

Holotype. Downie 1959, pl. 11, fig. 2; Mik(P)17001; from the Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Original diagnosis. (Downie 1959, p. 63). "A species of *Cymatiosphaera*, lemon-yellow colour, test surface granular, divided into eight rectangular, more or less equally sized, areas by membranes about one-third of the diameter in height, height of membrane varies giving a rectangular outline, test diameter about 30μ."

Emended diagnosis. Vesicle spherical to ellipsoidal, reticulate. Thin membranes give an overall subtriangular, square-rectangular or polygonal outline. Thickenings along the membrane bases produce a striate appearance and membranes define triangular, rectangular or polygonal fields. In examples with a subtriangular outline the membranes are convex to the vesicle surface. Excystment mechanism not observed, possibly a simple split.

Dimensions. V=22-33μm, M=6-11μm, F=12-23μm (10 specimens measured).

Remarks. This species shows a large number of morphologies, similar to those illustrated for *Cymatiosphaera heloderma* Cramer & Diez 1972 by Le Hérissé (1989, pl. 1, figs 5-8). The emended diagnosis includes forms where the membranes produce triangular, square-rectangular or more complex polygonal outlines and this variation is considered to represent the morphological continuum of a single species. Those forms illustrated as *C.* cf. *prismatica* by Le Hérissé (1989) are considered to display enough features (vesicle shape, size, membrane height and outline) to be placed in *C. octoplana* ; *C. prismatica* Deunff 1954a is clearly different and closely resembles some species of *Polyedrixium* (e.g. *Polyedrixium fragosulum* Playford 1977, pl. 16, figs 8-14). The holotype of *C. prismatica* possesses membranes that have edges that are straight or slightly concave to the vesicle surface, whereas forms attributed to *C. octoplana* herein have membranes that are convex to the vesicle surface. *C. heloderma* is differentiated from *C. octoplana* by its larger vesicle size (40-60µm vs' 23-30µm this study) and coarser reticulate ornament.

Specimens recovered in the present study have not been found with clear excystment structures, though a specimen illustrated as *C.* cf. *prismatica* by Le Hérissé (1989, pl. 1, figs 14-15) shows an unopened rupture with thickened lips. The junior synonym of *C. octoplana*, *C. wenlockia*, was reported from the Devonian of Belgium by Stockmans & Willière (1974, p. 34); no specimens were illustrated and thus the reference is tentatively included below as *C. octoplana* appears to be restricted to the Silurian.

Occurrence. Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959); Silurian, Belgium (Martin 1969); Tuscarora and Rose Hill formations, upper Llandovery Series, Pennsylvania (Cramer 1969a); Neahga Formation, upper Llandovery Series, Ontario and New York (Cramer & Diez 1970); Ross Brook Formation, lower-middle Llandovery Series, Nova Scotia (Cramer 1970b); Plum Creek and Racine formations, upper Llandovery and Wenlock-Ludlow series, USA (Cramer & Diez 1972); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Frasnian-Famennian stages, Belgium (Stockmans & Willière 1974); Aeronian Stage-Lower Elton Formation, middle Llandovery-lower Ludlow Series, Britain and Ireland (Aldridge *et al.* 1979); Upper Visby-Högklint formations, lower Wenlock Series, Gotland (Cramer *et al.* 1979); Hughley Formation, upper Llandovery Series-Elton Group, Ludlow Series, Welsh Borderland (Dorning 1981a); Wenlock Series, Ayrshire (Dorning 1982); lower Silurian, Ringerike, Norway (Dorning & Aldridge 1982); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Wenlock-Ludlow series, Austria (Priewalder 1987); lower Silurian, Ringerike, Norway (Smelror 1987); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); basal Wenlock Series (Upper Visby Formation) to the topmost Ludlow (Hamra Formation), Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: lower Llandovery-Prídolí series, ? Upper Devonian.

Cymatiosphaera paucimembrana sp. nov. Pl. 1, figs 18-19.

Name. Species name *paucimembrana*, from the latin *pauci* = few, *membrana* = membrane, refering to the small number of membranes visible on examples of this taxon.

Holotype. Pl. 1, fig. 18, GOG6/275-A (1)-O35/1, from the Middle Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Description. Vesicle spherical, laevigate under transmitted light, moderately thick walled. Vesicle divided into a few large fields (usually 3-4) by thin membranes. Excystment structure not observed.

Dimensions. V=15-20µm, T=22-30µm, W=1-1.5µm (11 specimens measured).

Remarks. This taxon can easily be mistaken for a pterospermellid, as the membranes of some specimens appear, at first glance, to be restricted to the equator. It is the very large nature of the fields and the low number of membranes that distinguish this taxon from any other species of *Cymatiosphaera* recovered herein.

Occurrence. Middle Elton Formation, Goggin Road.

Cymatiosphaera aff. **pavimenta** (Deflandre 1945) Deflandre 1954 Pl. 1, figs 14-15.

aff	1945	*Micrhystridium pavimentum* n. sp.; Deflandre, p. 68, pl. 3, figs 20-21, text-fig. 41.
aff	1954	*Cym. pavimenta* (Defl. 1945); Deflandre, p. 258 (no fig.).
aff	1990	*Cymatiosphaera pavimenta* (Deflandre 1945a) Deflandre 1954; Fensome *et al.*, p. 173 (no fig.).

Holotype. Deflandre 1945, pl. 3, fig. 21; AY 32; paratype, pl. 3, fig. 20; AY 15; from the Silurian, Montagne Noire, France.

Description. (Translation after Deflandre 1945, p. 30.). "Vesicle spherical, surface divided into polygonal lacunae by short muri; vesicle diameter 18 to 22µ, total diameter 23 to 27µ."

Description. Vesicle spherical to subspherical, finely reticulate with short, thin, membranes defining rectangular to polygonal fields and giving an overall circular or subcircular outline. Excystment by simple unornamented rupture.

Dimensions. V=20-22µm, M=0.5-2µm, F=7-14µm, W=0.3-1.5µm (9 specimens measured).

Remarks. The description after Deflandre (1945, p. 30), above, is an abbreviated translation of the original diagnosis, from which remarks on the specimens he recovered have been removed. Specimens have been assigned to *C.* aff. *pavimenta*, as they appear similar to the material illustrated by Deflandre (1944), but possess slightly fewer, larger fields, and lower membranes. *Cymatiosphaera blaisdonica* Dorning 1981a is separated from *C.* aff. *pavimenta* by its membrane height.

Occurrence. (as *C. pavimenta*) Silurian, Montagne Noire, France (Deflandre 1945); Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959); Silurian, France (Deunff 1959); San Pedro and La Vid formations, Silurian-Lower Devonian, NW Spain (Cramer 1964b); Ordovician-Silurian, Belgium (Martin 1966a, 1969); Famennian Stage, Belgium (Stockmans & Willière 1969); Llanvirn Series, Belgium (Paris & Deunff 1970); upper Silurian-lower Devonian, Belgium (Lefort & Deunff 1970); Upper Devonian, Belgium (Stockmans & Willière 1974); Much Wenlock Limestone-Lower Whitcliffe formations, Wenlock-Ludlow series, Ludlow (Lister & Downie 1974); Lower-Middle Devonian, Moose River Basin, Ontario, Canada (Playford 1977, as cf. *pavimenta*); Buildwas-Coalbrookdale formations, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); lower Silurian, Ringerike, Norway (Smelror 1987); lower Wenlock Series, Wenlock type area (Swire 1993); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); (as *C.* aff. *pavimenta*)

Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road. Known range: Ordovician-Upper Devonian.

Cymatiosphaera triangula sp. nov. Pl. 1, figs 16-17; Pl. 9, figs 10-11.

Name. Species name *triangula*, from the latin *triangulum* = triangle, referring to the triangular nature of the membranes.

Holotype. Pl. 1, fig. 16; TRENCH1/11-A (1)-L47/1; from the Lower Elton Formation, Goggin Road.

Diagnosis. Vesicle spherical, more commonly ellipsoidal; the wall of the vesicle is slightly thicker or considerably thicker than the membranes. The vesicle surface appears laevigate or irregularly ornamented and occasionally solid projections are found between the membranes. These membranes are almost transparent and are commonly extended into sharp points (commonly 4-7 per specimen), though rarely they may be rounded or appear bifurcate. Excystment by simple, unornamented rupture.

Dimensions. V=12-21μm, maximum membrane height=10-18μm (10 specimens measured).

Remarks. Superficially, this taxon resembles *Eisenackidium wenlockense*, which differs in having distinct processes, which are generally not connected by crests; *Polyedrixium fragosulum* Playford 1977 is much larger. This species has been assigned to *Cymatiosphaera* as specimens show a clear distinction between the membranes and vesicle (Pl. 9, fig. 11); species of *Polyedrixium* generally have an indistinct contact between the membranes and vesicle.

Occurrence. Common over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road); rare in the Lower and Middle Elton formations, Goggin Road.

Cymatiosphaera sp. A Pl. 1, figs 20-21.

Description. Vesicle spherical, appears laevigate or rarely faintly reticulate under transmitted light; membranes low, giving an overall polygonal outline and delineating polygonal fields. Excystment mechanism not observed.

Dimensions. V=19-24μm, M=2.5-5μm, F=3-8.5μm, W=0.5-1μm. (8 specimens measured).

Remarks. This taxon resembles several cymatiosphaerids which are distinguished from one another by their vesicle size, ornament and outline. The vesicle and fields of *C.* aff. *cornifera* are smaller and *Cymatiosphaera* sp. A lacks the central projections which are sometimes apparent on that taxon. The polygonal outline of this species separates it from *C.* aff. *pavimenta* and *C.* aff. *multisepta*, the latter of which also has more numerous, smaller fields. The overall larger size, height of membranes and width of fields separate *C.* sp. A from *C.* aff. *ledburica*.

Occurrence. Uppermost Middle Elton Formation, Goggin Road.

Cymatiosphaera sp. B — Pl. 2, fig. 1.

Description. Poorly preserved, vesicle ellipsoidal to subspherical, laevigate, divided into numerous, small, polygonal fields by very low membranes. Excystment mechanism not observed.

Dimensions. V=19-24μm, M=0.2-0.4μm, F=1.5-3μm, W= *c.* 0.5μm (9 specimens measured).

Remarks. The preservation of examples placed within this taxon is generally very poor and on most specimens the fields are hardly discernible. This taxon has, therefore, been retained in open nomenclature. In overall size, this taxon is similar to *C. multicrista* sp. nov., but differs in having larger fields and shorter membranes; *Cymatiosphaera eltonensis* Dorning 1981a is also similar, but has higher membranes.

Occurrence. Middle Elton Formation, Goggin Road.

Genus **Dictyotidium** Eisenack 1955 emend. Staplin 1961

1969 *Dictyosphaeridium* ; Timofeev, p. 18 (an invalid name)

Type Species. By original designation, *Leiosphaera dictyota* Eisenack 1938, p. 27-28, pl. 3, figs 8a-c; Beyrichienkalk, Silurian (?Prídolí Series), Baltic erratic . Holotype lost (Eisenack *et al.*, 1979a, p. 162).

Diagnosis. (Staplin 1961, p. 417). "Vesicle spherical; surface reticulate, ridges low, distinct, lacunar areas polygonal; some species with two distinctly smaller lacunae, one at each pole; small apiculae or spines may arise from the ridges; papillae may be present in the floors of lacunae."

Remarks. The genus *Melikeriopalla* was considered a junior synonym of *Dictyotidium* by Eisenack *et al.* (1979a, p. 155), but was retained by Colbath (1983, p. 259). He considered that the structures within each polygonal field on the holotype of the type species of *Melikeriopalla* may have been tubular canals or pseudopores, which he believed were lacking in *Dictyotidium* (see *Melikeriopalla* below). Rare examples of *Dictyotidium* have, however, been found with pore canals that pass through the vesicle wall (see *Dictyotidium faviforme* below). The genus *Dictyosphaeridium* Timofeev 1969, a junior homonym of *Dictyosphaeridium* W.Wetzel 1952, was considered a junior synonym of *Dictyotidium* by Cramer & Diez (1979, p. 76).

Dictyotidium biscutulatum Kiryanov 1978 — Pl. 2, fig. 7; Pl. 9, figs 13-14.

1978 *Dictyotidium biscutulatum* sp. nov.; Kiryanov, p. 39-40, pl. 5, figs 1a-b, 6a-b.

1978 *Melikeriopalla cataphracta*; Martin, p. 40, pl. 2, figs 1-3 (according to Priewalder 1987, p. 28).

1983 *Dictyotidium cataphractum* (Martin 1978) comb. nov.; Colbath, p. 257 (no fig.).

1990 *Dictyotidium biscutulatum* Kiryanov 1978; Fensome *et al.*, p. 193 (no fig.).

Holotype. Kiryanov 1978, pl. 5, figs 1a-b; Geological Museum IGN AN USSR no. 1920/643-3a; from the Wenlock Series-Gedinnian Stage, Podolia.

Diagnosis. (Kiryanov 1978, p. 40-In Russian).

Description. Vesicle spherical to ellipsoidal, thin walled, divided into rectangular and polygonal fields by low, thin, membranes perpendicular to the vesicle surface. Floor of each field ornamented by coarse reticulae which become finer, or are absent, in the parts closest to the membranes. Excystment by large, simple, unornamented rupture, which almost divides vesicle in two.

Dimensions. V=21-36μm, M=0.5-2μm, F=3.5-10.5μm, W ≤ 0.5μm (6 specimens measured).

Remarks. Specimens recovered are smaller than those previously recorded by Kiryanov (1978, V = 31-52μm), Colbath (1983, V = 45-57μm) and Le Hérissé (1989, V = 40-72μm).

Occurrence. Silurian, Podolia (Kiryanov 1978); Llandovery Series, Carnic Alps, Austria (Martin 1978); Bainbridge Formation, upper Ludlow-Prídolí series, Missouri (Colbath 1979, 1983); Llandovery-lower Wenlock and ? Prídolí series, Austria (Priewalder 1987); När borehole, Visby and Slite (units a and «Slite siltstone») formations, Llandovery-Wenlock series, Gotland (Le Hérissé 1989); rare in the Lower/Middle Elton formations, Goggin Road; not recovered from Pitch Coppice Quarry. Known range: Llandovery-Prídolí series.

Dictyotidium faviforme Schultz 1967 Pl. 2, figs 2, 4-5, 8; Pl. 9, figs 15-16.

1967 *Dictyotidium faviformis* n. sp.; Schultz, p. 183, pl. 1, fig. 16.

p. 1977 *Dictyotidium cavernosulum* sp. nov.; Playford, pl. 5, figs 7-8 (only).

1990 *Dictyotidium faviforme* Schultz 1967; Fensome *et al.*, p. 194 (no. fig.).

Holotype. Schultz 1967, pl. 1, fig. 16; Geological Institute of Köln; from the Retiolites Shales, upper Llandovery Series, Dalarne, Sweden.

Diagnosis. (Schultz 1967, p. 183-In German).

Description. Vesicle spherical to ellipsoidal, divided into small, polygonal or irregular, laevigate, fields by low ridges; ridges of generally uniform height and width, though on some specimens the ridges rise to form small peaks at the corners of the fields. Vesicle wall rarely possesses pore canals. Excystment by large, unornamented rupture.

Dimensions. V=15-66μm, F=0.2-2μm, W=0.5-3μm (23 specimens measured).

Remarks. The species *D. cavernosulum* Playford 1977 was considered a junior synonym of *D. faviforme* by Le Hérissé (1989), a synonymy rejected herein. *D. cavernosulum* was originally separated by the fineness of the reticulate ornament, which is clearly shown on the holotype (Playford 1977, pl. 5, fig. 5); two examples resembling *D. faviforme* were also, however, assigned to *D. cavernosulum* (Playford 1977, pl. 5, figs 7-8).

Small tubular pore canals that pass through the vesicle wall have been reported in examples recovered from the Silurian of Gotland (Le Hérissé 1989, p. 109, pl. 3, fig. 9). These pores are situated at the junction of the corners of some fields, in positions which may be occupied by small peaks or nodes in some specimens recovered herein. Pore canals have been observed in rare specimens in the present study (pl. 2, fig. 5).

Occurrence. Retiolites Shale, upper Llandovery Series, Sweden (Schultz 1967); Alger Formation, upper Llandovery Series, Ohio; Moccasin Springs Formation, Ludlow-Přídolí series; Osgood Formation, upper Llandovery Series, Indiana; Racine Formation, Wenlock-Ludlow series; Waldron Formation, upper Wenlock Series, Tennessee (Cramer & Diez 1972); Stooping River Formation, Emsian Stage, Ontario (Playford 1977); upper Llandovery (När borehole)-upper Ludlow series (basal Hamra Formation), Gotland (Le Hérissé 1989); Present in most samples from the Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: upper Llandovery Series-Emsian Stage.

Dictyotidium stenodictyum Eisenack 1965a — Pl. 2, figs 9-10; Pl. 9, figs 17-18.

	1965a	*Dictyotidium stenodictyum* n. sp.; Eisenack, p. 264, pl. 22, fig. 2, ? 3.
non.	1969	*Dictyotidium stenodictyum* Eisenack; Martin, p. 137-138, pl. 3, figs 139-140, pl. 6, fig. 276, pl. 7, figs 309, 314.
non.	1984	*Dictyotidium stenodictyum* Eisenack 1965; Le Hérissé, p. 230, pl. 2, figs 9-10.
non.	1989	*Dictyotidium stenodictyum* Eisenack; Le Hérissé, p. 111-112, pl. 4, figs 6-9.
	.1989	*Dictyotidium stellatum* n. sp.; Le Hérissé, p. 110-111, pl. 4, figs 1-5.
	1990	*Dictyotidium stenodictyum* Eisenack 1965c; Fensome *et al.*, p. 196 (no fig.).

Holotype. Eisenack 1965a, pl. 22, fig. 2; Sphaerocodian Marl, Silurian, Burgsvik, Gotland.

Diagnosis. (Eisenack 1965a, p. 264; translation by Eisenack *et al.* 1979a, p. 169). "A species of *Dictyotidium* with essentially a smaller polygonal reticulum than in *D. dictyotum.*"

Description. Vesicle spherical to ellipsoidal, thick walled; divided into triangular, polygonal and irregular areas (1-4.5µm diameter) by low ridges. Spaced irregularly over the surface are larger, solid, projections from which the ridges radiate, giving a star-like appearance; the vesicle is otherwise laevigate. Excystment by large rupture, with thickened lips, in vesicle wall.

Dimensions. V=44-73µm, Major projections=1-4µm, W=2-4.5µm (10 specimens measured).

Remarks. The holotype, illustrated by Eisenack (1965a, pl. 22, fig. 2), appears to have a reticulate vesicle onto which larger projections are scattered, an arrangement identical to *D. stellatum* Le Hérissé (1989) which is considered a junior synonym herein. Those specimens assigned to *D. stenodictyum* by Martin (1969) and Le Hérissé (1989) lack these larger projections and can probably be assigned to *D. dictyotum* Eisenack 1955.

The morphology of *D. stenodictyum* resembles that of *Pterosphaerula astrala* Cramer 1966a from San Pedro and Furuda formations, Silurian, NW Spain. Both taxa have vesicles which are covered by low ridges onto which larger projections are superimposed, though on *P. astrala* the ridges and projections are larger and the vesicle is smaller.

Occurrence. Llandovery-Ludlow series, Gotland (Eisenack 1965a); Llandovery Series, Llandovery type area (Hill 1974); Much Wenlock Limestone-Lower Elton formations, Wenlock-Ludlow series, Ludlow (Lister & Downie 1974); Much Wenlock Limestone Formation-Elton Group, Wenlock-Ludlow Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Llandovery Series (Telychian Stage), Wenlock Series (Högklint, Slite, Mulde and basal Klinteberg formations) and Ludlow Series (upper Hemse and Hamra formations), Gotland (Le Hérissé 1989); Much Wenlock Limestone Formation (Pitch Coppice Quarry); Much Wenlock Limestone-Middle Elton formation, Goggin Road. Known range: Llandovery-Ludlow series.

Genus **Duvernaysphaera** Staplin 1961

1964b *Helios* n. gen.; Cramer, p. 329.

Type Species. By original designation, *Duvernaysphaera tenuicingulata* Staplin 1961, p. 415-416, pl. 49, figs 10-11; Duvernay Member, Upper Devonian, Alberta, Canada.

Original Diagnosis. (Staplin 1961, p. 414-415). "Vesicle circular in outline, surrounded by an appresed diaphanous membrane that extends beyond the vesicle margin as a flange, the flange supported by simple rods or spokes arising from the vesicle that are present only in the equatorial plane, much like the fin of a fish."

Diagnosis. (Deunff 1964, p. 211, translation by Cramer & Diez 1972, p. 162). "Fossil planktonic microorganism, generally of a subcircular, starlike or square form, made up by transparent, hollow body which is slightly inflated in its centre and which is circular, square or in the form of a star. Equatorially, the central body is surrounded by a thin, transparent membrane. The general form and outline of this membrane is generally determined by the form of the central body. The membrane which surrounds the central body is made rigid by thickenings, sometimes by rays that stick out from the corners or from the rim of the central body. Diameter of the central body, 15 to 45 microns; thickness at its centre, 5 to 10 microns; length of membrane, 3 to 15 microns."

Remarks. The genus *Helios* was effectively considered a junior synonym of *Duvernaysphaera* when the type species, *Helios aranides*, was transferred to *Duvernaysphaera* by Cramer (1970b); this combination was not validly published, as the basionym was not fully referenced (Fensome *et al.* 1990, p. 205). The combination was validly published by Cramer & Diez (1972, p. 162-163) and *Helios* has also been considered a junior synonym of *Duvernaysphaera* by Le Hérissé (1989, p. 119-120); *Helios aranides* was retained by Pöthé de Baldis (1981, p. 241) and thus by Fensome *et al.* (1990, p. 245).

In the original diagnosis of Staplin (1961, p. 414-415) the vesicle shape was restricted to circular and the diagnosis was emended to include star-like and square vesicles by Deunff (1964, p. 211). This emended diagnosis, however, stated that the membrane was equatorial, whereas it encompasses the whole inner vesicle (see Le Hérissé 1989, fig. 11). For this reason the diagnosis of Deunff (1964) is not followed herein.

A complete reappraisal of this genus is beyond the present study, though a cursory examination of the relevant publications indicates that several species presently assigned to *Duvernaysphaera* do not belong there. For the purposes of this study, taxa have been assigned to *Duvernaysphaera* if they possess circular vesicles and an enveloping membrane. Those with square or rectangular inner vesicles, surrounded by a membranous outer wall, are assigned to *Quadratitum*.

The diagnosis of *Duvernaysphaera* fails to mention the method of excystment, which is via a rupture of the vesicle wall (see Le Hérissé 1989, fig. 11). This method of excystment is identical to that of *Quadratitum* (Le Hérissé 1989, p. 186). If the broader diagnosis of *Duvernaysphaera* is accepted, so that it contains square, polygonal and stellate forms, then both *Veliferites* Brito 1966 ex Brito 1967 and *Quadratitum* could be considered junior synonyms. The diagnosis of *Veliferites* states that the membrane is equatorial, which would exclude it from the concept of *Duvernaysphaera* and *Quadratitum* used herein, though re-examination of the type species may prove the membrane to completely surround the vesicle.

Duvernaysphaera aranides (Cramer 1964b) Le Hérissé 1989 Pl. 2, fig. 14.

1964b *Helios aranides* n. sp.; Cramer, p. 329-330, pl. 5, fig. 9, pl. 14, fig. 7, text-figs 36:1, 36:2.

1967 *Duvernaysphaera gothica* nov. sp.; Martin, p. 323, pl. 1, figs 6, 15.

1970b *Duvernaysphaera aranides* (Cramer 1964) New Combination; Cramer, Table 1, p. 746 (invalid combination).

1972 *Duvernaysphaera aranides* (Cramer 1964b) New Combination, emended; Cramer & Diez, p. 162-163, pl. 35, fig. 55.

1975 *Duvernaysphaera jelinii* n. sp.; Pöthé de Baldis, p. 495, pl. 4, figs 1-2, 4-5.

1981 *Duvernaysphaera gothica* Martin 1966; Pöthé de Baldis, p. 239, pl. 3, figs 1-2.

1981 *Helios aranides* Cramer; Pöthé de Baldis, p. 243, pl. 4, figs 10-12.

1989 *Duvernaysphaera aranides* (Cramer) Cramer & Diez emend.; Le Hérissé, p. 119-120, pl. 6, figs 11-15.

1990 *Duvernaysphaera gothica* Martin 1967; Fensome *et al.*, p. 205 (no fig.).

1990 *Helios aranides* Cramer 1964b; Fensome *et al.*, p. 245 (no fig.).

Holotype. Cramer 1964b, pl. 14, fig. 7; 1143; San Pedro Formation, Ludlow Series-lower Gedinnian Stage, NW Spain.

Diagnosis. (Translated from Le Hérissé, 1989). "Acritarchs of the genus *Duvernaysphaera* are characterised by a double layered wall; the internal layer, relatively thick, delineates the central wall of lenticular form with a circular outline with, at the equator, a ring of 9 to 16 radiating processes, short (p [process length] = $^1/_7$ d [vesicle diameter]), with equal length and equidistant; the width of processes varies from 1 to 2.5 μm; the processes are cylindrical, hollow and communicate freely with the central cavity. The surface of the central body is smooth or granulate. The external wall, thin and transparent, envelops the central body and processes; it is depressed and touches the internal wall. The mode of excystment, visible on the more flattened face, is represented by a simple slit, which crosses the central body and coincides with a tear in the external wall."

Description. Inner body circular, laevigate or granulate. In the centre of the inner body there may be an irregularly shaped thickened area, across which a linear fold may pass. Processes hollow, tapering, simple, open to vesicle interior. Outer membrane covers both vesicle and processes, sometimes extending beyond the processes suggesting that it is not firmly attached. Excystment mechanism not observed.

Dimensions. V=15-23μm, PL=6-8μm, PN=14-16 (10 specimens measured).

Remarks. The excystment mechanism of this species has been reported as simple split (Le Hérissé 1989, fig. 11). In examples recovered in this study no excystment structures have been recorded, linear folds have, however, been observed in the centre of the inner body at approximately the same position as the splits reported by Le Hérissé (1989).

Occurrence. San Pedro and Furada formations, Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer 1964b, 1966b, 1969b; Pöthé de Baldis 1974a); Tuscarora and Rose Hill formations, upper Llandovery Series, Pennsylvania (Cramer 1969b); Silurian, Belgium (Martin 1967, 1969); Devonian, NW Africa (Maglore 1968, Jardiné & Yapaudjian 1968); Ross Brook Formation, lower-middle Llandovery Series, Nova Scotia (Cramer 1970b); Upper Silurian, Argentina (Pöthé de Baldis 1971); Wenlock Series, subsurface material, Portuguese Guinea; subsurface, Saudi Arabia; Alger and Clemville formations, upper Llandovery Series, Quebec, Canada; middle Llandovery-Prídolí series, Florida subsurface; Osgood Formation, upper Llandovery, Indiana, Kentucky and Ohio; Plum Creek Formation, upper Llandovery, Kentucky; Quoddy Formation, upper Llandovery Series; Red Mountain Formation, lower-upper Llandovery, Alabama and Georgia; Rose Hill Formation, upper Llandovery, Pennsylvania and Virginia; Ross Brook Formation, Llandovery Series; Waldron Formation, upper Wenlock Series, Indiana and Tennessee (Cramer & Diez 1972); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Llandovery-Ludlow series, Algeria (Jardiné *et al.* 1974); Los Espejos Formation, Wenlock Series, Argentina (Pöthé de Baldis 1975); Silurian, Podolia (Kiryanov 1978); Upper Visby-Högklint formations, lower Wenlock Series, Gotland (Cramer *et al.* 1979); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); middle-upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); upper Llandovery- Ludlow series (Ludfordian Stage), Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone and Lower Elton formation, Pitch Coppice Quarry and Goggin Road; common in the Middle Elton Formation, Goggin Road. Known range: lower Llandovery Series-lower Gedinnian Stage.

Genus **Melikeriopalla** Tappan & Loeblich Jr. 1971

Type Species. By original designation, *Melikeriopalla amydra* Tappan & Loeblich Jr. 1971; from the Waldron Formation, Wenlock Series, Jennings County, Indiana.

Diagnosis. The diagnosis of Tappan & Loeblich Jr. (1971) is partly based on reticulo-cristate specimens (Tappan & Loeblich Jr. 1971, pl. 6, figs 1-2) which were incorrectly assigned to the type species *M. amydra.* The diagnosis is, therefore, not followed herein and without re-examination of the type material no emended diagnosis can be proposed.

(Tappan & Loeblich Jr. 1971, p. 396). "Vesicle spherical to subspherical; surface of vesicle cristate, divided into small, irregular, polygonal fields by low, apparently solid ridges or crests; fields may be secondarily subdivided by low and discontinuous ridges; wall thin, ornamented with small, scattered granules and short, discontinuous micro-ridges within the fields; excystment by simple rupture of the vesicle."

Remarks. The genus *Melikeriopalla* was considered a junior synonym of *Dictyotidium* by Eisenack *et al.* (1979a, p. 155), but was retained by Colbath (1983, 1987). The diagnosis of Tappan & Loeblich Jr. (1971) is unusable as it is partly based on incorrectly identified specimens, which do not belong within the type species (see below). *Melikeriopalla* is very similar to *Orygmahapsis* Colbath 1987, which may prove to be a junior synonym; the two are retained, however, pending re-examination of the type material.

Melikeriopalla amydra Tappan & Loeblich Jr. 1971 Pl. 2, figs 3, 11-12; Pl. 10, figs 1-4.

p.	1971	*Melikeriopalla amydra* n. sp.; Tappan & Loeblich Jr., p. 396, 398, pl. 6, figs 3, ?4 (only).
	1977	*amydrum* (Tappan et Loeblich 1971) *Dictyotidium*; Diez & Cramer, p. 3 (no fig.) (invalid combination).
	1979a	*Dictyotidium amydrum* (Tappan & Loeblich 1971); Eisenack *et al.*, p. 157-158.
	1990	*Dictyotidium amydrum* (Tappan & Loeblich Jr. 1971) Eisenack *et al.* 1979; Fensome *et al.*, p. 193 (no fig.).

Holotype. Tappan & Loeblich Jr. 1971, pl. 6, fig. 3; Waldron Formation, Wenlock Series, Jennings County, Indiana.

Diagnosis. The diagnosis of Tappan & Loeblich Jr. (1971) is partly based on reticulo-cristate specimens (Tappan & Loeblich Jr. 1971, pl. 6, figs 1-2) which were incorrectly assigned to the type species *M. amydra.* The diagnosis is, therefore, not followed herein and without examination of the type material, to ascertain the wall structure, no emended diagnosis can be proposed.

(Tappan & Loeblich Jr. 1971, p. 396, 398). "Vesicle spherical to subspherical; surface of vesicle reticulocristate, divided by low, apparently solid ridges into small, irregular, polygonal fields, four to six sided and commonly 2-3μ across. Commonly the fields are subdivided by low and discontinuous ridges that give the periphery a serrate appearance. Wall thin, about 1μ in thickness; surface sculpture cristate, with small scattered granules and discontinuous micro-ridges within the fields; excystment by a simple rupture of the vesicle."

Description. Vesicle spherical to ellipsoidal, moderately thick walled; surface divided into subpolygonal or subspherical fields by low ridges of uniform height and irregular width. The centre of each field appears to posses a small node (0.5-1μm diameter), or small pore which passes partly though the vesicle wall. The development of pores in the vesicle wall is variable; specimens with no pores and specimens with numerous pore canals can be found. Small, thin walled examples commonly lack larger pore canals; specimens with thicker walls can possess a few pore canals and examples with very thick vesicles have pore canals in the centre of every field, between which a fine, secondary porous structure is developed. Excystment mechanism not observed.

Dimensions. V=26-74μm, F=1.5-4μm, W=1-4.5μm (11 specimens measured).

Remarks. The reticulo-cristate specimens illustrated by Tappan & Loeblich Jr. (1971, pl. 6, figs 1-2), which are herein excluded from *M. amydra*, lack the central node structure present on the holotype and possess fields with scattered granulations that are subdivided by low, discontinuous ridges similar to *Dictyotidium venulosum* Playford in Playford & Dring 1981. Specimens assigned to *M. amydra* herein show a range of vesicle size, wall thickness and pore canal development. Smaller, thinner walled examples commonly lack pore canals below the central node, though it is impossible to ascertain whether a finer structure of pores is present. Some specimens have thicker walls but show only the development of pore canals beneath a few of the nodes. Finally, larger thicker walled specimens may have a pore canal beneath every node and may also show a fine porous structure between the nodes (Pl. 2, fig. 3); this is similar to the wall structure present in some tasmanitids. These thick walled specimens could be assigned to *Orygmahapsis fistulosa* (Colbath 1983) Colbath 1987.

O. fistulosa was distinguished from *M. amydra* by the presence of a thicker vesicle wall, lack of secondary ridges subdividing the fields, and later, by the occurrence of tubular canals (Colbath 1983, 1987). A personal communication was also cited from G. D. Wood, who, having examined numerous specimens of *M. amydra* from the Wenlock Series of the USA, stated that no pseudopores were present (Colbath 1987, p. 65); the holotype was not re-examined. Confusion has arisen, however, as Colbath (1983, p. 259; 1987, p. 65) incorrectly stated that *M. amydra* has a reticulo-cristate ornament, referring to those specimens, now excluded, illustrated by scanning electron microphotographs (see above). Taking into account the variation of this taxon, *O. fistulosa* is, in effect, treated as a junior synonym of *M. amydra* herein, though no formal synonymy is proposed.

The transfer of this taxon to *Dictyotidium* was attributed to Diez & Cramer 1977 by Dorning (1981a). The combination was, however, not validly published as the basionym was not fully referenced.

Occurrence. (*M. amydra* and *O. fistulosa*). Waldron Formation, Wenlock Series, Tunnel Mill, Indiana (Tappan & Loeblich Jr. 1971, as *M. amydra*); Much Wenlock Limestone Formation-Elton Group, upper Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a, as *D. amydrum*); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983, as *D. amydrum*);

Bainbridge Formation, Přídolí Series, Missouri; Ludfordian Stage, Ludlow Series, Ludlow (Colbath 1983, 1987, as *O. fistulosa*); Much Wenlock Limestone Formation (Pitch Coppice Quarry); Much Wenlock Limestone-Middle Elton formations, Wenlock-Ludlow series, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock-Přídolí series.

Genus **Polyedrixium** Deunff 1954a ex Deunff 1961 emend. Deunff 1971

1969 *Senzeillea*; Stockmans & Willière, p. 40.
.1970 *Crameria* gen. nov.; Lister, p. 61-62.

Type Species. By original designation, *Polyedrixium deflandrei* Deunff 1954a, p. 1065, fig. 8; from the Devonian of Ontario (a *nomen nudum*, validly published by Deunff 1961, p. 216).

Diagnosis. (Deunff 1971, p. 17 translation by Eisenack *et al.* 1976, p. 571). "Organic microplanktont [*sic*] more or less transparent, supple and stainable of which the colour varies according to the degree of fossilization. The vesicle is polyhedral with faces that are generally made up by layers of organic material of uneven thickness, they are often bent inwards so delimiting a chamber of variable volume. The edges of the faces may or may not be provided with border membranes (1); these bear often an ornamentation of more or less strongly developed crenulations (2); these are frequently hollow or open distally. The angles of the vesicle continue in the form of angular floral ornaments (3) or are digitate, which communicate, in the same manner as the crenulate expansions, with the body cavity. The total diameter falls between 10 and 150 μ."

Remarks. The genus *Senzeillea* Stockmans & Willière 1969 is considered to be a junior synonym, by implication, of *Polyedrixium*, as its type species is regarded as a junior synonym of *Polyedrixium pharaone* Deunff 1954a ex Deunff 1961 (see Lu Lichang & Wicander 1988, p. 127, Fensome *et al.*, p. 452). It has been recognised that *Eisenackidium* and *Crameria* are morphologically akin to *Polyedrixium*, though it was felt by Playford (1977, p. 33) that the genera could only be reassigned after the re-examination of the type species of *Eisenackidium*, which he believed to be senior to *Crameria*. He questioned the true nature of the nerve like structures found in species of *Eisenackidium*, which are also found in species of *Polyedrixium*; for example the nerve-like structures of *P. pharaone* result from the junction of flap-like elements (Playford 1977, p. 35).

The type species of *Crameria*, *Crameria duplex* (Cramer 1964b) Lister 1970 is morphologically similar to *P. pharaone*. The holotype of *C. duplex* appears to lack between process membranes and the diagnosis (Cramer 1964b, p. 287) states that there are "no crests between the processes". The holotype of *P. pharaone* from the Devonian of Canada (Deunff 1954a, fig. 13) also appears to lack membranes between the processes. Membranes were, however, clearly illustrated by Playford (1977, e.g. pl. 17, fig. 7), although in some forms they are highly reduced (e.g. Playford 1977, pl. 17, fig. 4). It appears that the population of *P. pharaone* has a range of morphologies from examples with low, or non-existent, membranes, to specimens where the membranes are clearly obvious. Some of the specimens illustrated as ?*Baltisphaeridium duplex* n. sp. from the Devonian of NW Spain (Cramer 1964b, pl. 5, figs 1-2 only), including the holotype, are considered to represent the membrane free end of this spectrum. Thus *Crameria duplex* is considered to be a junior synonym of *P. pharaone*. This proposed synonymy is further strengthened by the remarks of Eisenack *et al.* (1973, p. 434), who state that "there is a tendency for the development of crestlike interconnections on the central body between the 'ribs' of the processes. This tendency is quite pronounced in *E. duplex* and *E. carminae*."

Muraticavea Wicander 1974, is also morphologically similar to some species of *Polyedrixium*, and the type species of this genus was considered to be a possible junior synonym of *Polyedrixium robustum* Deunff 1971 by Eisenack *et al.* (1979b, p. 49). Originally, *Muraticavea* was separated from *Polyedrixium* by the lack of serrated edges and projections from the vesicle (Wicander 1974, p. 14). Although *Muraticavea* is still considered separate, one of the taxa assigned to it, *Muraticavea wenlockia*, has already been transferred to *Polyedrixium* (see below).

Polyedrixium wenlockium (Dorning 1981a) Le Hérissé 1989 Pl. 2, fig. 13.

	1981a	*Melikeriopalla wenlockia* n. sp.; Dorning, p. 181, 202, table 1 (no fig.) (*nomen nudum*).
v*	1981a	*Muraticavea wenlockia* n. sp.; Dorning, p. 195-196, pl. 2, figs 10, 11.
	1983	*Melikeriopalla wenlockia* Dorning 1981; Dorning, p. 33 (no fig.) (*nomen nudum*)
	1989	*Polyedrixium wenlockium* (Dorning 1981) n. comb.; Le Hérissé, p. 181, pl. 20, figs 13-16.
	1990	*Muraticavea wenlockia* Dorning 1981; Fensome *et al.*, p. 359 (no fig.).

Holotype. Dorning 1981a, pl. 2, fig. 10; LE4K, F35/0, MPK 2921; Lower Elton Formation, Ludlow Series, Ledbury Hill, Herefordshire (SO 716 384).

Diagnosis. (Dorning 1981a, p. 195). "Vesicle subpolygonal, 40-80 μm across, wall laevigate; flanges 18-22 μm long, 4-6 μm high, laevigate, divide the vesicle into polygonal areas up to 25 μm across. Overall diameter 50-90 μm. Excystment method not observed."

Description. Vesicle poorly defined, polygonal to subpolygonal, laevigate. The surface of the vesicle is divided into large polygonal fields by low membranes. On some specimens, under transmitted light a membrane-vesicle contact may be distinguished, though this is not always possible. Excystment mechanism not observed.

Dimensions. V=42-78μm, M=2-6μm, F=25-49μm (10 specimens measured).

Remarks. This species was listed as *Melikeriopalla wenlockia* by Dorning (1981a, p. 181, 202, table 1 no. 87; 1983, p. 33). The transfer of this taxon to *Polyedrixium* by Le Hérissé (1989, p. 181) was based on its polygonal vesicle shape.

Occurrence. Much Wenlock Limestone-Lower Elton formation, upper Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983, listed as *Melikeriopalla wenlockia*, illustrated as *Muraticavea wenlockia*); Mulde Formation, uppermost Wenlock Series, Gotland (Le Hérissé 1989); Silurian, Argentina

(Rubinstein 1993); Much Wenlock Limestone-Lower Elton formation, Pitch Coppice Quarry and Goggin Road. Known Range: upper Homerian-lower Gorstian stages.

Genus **Pterospermella** Eisenack 1972

Type species. By original designation, *Pterospermopsis aureolata* Cookson & Eisenack 1958, p. 49, pl. 9, figs 10-12; Meadow Station Bore No. 9, Birdrong Formation (? Grierson Member), Lower Cretaceous (Upper Neocomian or Lower Aptian),Western Australia.

Diagnosis. (Eisenack 1972, p. 597-In German).

Remarks. The genus *Pterospermella* was described by Eisenack (1972), who transferred to it all the species of *Pterospermopsis* W.Wetzel 1952 except the holotype, which was already considered a damaged chorate dinoflagellate cyst (Morgenroth 1968, see also Fensome *et al.* 1990, p. 429 and Colbath & Grenfell 1995, p. 293). Sarjeant (1976, 1984) and Le Hérissé (1989) have both considered *Pterospermopsis* to be senior over *Pterospermella.*

Pterospermella foveolata Lister ex Dorning 1981a Pl. 2, fig. 19.

	.1968	*Pterospermopsis martinii* Cramer; Cramer & Diez, p. 574, pl. 21, figs 82-87.
	1973a	*Pterospermopsis* cf. *P. martinii* Cramer and Cramer 1968; Thusu, p. 804, pl. 106, fig. 15.
	1974	*Pterospermopsis foveolata*; Hill, p. 13 (no fig.) (*nomen nudum*).
v*	1981a	*Pterospermella foveolata* Lister n. sp.; Dorning, p. 197, pl. 3, fig. 18.
	.1984	*Pterospermella martinii* Cramer 1967; Le Hérissé, p. 230-231, pl. 2, figs 11-12, pl. 3, figs 1,4.
	.1989	*Pterospermopsis martinii* Cramer; Le Hérissé, p. 78-79, pl. 4, figs 10-11.
	1990	*Pterospermella foveolata* Dorning 1981; Fensome *et al.*, p. 426 (no fig.).

Holotype. Dorning 1981a, pl. 3, fig. 18; WG46K, L37/3, MPK 2944; from the Upper Flaxly Beds, Ludlow Series, Wood Green, May Hill, Gloucestershire (SO 695 165).

Diagnosis. (Dorning 1981a, p. 197). "Vesicle subspherical, 20-25 µm across, granulate; one equatorial flange, thin, laevigate 10-15 µm high, often with numerous radial folds near the vesicle margin. Excystment by straight split in the vesicle wall."

Description. Vesicle spherical or ellipsoidal, thicker walled than the equatorial membrane which surrounds it. The vesicle surface appears reticulate under transmitted light, foveolate with a SEM. Under transmitted light the apparent size of the ornament is related to position on the vesicle, with the reticulae in the centre of the vesicle often appearing considerably smaller than those around the rim. The membrane is very thin, generally poorly preserved and often has radial folds. Excystment by rupture of the vesicle wall, with thickened lips.

Dimensions. V=19-34µm, FL=12-21µm, W=0.75-1µm (10 specimens measured).

Remarks. This species was considered a junior synonym of *Pterospermopsis* (now *Pterospermella*) *martinii* Cramer 1966a by Le Hérissé (1989, p. 78). Those forms illustrated as *P. martinii* by Le Hérissé (1984, 1989) are considered here to belong in *P. foveolata*, as the original diagnosis and remarks of *P. martinii* state that the central body and membrane are of equal thickness and unornamented. *Pterospermella reticulata* Loeblich Jr. & Wicander 1976 was also considered a junior synonym of *P. martinii* by Le Hérissé (1989, p. 78); this synonymy is rejected as *P. reticulata* also has an ornamented vesicle. *P. reticulata* and *P. foveolata* may be synonymous but the two taxa are retained, as *P. reticulata* is much larger than *P. foveolata* (total diameter = 56-66µm vs' 31-55µm). If the two species were synonymous, *P. reticulata* would be the senior name as *P. foveolata* (based on an unpublished thesis taxon of Lister) was not validly published until 1981.

Occurrence. Ludlow Series, Silurian, León, NW Spain (Cramer & Diez 1968, as *P. martinii*); upper Ludlow Series, N Spain (Cramer 1969b, as *P. martinii*); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a, as *P.* cf. *martinii*); Hughley Shales-Buildwas Formation, upper Llandovery-Wenlock series, Welsh Borderland (Hill 1974); Ludlow Series, Algeria (Jardiné *et al.* 1974); Hughley Shales-Bringewood Group, upper Llandovery-Ludlow Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-Wenlock series, Gotland (Le Hérissé 1984, as *P. martinii*); upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); lower Silurian, Ringerike, Norway (Smelror 1987); Lower Visby-Hemse formations, upper Llandovery-lower Ludlow series, Gotland (Le Hérissé 1989, as *P. martinii*); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: upper Llandovery-Ludlow series.

Pterospermella sp. A Pl. 2, fig. 17.

Description. Vesicle spherical, laevigate, slightly thicker walled than the surrounding equatorial membrane which is very thin and possesses numerous radial folds. Excystment mechanism not observed.

Dimensions. V=12-18µm, FL=5-12µm (10 specimens measured).

Remarks. Overall size and vesicle ornamentation separates this taxon from *P. foveolata*, which is larger and has a thicker, ornamented, vesicle. Comparisons with the probably related modern genus *Pterosperma* (Parke *et al.*) may indicate that those forms assigned to *Pterospermella* sp. A may well be small examples of *P. foveolata*. The life cycle of *Pterosperma*, as illustrated by Tappan (1980, fig. 10.7), shows that the size of the phycoma increases with maturity and can have a range of sizes between 10µm and 175µm (Tappan 1980, p. 808).

Occurrence. Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road.

Pterospermella sp. B Pl. 2, figs 15-16.

Description. Vesicle spherical to ellipsoidal, thicker walled than membrane, laevigate or granulate, often possessing a linear fold across the centre of the vesicle; vesicle surrounded by thinner membrane. The membrane is attached to the equator of the vesicle, though the overall morphology is rarely symmetrical and the vesicle is commonly displaced to one side. Excystment by unornamented rupture.

Dimensions. V=15-20μm, T=21-30μm, W=0.25-0.7μm (15 specimens measured).

Remarks. This taxon is similar to *Pterospermella pertonense* Dorning 1981a, of which it may be a junior synonym. The topotype material of *P. pertonense* appears to show a vesicle completely encompassed by a thin membranous sack; *Pterospermella* sp. B has a vesicle surrounded by an equatorial flange.

Occurrence. Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road; absent from the remaining Lower Elton Formation, with scarce occurrences in the Middle Elton Formation, Goggin Road.

Genus **Quadratitum** Cramer 1964b emend. Cramer & Diez 1972

1976 *Phoenisphaeridium* Deunff in Eisenack *et al.*, p. 655 (*nomen nudum*).

Type Species. By original designation, *Quadratitum fantasticum* Cramer 1964b, p. 334, pl. 14, figs 3-4, text-figs 37:1-3; from the San Pedro Formation, Ludlow Series-lower Gedinnian Stage, Oblanca de Luna, NW Spain.

Diagnosis. (Cramer & Diez 1972, p. 170). "Complex acritarch, consisting of inner and outer membrane (the ectoderm and periderm respectively). In undamaged condition, the periderm is spherical to ellipsoidal. It is attached to the square central body, at the four angles. The periderm [*sic* = ectoderm in Eisenack *et al.* 1976, p. 653] is psilate to slightly inflated, pillow-shaped, rectangular to square, and is attached at its corners to the periderm. The collapse of the body cavity may cause a consistent set of folds to form that are more or less similar to the letter H squeezed at the place of the horizontal bar. The corners of the central body may be slightly drawn-out and may form short productions; these productions are hollow at the proximal part and their cavity is continuous with the central body cavity. Whether the body cavity is open at the attachment points of the two membranes and thus communicates freely with the outside, could not be determined. No preferential patterns of splitting, nor pylome structures were found."

Remarks. The emended diagnosis of Cramer & Diez (1972, p. 170) incorrectly cites the shape of the central body (ectoderm) as that of the periderm (see above). The nature of the thin membrane was originally used to distinguish this genus from *Duvernaysphaera*. It was stated that the membrane encompassed the whole inner vesicle in *Quadratitum*, whereas, in *Duvernaysphaera*, the periderm "surrounds no more than a portion of one hemisphere of the central body" (Cramer & Diez 1972, p. 170).

This appears to be a reference to the emended diagnosis of Deunff (1964), which stated that the membrane of *Duvernaysphaera* was equatorial (see *Duvernaysphaera*-Remarks above).

In both genera, however, the membrane surrounds the inner vesicle. Due to the uncertainty surrounding the generic diagnosis of *Duvernaysphaera*, those forms recovered in the present study with square or rectangular inner vesicles have been assigned to *Quadratitum*, which may prove, after further work, to be a junior synonym of *Duvernaysphaera*.

The genus *Veliferites* Brito 1966 ex Brito 1967 has been regarded as a junior synonym of *Duvernaysphaera* (see Fensome *et al.* 1990, p. 509) and may also be considered synonymous with *Quadratitum*. The diagnosis of *Veliferites* refers to the vesicle having a transparent, equatorial membrane, whereas both *Duvernaysphaera* and *Quadratitum* have membranes that are not restricted to the equator. Until the type species of *Veliferites* is re-examined and the true nature of the outer wall/membrane established, no definite synonymy can be proposed.

Quadratitum fantasticum Cramer 1964b Pl. 2, fig. 18.

1964b *Quadratitum fantasticum*; Cramer, p. 334, pl. 14, figs 3-4, text-figs 37:1-3.

1975 *Veliferites jachalensis* n. sp; Pöthé de Baldis, 496, pl. 4, fig. 6, 8-9.

1976 *Phoenisphaeridium interpositum* Deunff; Eisenack *et al.*, p. 655 (*nomen nudum*).

1976 *Phoenisphaeridium involutum* Deunff; Eisenack *et al.*, p. 655 (*nomen nudum*).

1990 *Quadratitum fantasticum* Cramer 1964b; Fensome *et al.*, p. 437 (no fig.).

Holotype. Cramer 1964b, pl. 14, fig. 3; sample 1141; San Pedro Formation, Ludlow Series-lower Gedinnian Stage, Oblanca de Luna, NW Spain.

Diagnosis. (Cramer 1964b, p. 334). "Central body moderately thin and moderately transparent, psilate at 1200 x magnification. The central body has a square outline. Enveloping membrane very thin and transparent, smooth, attached at the corners of the central body. Membrane usually damaged."

Description. Vesicle laevigate, square to rectangular, thicker walled than outer body, rarely extended at the corners to form short processes. The vesicle is totally encompassed by a thin, spherical, almost transparent, apparently laevigate, outer body; often the only remnants of the outer body are those sections attached to the corners of the inner vesicle. Excystment mechanism not observed.

Dimensions. V=11-18µm, T=25-30µm (10 specimens measured).

Remarks. The taxa *P. interpositum* and *P. involutum* were included in synonymy with *Q. fantasticum* by Eisenack *et al.* (1976); they are both *nomina nuda*, being published in a preprint distributed by the CIMP (Eisenack *et al.* 1976, p. 655). *Duvernaysphaera oa* Loeblich Jr. & Wicander 1976 and *Quadratitum ibericum* Pöthé de Baldis 1981 were included in synonymy by Le Hérissé (1989, p. 186). The diagnosis of *D. oa* states that the vesicle is surrounded by a thin, equatorial flange. This would exclude it from *Quadratitum*, and also *Duvernaysphaera*, and the author believes that it should be excluded from synonymy until the holotype has been re-examined and the true nature of the membrane established. *Q. ibericum* is also not included, as the corners of the vesicle are extended into quite long processes, whereas the processes of *Q. fantasticum* are very short, if developed at all.

Occurrence. Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer 1964b, 1966b; Cramer *et al.* 1976); Tuscarora and Rose Hill formations, upper Llandovery Series, Pennsylvania (Cramer 1969b); Devonian, Tunisia (Deunff 1966); Devonian, Algeria (Jardiné & Yapaudjian 1968); Silurian, Belgium (Martin 1967, 1969); Ludlow Series, France (Deunff *et al.* 1971); Llandovery-Prídolí series, Florida borehole material; Osgood Formation, upper Llandovery Series, Kentucky; Red Mountain Formation, lower-upper Llandovery Series, Georgia and Alabama; Rose Hill Formation, upper Llandovery Series, Pennsylvania and Virginia; St. Clair Formation, upper Llandovery-lower Ludlow Series, Missouri; Waldron Formation, upper Wenlock Series, Kentucky (Cramer & Diez 1972); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Acacus Formation, Wenlock-Ludlow series, Libya (Richardson & Ioannides 1973); Lower Elton-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Ludlow Series-Gedinnian Stage, Algeria (Jardiné *et al.* 1974); Ludlow Series, Bolivia (Cramer, Diez & Cuerda 1974); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1975, 1981); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-Ludlow (? Prídolí) series (Hamra Formation), Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: lower Llandovery Series-Gedinnian Stage.

Genus **Tasmanites** Newton 1875

Pl. 8, fig. 9.

Type species. By original designation, *Tasmanites punctatus* Newton 1875, p. 337, pl. 10, figs 2-9; Permian, Mersey River, Tasmania.

Original Discussion. (Newton 1875, p. 341; from Eisenack *et al.* 1979b, p. 231). "When the separated discs are viewed by reflected light, they appear as more or less circular bodies, somewhat thickened towards the circumference, many of them having their surfaces raised into irregular folds....The more perfect discs are seen to be surrounded by a double contour line-the optical expression of the fact that these discs are really thick-walled sacs. The saccular character is best seen in transverse section or when the sac is broken. A closer examination enables one to see that the walls of these sacs are not homogeneous. Numerous dots are scattered over the surface, which become somewhat elongated towards the edges of the disc. When examined with a power of about 250 diameters, the dots can be resolved into minute circles about one three-thousandth of an inch in diameter with a still smaller dot in the centre. These structures are best seen in the discs of the White Coal. It may be thought that these structures are comparable to the granules shown on the surface of some of the macrospores of *Flemingites*; but the study of transverse sections shows at once that these dots are not mere surface markings, for they can be distinctly traced as minute lines (tubes?) passing from the outer to the inner surface.(...), but owing to the section not being in quite the same plane as the lines, they do not appear to extend quite through. In addition to the fine lines, the walls of the sacs exhibit obscure longitudinal markings, which give them a laminated appearance....The discs vary in diameter....from about one-eightieth to one-fiftieth of an inch. Mr. MacNaughton speaks of a thin outer crust of these discs, which may be seen when they are ruptured. I have examined all my preparations, both sections and separated discs, in order to distinguish this outer coat, but have been unable to do so. One easily recognizes in transverse sections that the walls of the sacs vary much as regards thickness: and...some may be seen to be much more transparent than the rest; but I have failed to see any real difference between the thicker and the thinner sacs, or to find them in anything like the relation of an inner and outer coat. Nearly all the sacs are so compressed that their walls are brought into contact; but occasionally on may be found similar to containing a quantity of black material differing in appearance from the surrounding matrix and which appears to consist of minute rounded particles about three-thousandth of an inch in diameter."

Diagnosis. (Eisenack 1958a, p. 2; translation by Eisenack *et al.* 1979b, p. 231-232). "Hollow spherical, generally comparatively thick-walled and of a very resistant, yellowish to dark red-brown hyaline organic substance consisting of organic remains which often are preserved in a disc-shaped compressed state or also irregularly folded. Wall with more or less numerous pores which rarely penetrate the entire wall, but often either end blindly in the thick wall from the outside or from the inside. Pylome present, however usually uncommon. The wall pores are not always visible in each specimen of a species; it is essential that they should occur in the majority of the species."

Remarks. A list of taxa that have been considered synonymous with this genus is given in Fensome *et al.* (1990, p. 471). The diagnosis of Eisenack (1958a, p. 2) has been considered an emendation of the genus by some authors, though others consider that it was not intended as such (see Fensome *et al.*, p. 471).

Group **ACRITARCHA** Evitt 1963

Genus **Ammonidium** Lister 1970

Type species. By original designation, *Baltisphaeridium microcladum* Downie 1963, p. 645, pl. 92, fig. 6; sample BS/3, Wenlock Shales (= Buildwas Formation), Wenlock Series, Harley Brook, Wenlock Edge, Shropshire.

Diagnosis. (Lister 1970, p. 48). "Vesicle hollow, spherical to ellipsoidal, single-walled; vesicle wall smooth or sculptured. Processes numerous, evenly spaced, more or less rigid, hollow, tapering, communicating freely with the vesicle cavity; distally the processes have equifurcate terminations. Excystment by cryptosuture, apical or near-equatorial."

Remarks. Species of *Multiplicisphaeridium* differ in having processes that display a great variation in style of branching; species of *Ammonidium* have branches that are restricted to the very distal process extremities.

Ammonidium waldronense (Tappan & Loeblich Jr. 1971) Dorning 1981a Pl. 2, fig. 20; Pl. 10, fig. 5.

1970 *Ammonidium microcladum* (Downie 1963) comb. nov.; Lister, p. 49-50, pl. 1, figs 1-5, 7-11, text-figs 17a-d.

1971 *Caiacorymbifer waldronensis* n. sp.; Tappan & Loeblich Jr., p. 393, pl. 3, figs 1-8.

1973 *Multiplicisphaeridium waldronensis* (Tappan & Loeblich 1971); Eisenack *et al.*, p. 487-488.

1981a *Ammonidium waldronense* n. comb.; Dorning, p. 183 (no fig.).

.1989 *Ammonidium microcladum* (Downie, 1963); Le Hérissé, p. 82-84, pl. 5, figs 7-13.

1990 *Ammonidium waldronense* (Tappan & Loeblich Jr. 1971) Dorning 1981; Fensome *et al.*, p. 60 (no fig.).

Holotype. Tappan & Loeblich Jr. 1971, pl. 3, fig. 1, isotypes pl. 3, figs 2-8; holotype: 69-63(8)31.9-96.1, isotypes: 69-63(13)31.7-109.3, 69-63(13)46.6-98, 69-63(SEM 2966-2967), 69-63(SEM 2732-2733, 2744); from Waldron Formation, upper Wenlock Series, Tunnel Mill, Indiana.

Diagnosis. (Tappan & Loeblich Jr. 1971). "Vesicle ovate to subcircular in outline, ornamented with numerous processes, more than 40 visible from one side; processes hollow and communicating freely with the vesicle interior, 5-10μ in length, rather rigid, up to about 2μ in diameter at the base, tapering slowly to a furcate tip. With the light microscope the true nature of the termination is barely indicated, but with the scanning electron microscope the distal termination is shown to be a division into six small aculeate branches up to 0.35μ in length arranged in a rosette. Wall thin, slightly less than 1μ in thickness; both vesicle and process walls laevigate; excystment by a simple rupture and splitting of the vesicle wall."

Description. Vesicle single walled, spherical to ellipsoidal, foveolate. Processes numerous, evenly spaced, hollow, open to the vesicle interior, rigid or slightly flexuous, smooth, narrow, slightly tapering with closed tips and expanded bases. Tips poorly preserved, bifurcate or with a rosette arrangement of up to six small spines which do not appear to be secondary branched. Excystment by unornamented rupture.

Dimensions. V=20-32μm, PL=7.5-13μm, PØb=1-3μm (10 specimens measured).

Remarks. Although the diagnosis of Tappan & Loeblich Jr. (1971) states that the vesicle of *A. waldronense* is laevigate, the holotype and two isotypes, illustrated by transmitted light microphotographs (Tappan & Loeblich Jr. 1971, pl. 3, figs 1-3), clearly have ornamented vesicles. The two isotypes illustrated with scanning electron microphotographs have laevigate vesicles and probably represent a separate species.

A. waldronense was considered a junior synonym of *A. microcladum* by Le Hérissé (1989, p. 82). After examining the holotype of *A. microcladum* (Downie 1963, pl. 92, fig. 6) it is clear that *A. microcladum* and *A. waldronense* are two very distinct taxa. The processes of *A. microcladum* have a much more columnar aspect, with the tips being more complexly branched; the vesicle of *A. microcladum* appears faintly ornamented, but lacks the distinct foveolae of *A. waldronense*. Those specimens figured as *A. microcladum* by Lister (1970) and Le Hérissé (1989) clearly belong in *A. waldronense*.

An intraspecific variation was distinguished by Le Hérissé (1989, p. 83), with two extremes:

1.) Forms with small vesicles and more numerous, narrow, shorter processes.

2.) Forms with larger vesicles and fewer, wider, longer processes with longer branches.

This intraspecific variation was also reported to be apparent in *Salopidium granuliferum* and *Gracilisphaeridium encantador* Cramer 1970a by Le Hérissé (1989, p. 82). The taxa *S. granuliferum* and *G. encantador* closely resemble *A. waldronense* and the three taxa are distinguished from each other by the nature of their process terminations. *S. granuliferum* has simple, unbranched processes, *A. waldronense* has a variable number of branches arranged in a rosette and *G. encantador* has a rosette of branches which are joined together, forming a series of loops.

Occurrences. Much Wenlock Limestone Formation and Elton Group, Wenlock-Ludlow series, Ludlow and Millichope areas; Elton Group, Ledbury (Lister 1970, as *A. microcladum*); Waldron Formation, upper Wenlock Series, Indiana (Tappan & Loeblich Jr. 1971); Much Wenlock Limestone-Lower Leintwardine formations, Wenlock-Ludlow series, Ludlow (Lister & Downie, 1974, as *A. microcladum*); Coalbrookdale Formation-Elton Group, Wenlock-Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock-Ludlow series.

Ammonidium sp. A — Pl. 2, fig. 21; Pl. 10, figs 6-7.

Description. Vesicle spherical to ellipsoidal, thin walled, foveolate. Processes numerous, short, hollow, open to the vesicle interior and tapering to branched tips. The branches are short and spinose, arranged in a rosette around the tip of the process. In poorly preserved specimens, the process tips appear to be capitate. Excystment mechanism not observed.

Dimensions. V=18-24µm, PL=2-7µm, PØb=0.5-1.5µm (10 specimens measured).

Remarks. This taxon appears nearly identical to *A. waldronense*, but differs in having shorter processes, with less well developed branching at the process tips. *Ammonidium rigidum* var. *ludloviensis* Lister 1970 has a laevigate vesicle and slighlty larger processes bases. *Ammonidium listeri* Smelror 1987, from the early Silurian of Norway, is similar to *Ammonidium* sp. A, but has a laevigate vesicle. *Ammonidium* sp. 1 and *Ammonidium* sp. 2 of Turner *et al.* (1995), from the Coalbrookdale Formation, Wenlock Series, of Shropshire, are also similar, but again differ in having laevigate vesicles.

Occurrence. Middle Elton Formation, Goggin Road. Known range: Middle-Upper Elton formations, Ludlow Series.

Genus **Baltisphaeridium** Eisenack 1958b ex Eisenack 1959 emend. Staplin, Jansonius & Pocock 1965 emend. Eisenack 1969 emend. Eiserhardt 1989

Type Species. By original designation, *Ovum hispidum* var. *longispinosum* Eisenack 1931, p. 110-111, pl. 5, figs 6-17; Ordovician, Baltic erratic. [Holotype lost (Eisenack 1959, p. 194), neotype designated (Eisenack 1959, p. 194, pl. 15, fig. 1; *Baltisphaeridium longispinosum* forma *filifera*), Chasmops-Kalk, Böda, Öland, Sweden.]

Diagnosis. (Eiserhardt 1989, p. 89-90). "1. Features of importance (represented by type material) are: Primary form of the vesicle is spherical with some tendency to polygonality. A multi-layered membrane composition is possible-but not proven. Angular proximal process contact with the vesicle, but tendency to basal expansion is represented. The processes are homomorph, simple, evenly distributed over the vesicle, hollow and distally closed; no communication between processes and central bodies cavity. In typical cases the processes are long and slender, with narrow central lumen and solid base, which seems to be derivated [*sic*] from the process membrane. Process membrane more delicate and transparent than vesicle membrane.

2. Supplemented generic inventory by deducted features: Variation of vesicle geometry tends to two different final stages; these are i) a perfect spherical outline, ii) a vesicle outline of distinct irregular polygonality. Even very thin and transparent vesicle membranes are reliably deducted [*sic*]. If vesicle membrane is developed in this way, the process membrane is reduced analogically [*sic*]. Unsymmetrical process distribution and heteromorphous process outline (i.e. rare bifurcations and variation in process size) are truly within generic bounds. In the course of process multiplying, the reduction of process length seems to be a frequent attendant phenomenon. If developed, membrane ornamentation is a fine one (i.e. microgranulate, -echinate etc.).

3. Features of presumed congenerity are (present state of knowledge):

a) processes with hollow bases,

b) solid processes (if they can considered being derivated [*sic*] from hollow types),

c) hollow processes with initial communication to the vesicle cavity (but only if such perforated base can be declared as being derivated [*sic*] from a proximally closed process type)".

Remarks. The nature of the excystment opening (pylome) separates *Baltisphaeridium* from *Baltisphaerosum* Turner 1984 (rupture). The processes of *Baltisphaeridium* are generally simple; those of *Leptobrachion* and *Cymbosphaeridium* have branched tips; *Eisenackidium* generally has broader based processes, some of which appear to possess a nerve-like structure parallel to their longest axis; *Oppilatala* has hollow processes which do not communicate with the vesicle cavity, however, the vesicle is single walled and the processes are plugged within their length.

Baltisphaeridium muldiensis Le Hérissé 1989 Pl. 2, fig. 22; Pl. 10, figs 8-10.

v. 1970 *Baltisphaeridium* sp. nov; Lister 1970, p. 59, pl. 2, figs 13, ? 15.

1989 *Baltisphaeridium muldiensis* n. sp.; Le Hérissé p. 85, pl. 5, figs 17, 18, pl. 6, figs 1, 2.

Holotype. Le Hérissé 1989, pl. 5, figs 17-18, pl. 6, fig. 2; G662 B1, SGU 7318, P41/3; from the Mulde Formation, Wenlock Series, Bjärges. 1, Gotland.

Diagnosis.(Translated from Le Hérissé 1989, p. 85). "This species of the genus *Baltisphaeridium* is small in size, with a spherical vesicle and thick wall adorned with 30-40 narrow, cylindrical, hollow, transparent processes, the majority of which are simple, though some are branched; the longer the processes the smaller the diameter of the vesicle. The processes have a sharp angular contact with the vesicle and do not communicate with the central cavity; they are neither plugged nor narrowed at the base. Under the SEM the trunk of the processes appear ornamented with longitudinal crests in relief; the surface of the vesicle being densely and irregularly microgranulate."

Description. Vesicle spherical, rarely ellipsoidal, laevigate or microgranulate, moderately thick walled (~1.5μm), commonly bearing small circular structures. Processes thin, cylindrical, hollow, flexuous, tapering from an angular contact with the vesicle; most processes simple, some rarely bifurcate $^1/_4$-$^2/_3$ along their length. Processes can be laevigate, though most have striate bases; on some specimens the striae extend to the process tips. The processes do not communicate with vesicle interior, though they are not plugged. Excystment mechanism not observed.

Dimensions. V=20-26μm, PL=10-21μm, PØb=1-3μm, PN=10-16 (10 specimens measured).

Remarks. This species was described as having 30-40 processes by Le Hérissé (1989), but the holotype (pl. 5, fig. 17-18, pl. 6, fig. 2) has considerably fewer. It may be that Le Hérissé also counted the circular structures on the vesicle surface, which appear to be the bases of broken processes, though these still do not occur in sufficient numbers. These circular structures, which are identical on all specimens, are seen on almost all examples recovered; they have diameters equal to the base of the processes and end with smooth surfaces, not ragged terminations. These structures are similar to those seen on the holotype of *Lanveocia formosa* Deunff 1978, from the Devonian. The specimen, illustrated by scanning electron microscopy (Deunff 1978, pl. 1, figs 1, 4; re-illustrated in Eisenack *et al.* 1979a, p. 273), clearly shows circular structures resulting from the breakage of processes, and also shows one of the processes cleanly breaking away. The diagnosis of the genus *Lanveocia* on the basis of striations on the processes, which are only visible with a SEM, was questioned by Le Hérissé (1989, p. 86), though he did not synonymise *Lanveocia* and *Baltisphaeridium.* He compared *B. muldiensis* to *Baltisphaeridium distentum* Playford 1977, which also has striate processes, and considered that his new species displayed enough features to be included in *Baltisphaeridium.*

Occurrence. Mulde, Klinteberg and Hemse formations (Homerian and lower Gorstian stages), Gotland (Le Hérissé 1989). Much Wenlock Limestone, Lower and Middle Elton formations, Pitch Coppice Quarry and Goggin Road. Known range: Homerian-lower Gorstian stages.

Baltisphaeridium muldiensis var. A Pl. 3, fig. 1.

Description. Vesicle spherical, moderately thick walled (~1.5μm), laevigate under transmitted light, bearing numerous circular structures. Processes long, flexuous, hollow, tapering to simple tips, not communicating with vesicle interior but not obviously plugged; processes appear laevigate under transmitted light. Excystment opening not observed.

Dimensions. V=24μm, PL=30μm, PØb=1.5μm, PN=14 (1 specimen measured).

Remarks. This taxon is separated, and differs, from typical *B. muldiensis* in having much longer processes. It does, however, have the circular structures on the vesicle surface that are characteristic of *B. muldiensis.*

Occurrence. From a single sample in the Lower Elton Formation, Goggin Road.

Baltisphaeridium ? spinatum sp. nov. Pl. 8, figs 21-23; Pl. 12, figs 15-16.

Name. Species name *spinatum*, after the latin *spina* = spine, refering to the spinose nature of the processes.

Holotype. Pl. 8, figs 21-22; GOG5/245-A (1)-R44/2; from the Middle Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle spherical, dark, covered with numerous processes, or where the processes have broken, by thickened, circular hoops. Processes simple, spinose, hollow. Excystment via a pylome (3-5μm diameter).

Dimensions. V=10-13μm, PL=2-6.5μm, W=0.25-1μm (14 specimens measured).

Remarks. Specimens assigned to this species may occur as isolated individuals or clusters (upto four specimens have been found associated together). This species has been provisionally assigned to Baltisphaeridium because it is difficult to ascertain whether the process cavities are open or closed to the vesicle interior. Under transmitted light they appear closed; with a SEM, broken processes suggest some are open and others closed (Pl. 12, fig. 16). Excystment occurs via a small circular pylome, which is typical of species of *Baltisphaeridium.*

Occurrence. First recorded at the Lower/Middle Elton formation boundary at Goggin Road (samples TRENCH4/LE2-A-TRENCH4/ME2-A), and has sparse occurences higher in the Middle Elton Formation.

Baltisphaeridium sp. A Pl. 3, fig. 2.

Description. Vesicle spherical to ellipsoidal, thin or moderately thick walled (0.25-1.5μm), laevigate under transmitted light. Over the vesicle surface are numerous circular structures, which are the bases of processes which have broken off. Processes numerous, hollow, closed to vesicle interior, evenly distributed, laevigate under transmitted light, straight or flexuous, with most tapering to simple tips, though some may bifurcate (either proximally or distally). Excystment mechanism not observed.

Dimensions. V=18-26μm, PL=8-17μm, PØb=0.75-2μm, PN=26-37 (4 specimens measured).

Remarks. The greater number of processes and circular structures present on specimens of this taxon separate it from *B. muldiensis.*

Occurrence. Lower Elton Formation (Pitch Coppice Quarry); lowermost Lower Elton Formation, with rare occurrences in the Middle Elton Formation, Goggin Road.

Genus **Buedingiisphaeridium** Schaarschmidt 1963 emend. Lister 1970 emend. Sarjeant & Stancliffe 1994

1977 *Adara*; Fombella, p. 117. (according to Sarjeant & 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 & 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 μm."

Remarks. The diagnosis given by Staplin *et. al.* (1965, p. 179) was considered to be a translation of the original diagnosis of Schaarschmidt (1963) by Lister (1970, p. 59). Staplin *et al.* (1965) did not indicate this, nor did they indicate that their diagnosis was an emendation. The proposals of Staplin *et al.* (1965) were, however, followed in the emendation of Sarjeant & Stancliffe (1994, p. 24). The relationship between *Buedingiisphaeridium* and *Lophosphaeridium* was briefly discussed by Sarjeant & Stancliffe (1994, p. 32), who retained both genera until the morphology of the type species of *Lophosphaeridium* was more clearly understood.

Buedingiisphaeridium pyramidale Lister 1970 Pl. 3, figs 3-4.

v. 1970 *Buedingiisphaeridium* sp. nov.; Lister, p. 61, pl. 3, fig. 9.
v* 1970 *Buedingiisphaeridium pyramidale* sp. nov.; Lister, p. 61, pl. 3, figs 11-14, text-figs 17h, 20e.
1981a *Tylotopalla pyramidale* n. comb.; Dorning, p. 200 (no fig.).
1990 *Tylotopalla pyramidalis* (Lister 1970) Dorning 1981; Fensome *et al.*, p. 500 (no fig.).

Holotype. Lister 1970, pl. 3, fig. 12; MPK 82; Lower Elton Formation, Ludlow Series, MD12, Millichope, Shropshire.

Diagnosis. (Lister 1970, p. 61). "Vesicle hollow, subspherical, thin-walled; wall unilayered, smooth to faintly striate; numerous hollow pyramidal outgrowths ornament the test; the tips of these outgrowths appear to be solid; their bases are coincident. Excystment is by cryptosuture, apical or near-equatorial. Total dehiscence, resulting in a removal of the operculum, was not seen."

Description. Vesicle very thin, single walled, spherical to ellipsoidal, laevigate. Processes numerous, laevigate, hollow, open to vesicle interior, rarely appearing striate, heteromorphic (conical, rounded, or comprising only the small thickened tips evident on all processes). Within a single specimen all of the different process morphologies can occur, although a single type dominates. Excystment by unornamented rupture.

Dimensions. V=23-36μm, PL=0.2-2.5μm, PØb=0.2-3μm (10 specimens measured).

Remarks. The supposed echinate nature of the processes on the holotype was used to transfer this species to *Tylotopalla* (Dorning 1981a, p. 200). None of the processes on the holotype or the specimens recovered herein are echinate and the transfer of the species to *Tylotopalla* by Dorning (1981a) is rejected and the species retained in *Buedingiisphaeridium.*

The morphology of the late Arenig taxon *Beudingiisphaeridium fuscipetiolatum* (Cramer & Diez 1977, p. 353, pl. 3, figs 1-5, text-fig. 3:1) Hu Yunxu 1986 closely resembles that of *B. pyramidale*. The processes display the same heterogeneity on a single specimen; they are, however, more irregularly distributed and have larger solid tips which extend further down the processes, which can be occasionally completely solid (e.g. Cramer & Diez, pl. 3, fig. 1). The vesicle diameter of *B. fuscipetiolatum* is also larger than *B. pyramidale* (V = 45-55μm vs' 23-36μm this study).

Occurrence. From one horizon at the top of the Lower Elton Formation, Ludlow and Millichope areas (Lister 1970); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Elton Group (upper $^{2}/_{3}$ of biozone L1), Ludlow Series, Welsh Borderland (Dorning 1981a). In the present study the species has been recorded at two distinct levels; the Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road and the uppermost Lower Elton Formation, Goggin Road. Known range: Llandovery-lower Gorstian stages.

Buedingiisphaeridium reticulum sp. nov. Pl. 3, fig. 5.

Name. Species name *reticulum*, from the latin *reticulum*, refering to the reticulate pattern present on the vesicle surface, which is produced by the closely spaced processes.

Holotype. Pl. 3, fig. 5; GOG2/69-A (1)-G45/3; from the Lower Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle spherical to ellipsoidal, thick walled (1-2μm). Processes numerous, solid, covering the entire vesicle to produce a reticulate pattern when viewed from above; heteromorphic on a single specimen, rounded, conical or columnar with flattened tips. Excystment by unornamented rupture.

Dimensions. V=22-39μm, PL=1-3μm, PØb=1.5-2.5μm (9 specimens measured).

Remarks. This species is distinguished from *B. pyramidale* by its thicker vesicle wall and denser arrangement of processes, which can often give a characteristic reticulate appearance.

Occurrence. Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road.

Genus **Carminella** Cramer 1968a

Type Species. By original designation, *Carminella maplewoodensis* Cramer 1968a, p. 67, pl. 1, fig. 7; from the Maplewood Formation, upper Llandovery Series, New York.

Diagnosis. As for type species (see below).

Remarks. This genus is represented by a single species and the generic diagnosis is identical with that of the type species (Cramer 1968a).

Carminella maplewoodensis Cramer 1968a Pl. 3, fig. 6.

1968a *Carminella maplewoodensis* n. sp.; Cramer, p. 67, pl. 1, fig. 7.
1969b *Carminella inaple woodensis* Cramer 1968 [*sic*]; Cramer, p. 75, pl. 9, fig. 3.
1990 *Carminella maplewoodensis* Cramer 1968a; Fensome *et al.* p. 140 (no fig.).

Holotype. Cramer 1968a, pl. 1, fig. 7; slide F-3201; from the Maplewood Formation, upper Llandovery Series, New York.

Diagnosis. (Cramer 1968a, p. 67). "Central body spherical, hollow. Central body wall probably unilayered, thin, and often wrinkled. No openings other than accidental ones were observed. The vesicle wall is covered with numerous processes which are arranged in a fairly regular equidistance pattern. The processes are 0.5 micron or less thick and are of a variable length. The bases of the processes are distinctly broadened, giving the central body wall a goose pimply appearance. The process distribution symmetry is pronouncedly bipolar: at both poles there are bald spots and the equator is the divide of two curvature directions of the processes. The processes point towards the pole nearest to them. The length of the processes decreases gradually from pole to equator. At the poles they are up to 25 microns long; at the equator 5 microns or less. It is likely that the processes are solid; their expanded bases, however, might be hollow. Apart from the processes, the central body wall is psilate. The processes are attached distally to a very thin cylindrical membrane (less than 0.3 micron thick). The axis of this membrane is parallel to the N-S axis of the central body; the membrane is open at both ends, and has a smooth, not crenulate termination. Due to its thinness, the membrane is usually wrinkled and tends to collapse above the poles. The membrane is psilate and is of uniform thickness. The exact way of attachment of the processes to the membrane could not be ascertained with an ordinary light microscope, but it is certain that no such structures as are found at the distal terminations of *Tunisphaeridium* are present."

Description. Vesicle spherical to ellipsoidal, with a single, extremely thin, laevigate wall, which is wrinkled in appearance. At each pole, thin, wiry, solid processes support a fine, wrinkled, membrane that encircles the vesicle. The processes do not expand distally and their length decreases towards the equator from a maximum at the poles; the vesicle between the poles is unornamented. Excystment mechanism not observed.

Dimensions. V=40-49μm, PL=maximum of 20μm (2 specimens observed).

Remarks. Specimens recovered in the present study are smaller than the type material (V = 40-50µm vs' 60-70µm), but do fall within the size range of the hypotypes recovered from the Maplewood Formation by Loeblich Jr. (1970, p. 713; V = 40-55µm).

Riculasphaera fissa Loeblich Jr. & Drugg 1968, from the Lower Devonian, Haragan Formation, Oklahoma, is similar to *C. maplewoodensis*. Both possess encircling, membranous, polar extensions, though in *R. fissa* some of these extensions are bag-like, being nearly completely closed. *R. fissa* also possesses a complete rupture type of excystment opening, which almost divides the vesicle in two.

Occurrence. Maplewood Formation, upper Llandovery Series, New York (Cramer 1968a); Silurian, NW Spain (Cramer 1969b); Llandovery-Prídolí series, Florida borehole material; Osgood Formation, upper Llandovery Series, Kentucky; Rose Hill Formation, upper Llandovery Series, Pennsylvania and Virginia (Cramer 1971; Cramer & Diez 1970, 1972; Loeblich Jr. 1970); Los Espejos Formation, Wenlock Series, Argentina (Pöthé de Baldis 1975); Tanezzuft Formation, Wenlock Series, subsurface North Africa (Richardson & Ioannides 1973); Hughley Shales, upper Llandovery-Leintwardine Group, upper Ludlow series, Welsh Borderland (Dorning 1981a); middle-upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); upper Llandovery Series, Canada (Achab 1976); Devonian, Paraguay (Pöthé de Baldis 1974b); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Llandovery-Wenlock series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Rare in the Lower/Middle Elton formations, Goggin Road. Known range: upper Llandovery-Prídolí series.

Genus **Comasphaeridium** Staplin, Jansonius & Pocock 1965

1970 *Elektoriskos* Loeblich, n. gen.; Loeblich, p. 717.
1991 *Globosphaeridium* n. gen.; Moczydlowska, p. 54.

Type Species. By original designation, *Micrhystridium cometes* Valensi 1949, p. 545, fig. 5, no. 6; from the Bathonian Stage, Upper Jurassic, France.

Diagnosis. (Staplin *et al.* 1965, p. 192). "Vesicles spherical to ellipsoidal, sometimes of large size; with densely crowded, thin, solid, usually simple, more or less flexible hair-like spines."

Remarks. The type species of this genus, *C. cometes*, is described from the Jurassic, which raises the possibility that it may be a cyst of a dinoflagellate (e.g. *Cleistosphaeridium*).

The taxa *Elektoriskos* Loeblich Jr. (1970, p. 717) and *Comasphaeridium* Staplin *et al.* (1965, p. 192) were distinguished by the lack of densely crowded, hair-like processes on *Elektoriskos* (Loeblich Jr. 1970, p. 717). A comparison of the diagnoses of *Elektoriskos* and *Comasphaeridium* led Eisenack *et al.* (1976, p. 245) to consider *Elektoriskos* a junior synonym of *Comasphaeridium*. The genus was retained, however, by Wicander & Wood (1981, p. 36), though no reasons were given and no discussion on the relationship with *Comasphaeridium* entered into. Process spacing was cited as insufficient evidence for generic separation by Sarjeant & Stancliffe (1994, p. 67) and they agreed with Eisenack *et al.* (1976) in considering *Elektoriskos* to be a junior synonym of *Comasphaeridium*. The genera *Globosphaeridium* Moczydlowska 1991 (p. 54) and *Heliosphaeridium* Moczydlowska 1991 (p. 58) were also considered junior synonyms of *Comasphaeridium* by Sarjeant and Stancliffe (1994, p. 25). The processes of *Heliosphaeridium* are, however, hollow, open to the vesicle interior and occasionally branched, and the genus is considered here to be distinct from *Comasphaeridium* and *Filisphaeridium*.

The genera *Comasphaeridium* and *Filisphaeridium* were emended by Sarjeant & Stancliffe (1994, p. 25, 28), who used the difference in process nature and the process length : vesicle diameter ratio to distinguish the two taxa. This method is considered impractical, for example *Tricholigotriletum timofeevii* Stockmans & Willière 1962a (considered synonymous with *F. williereae* by Stockmans & Willière 1974) has a process:vesicle ratio of 0.18-0.29, which, under the diagnoses of Sarjeant & Stancliffe (1994), would place it in either *Comasphaeridium* or *Filisphaeridium*. It would seem sensible to divide the two genera on the presence or absence of structures at the distal ends of the processes, placing those forms with predominantly simple processes in *Comasphaeridium* and those with branched, capitate, clavate or thickened tips in *Filisphaeridium*; this would follow, in essence, the original designation of the genera in Staplin *et al.* (1965, p. 192).

Comasphaeridium brevispinosum (Lister 1970) comb. nov. Pl. 3, fig. 7.

1970 *Filisphaeridium brevispinosum* sp. nov.; Lister, p. 72-73, pl. 7, figs 5-10, text-fig. 22.

1979 *Elektoriskos brevispinosum* (Lister) nov. comb.; Vanguestaine, p. 247, pl. 3, fig. 18, pl. 4, fig. 14.

1984 *Comasphaeridium brevispinosum* (Lister 1970); Sheshagova, p. 31, pl. 22, fig. 8 (invalid combination)

1990 *Elektoriskos brevispinosum* (Lister 1970) Vanguestaine 1979; Fensome *et al.*, p. 209. (no fig.).

1994 *Filisphaeridium brevispinosum* Lister 1970; Sarjeant & Stancliffe, p. 29 (no fig.).

Holotype. Lister 1970, pl. 7, fig. 8; MPK 135; from the Upper Whitcliffe Formation, Ludlow Series, LD22, Whitcliffe, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 72). "Vesicle smooth, thin-walled, hollow, spherical; numerous solid hair-like processes, up to 10% of vesicle diameter in length; within a given individual, processes are of equal length and spacing. Excystment by cryptosuture."

Description. Vesicle spherical to ellipsoidal, with a very thin wall and numerous simple, solid, straight or flexuous, wiry processes, which have slightly expanded bases. Excystment by unornamented rupture of the vesicle wall.

Dimensions. V=20-36μm, PL=2-8μm (9 specimens measured).

Remarks. The combination *C. brevispinosum* was not validly published by Sheshagova (1984) as the basionym was not fully referenced (Fensome *et al.* 1990, p. 149). This taxon has been transferred to *Comasphaeridium* on the grounds that it has a thin spherical to ellipsoidal vesicle with a dense arrangement of simple, wiry, solid processes (see *Comasphaeridium*-Remarks above).

In the Ludlow area the number, length and density of processes have been reported to increase from the Lower Elton-Downton Castle Sandstone formations, with the most densely setose forms occurring from the Upper Whitcliffe Formation (Lister 1970, text-fig. 22).

Occurrence. Much Wenlock Limestone-Downton Castle Sandstone formations (upper Wenlock-Prídolí series, Ludlow, Shropshire (Lister 1970, Lister & Downie 1974); Siegenian Stage, Belgium (Vanguestaine 1979); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); Silurian, Argentina (Rubinstein 1993); most abundant over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), being rare in the remaining Lower Elton Formation (Goggin Road). Known range: Wenlock Series-Siegenian Stage.

Comasphaeridium williereae (Deflandre & Deflandre-Rigaud 1965 ex Lister 1970) Sarjeant & Stancliffe 1994 Pl. 3, fig. 8.

1963 *Baltisphaeridium* aff. *polytrichum* (Valensi 1947); Stockmans & Willière, p. 460, pl. 3, figs 24, 25, text-fig. 16.

1965 *Micrhystridium williereae*; Deflandre & Deflandre-Rigaud, fiche 2347. (*nomen nudum*).

1969a *Baltisphaeridium chiggerum* Cramer 1968; Cramer, pl. 70, fig. 18. (*nomen nudum*).

1969a *Micrhystridium chiggerum* Cramer 1968a; Cramer, p. 486 (no fig.) (*nomen nudum*).

1970a *Comasphaeridium williereae* (Deflandre & Deflandre-Rigaud 1965); Cramer, p. 121-122, text-fig. 37. (*nomen nudum*).

1970 *Filisphaeridium williereae* (G. & M. Deflandre 1965) comb. nov. emend.; Lister, p. 73, pl. 7, figs 1-4. (November).

1970 *Elektoriskos pogonius* n. sp.; Loeblich Jr., p. 718-719, figs 13A, B. (December).

1976 *Comasphaeridium williereae* Cramer 1970; Eisenack *et al.*, p. 135-137. (illegitimate)

1979 *Elektoriskos williereae* (Deflandre & Deflandre-Rigaud) comb. nov.; Vanguestaine, p. 247, pl. 1, figs 13, 14, pl. 3, fig. 20.

1990 *Elektoriskos williereae* (Deflandre & Deflandre-Rigaud 1965a *ex* Lister 1970) Vanguestaine 1979; Fensome *et al.*, p. 210 (no fig.).

1994 *Comasphaeridium pogonium* (Loeblich Jr. 1970a) comb. nov.; Sarjeant & Stancliffe, p. 27 (no fig.).

1994 *Comasphaeridium williereae* (Deflandre & Deflandre 1965 *ex* Lister 1970) comb. nov.; Sarjeant & Stancliffe. p. 27 (no fig.).

Holotype. Stockmans & Willière 1963, pl. 3, figs 24, 25 (as *Baltisphaeridium* aff. *polytrichium* (Valensi 1947)); from the Llandovery Series, borehole material, Belgium; designated by Lister (1970, p. 73).

Diagnosis. (Lister 1970, p. 73). "Vesicle hollow, subspherical to elongate polygonal; vesicle wall unilayered, thin; numerous slender, solid, flexuous processes about 40% of vesicle diameter in length; distally the processes most often taper to a point but occasionally branch. Excystment by cryptosuture."

Description. Vesicle laevigate, spherical to ellipsoidal, extremely thin walled. A dense arrangement of solid, wiry, flexuous processes, with slightly expanded bases, covers the vesicle surface. Excystment by large, unornamented rupture.

Dimensions. V=22-37µm, PL=8-14µm, PØ=0.3µm, PN > 35 (6 specimens measured).

Remarks. The invalidly published species (no holotype or diagnosis) *M. williereae* Deflandre & Deflandre-Rigaud 1965 was validated as *F. williereae* by Lister (1970, p. 73), who designated the single specimen referred to as *B.* aff. *polytrichum* (Valensi 1947) Stockmans & Willière 1963 (pl. 3, figs 24, 25) as holotype. The name *C. williereae* (Deflandre & Deflandre-Rigaud 1965) was invalidly published by Cramer (1970a), as no holotype was designated. There was an attempt to validate this name in Eisenack *et al.* (1976, p. 136), who designated the holotype as *B. chiggerum* (Cramer 1969a, pl. 70, fig. 18) and cited the diagnosis as that given by Cramer (1970a, p. 121). The taxon *F. williereae* (Deflandre & Deflandre-Rigaud 1965) Lister 1970 was, however, included in synonomy with *C. williereae* Cramer 1970a in Eisenack *et al.* 1976. Thus *C. williereae* Cramer 1970a in Eisenack *et al.* 1976 is a junior synonym of *F. williereae* (Deflandre & Deflandre-Rigaud 1965) Lister 1970, as is, by implication, *B.* (al. *M*) *chiggerum.*

E. pogonius was considered by Eisenack *et al.* (1976, p. 135) to be a junior synonym of *C. williereae* Cramer 1970a in Eisenack *et al.* 1976, and would be, by implication, a junior synonym of *C. williereae* used herein. In proposing *E. pogonius*, Loeblich Jr. (1970, p. 718) included *B.* (al. *M.*) *chiggerum* in synonymy. The possibility that *E. pogonius* and *M. williereae* were conspecific was raised by Loeblich Jr. (1970, p. 718), who cited the lack of knowledge about the nature of the processes on *M. williereae*, whether they were solid or hollow, as the reason for his uncertainties. Since the size range and description of *E. pogonius* is nearly identical to that of *F. williereae* in Lister (1970, p. 73), *E. pogonius* is considered to be a junior synonym of *C. williereae* herein.

The possibility that *F.* (now *Comasphaeridium*) *williereae* and *Elektoriskos* (now *Comasphaeridium*) *aurora* Loeblich Jr. 1970 were conspecific, was raised by Miller & Eames (1982, p. 237), who stated that the hair-like, acuminate, processes were similar on both species. The vesicle diameter of *E. aurora* is larger than *F. williereae* (type material: 41-47µm vs' 24-40µm); the process lengths, however, fall with the same range (13µm and 9-14µm respectively). The morphology and diagnoses of the two species are very similar, they are, however, both retained until examination of the holotypes.

Occurrence. Llandovery Series, borehole material, Belgium (Stockmans & Willière 1963); Upper Llandovery-Wenlock series, Belgium (Martin 1966a, 1969); Formigoso, San Pedro and Furada formations, Llandovery Series-lower Gedinnian Stage, Spain (Cramer & Diez 1968, Cramer 1970a); subsurface material (middle-upper Silurian), Libya and Saudi Arabia (Cramer 1970a); Red Mountain Formation, upper Llandovery Series, Georgia and Alabama; Ross Brook Formation, lower-middle

Llandovery Series, Nova Scotia; Rose Hill Formation, upper Llandovery Series, Pennsylvania and Virginia; Florida borehole material (Llandovery-Přídolí series); Power Glen Formation, lower Llandovery Series, Niagara escarpment, New York and Ontario; Neahga Formation, upper Llandovery Series, Niagara escarpment, New York and Ontario; Crab Orchard Formation, upper Llandovery Series, Kentucky; Maplewood Formation, upper Llandovery Series, Rochester, New York and Niagara escarpment; Plum Creek Formation, upper Llandovery Series; Red Mountain Formation, lower-upper Llandovery Series; Ross Brook Formation, lower-upper Llandovery Series, Nova Scotia; Saint Clair Formation, upper Llandovery-lower Ludlow series, Missouri (Cramer 1968b, 1969a, 1969b, 1970a & b, Loeblich Jr. 1970, Cramer & Diez 1972); Rochester Formation, Wenlock Series, southern Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); mainly from the Lower Elton Formation and rarely in other horizons up to the Whitcliffe Group, Ludlow and Millichope areas (Lister 1970); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Přídolí series, Ludlow (Lister & Downie 1974); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Siegenian-Emsian stages, Belgium (Vanguestaine 1979); Medina Group, lower Llandovery Series, New York (Miller & Eames 1982); Silurian, Siberia (Sheshegova 1984); Llandovery Series, Llandovery type area (Hill & Dorning 1984); lower Silurian, Ringerike, Norway (Smelror 1987); Slite-Sundre formations, Wenlock-Přídolí series, Gotland (Le Hérissé 1989). Most common over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry & Goggin Road), rarely occurring in the Middle Elton Formation (Goggin Road). Known range: lower Llandovery Series-Emsian Stage.

Genus **Cymbosphaeridium** Lister 1970

Type Species. By original designation, *Cymbosphaeridium bikidum* Lister 1970, p. 64-65, pl. 6, figs 1-9, text-figs 18a-c, f, k, 21; from the Upper Bringewood Formation, Ludlow Series, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 63). "Vesicle hollow, subspherical, double-walled; inner wall is closely appressed to the outer wall, and is continuous across the proximal part of the process. The processes are few and variable in number, hollow, tubiform, closed distally and formed from the outer wall only. The reflected plate formula follows the pattern of apical, pre-equatorial, post-equatorial, antapical. Excystment is by obvious suture, resulting in the release of an apical operculum consisting of a single plate."

Remarks. This genus is distinguished from *Multiplicisphaeridium* by its two walled nature and from *Baltisphaeridium* by its branching processes. This branching, which is typically cauliflorate, distinguishes it from *Leptobrachion*. Dorning (1981a, p. 186) regarded the double walled nature and circular pylome as characters not of essential importance, considering the primary characteristics to be the tubular processes and cauliflorate terminations. Other authors, however, (e.g. Hill 1978) have considered that the main criterion for distinguishing *Cymbosphaeridium* is the presence of a double wall.

Cymbosphaeridium pilar (Cramer 1964b) Lister 1970 Pl. 3, figs 9-10.

1964b *Baltisphaeridium pilar* n. sp.; Cramer p. 286, pl. 1, figs 1-2, text-fig. 14:1.

1966b *Baltisphaeridium pilaris* Cramer 1964 *Baltisphaeridium pilar*, in Cramer 1964b; Cramer, p. 30-33, pl. 1, figs 1-9, pl. 2, figs 3, 5-11, text-figs 2, 3.

1968 *Baltisphaeridium* (*Priscogalea* ?) *pilaris*; Jardiné & Yapaudjian, p. 439, pl. 3, figs 17-18.

1970 *Cymbosphaeridium pilar*; Lister, p. 63 (no fig.).

1973 *Multiplicisphaeridium pilaris* (Cramer 1964); Eisenack *et al.*, p. 725-727.

1978 *Cymbosphaeridium pilar* (Cramer, 1964b) Lister, 1970; Hill, p. 181-182, pl. 1, figs 1-4.

1990 *Cymbosphaeridium pilar* (Cramer 1964b) Lister 1970; Fensome *et al.*, p. 177 (no fig).

Holotype. Baltisphaeridium pilar Cramer 1964b, pl. 1, fig. 1; from 1165, San Pedro Formation, Ludlow Series, Oblanca de Luna, NW Spain.

Diagnosis. (Cramer 1964b, p. 286). "Central body and processes hollow, with not uniform walls. The central body is roughly spherical. It has a moderately thin wall, that is moderately transparent to not transparent. The wall of the central body is scabrate to irregularly rugulate. The central body is usually less transparent than the processes. The processes have the form of slender pilars and branch at the tips. They are psilate at 1200 x magnification. Number of processes 3 to 10 (5 to 6)."

Description. Vesicle spherical to ellipsoidal, scabrate; vesicle slightly thicker than processes or moderately thick walled. Processes thin, columnar, laevigate, hollow, closed to vesicle interior, with digitate branching at the tips (up to 2nd order). Excystment mechanism not observed.

Dimensions. V=20-36μm, PL=17-25μm, PØb=2.5-4.5μm, PN=7-11 (8 specimens measured).

Remarks. The specific epithet of this taxon was changed, without reason, to *pilaris* by Cramer (1966b); both Hill (1978, p. 181) and Fensome *et al.* (1990) have stated that the species name should be spelt *pilar.* A single, three dimensionally preserved specimen recovered in this study appears to possess a large, unornamented rupture, which almost divides the vesicle in two (Pl. 3, fig. 10). The diagnosis, however, identifies the method of excystment as a circular pylome; no examples with pylomes have been recovered herein. The taxon *C. pilar* var. *typicum* Cramer 1970a, was considered a junior synonym of the autonym *C. pilar pilar* by Fensome *et al.* (1990, p. 177), as it was believed that the holotype of *C. pilar* was included in synonymy with *C. pilar typicum* by Eisenack *et al.* (1973, p. 731). The holotype was not, however, included in synonymy with *C. pilar* by Eisenack *et al.* (1973) and thus the variety *C. pilar typicum* must be considered distinct from *C. pilar pilar.*

Occurrence. San Pedro and Furada formations, Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer 1964b, 1966a & b, 1969b; Cramer & Diez 1968); Silurian, Belgium (Martin 1967, 1969); lower Ludlow Series, Algeria (Maglore 1968); Maplewood Formation, upper Llandovery Series, New York (Cramer 1968a, as cf. *pilaris*); Ludlow Series-lower Gedinnian Stage, Algeria (Jardiné & Yapaudjian 1968); upper Silurian, Libyan subsurface material; middle-upper Silurian subsurface material, Florida; Osgood and Alger formations, upper Llandovery Series, Indiana and Ohio; Red Mountain Formation, lower-upper Llandovery Series, Georgia & Alabama (Cramer 1968b, 1970a);

Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974, 1978); Lower Bringewood Formation, Ludlow (Lister & Downie 1974); Siegenian-Emsian stages, Belgium (Vanguestaine 1979); Leintwardine-Whitcliffe groups, Ludlow Series, Welsh Borderland (Dorning 1981a); Gedinnian Stage, France (Moreau-Benoît & Poncet 1982); Llandovery-Ludlow series, Jordan (Keegan *et al.* 1990); Silurian, Argentina (Rubinstein 1993); from a single sample in the Middle Elton Formation, Goggin Road. Known range: Llandovery Series-Emsian Stage.

Cymbosphaeridium sp. A Pl. 3, fig. 11; Pl. 10, figs 11-12.

Description. Vesicle spherical to ellipsoidal, moderately thick walled, with a coarsely granulate surface. The vesicle has a variable number of processes, which are thinner walled than the vesicle, laevigate, hollow, columnar or rarely tapering. Most of the processes have tips that branch to 1st or 2nd order, though some may be simple; the processes are closed to vesicle cavity. Excystment mechanism not observed.

Dimensions. V=22-29μm, PL=7-12μm, PØb=0.75-2μm, W=1.5-2.5μm, PN=20-48 (7 specimens measured).

Remarks. This species resembles *Baltisphaeridium cariniosum* Cramer 1964b, which differs in having shorter processes.

Occurrence. From the middle-upper Lower Elton Formation, Goggin Road.

Genus **Dateriocradus** Tappan & Loeblich Jr. 1971

Type Species. By original designation, *Dateriocradus polydactylus* Tappan & Loeblich Jr. 1971, p. 396, pl. 5, figs 1-7; Waldron Formation, upper Wenlock Series, Indiana.

Diagnosis. (Tappan & Loeblich Jr. 1971, p. 396). "Central vesicle subtriangular in outline, commonly with three long hollow processes in plane of vesicle, rarely a forth arising from the broad face of the vesicle; processes distally bifurcating up to the fifth or sixth order; wall surface laevigate; excystment by development of an epityche, an arcuate splitting of the wall resulting in a flaplike opening between two processes similar to that in *Veryhachium*."

Remarks. This genus is similar in morphology to *Evittia* and *Multiplicisphaeridium*; species of *Evittia* have digitate, not ramified, branches, those of *Multiplicisphaeridium* do not possess triangular or tetrahedral vesicles.

Dateriocradus cf. **monterrosae** (Cramer 1969a) Pöthé de Baldis 1981 Pl. 3, fig. 12; Pl. 10, fig. 13.

1969a *Baltisphaeridium monterrosae* n. sp.; Cramer, p. 490, pl. 70, figs 5-7.

p. 1970a *Dateriocradus monterrosae* Cramer 1969; Cramer, p. 129-130, pl. 8, fig. 128 (only).

1971 *Dateriocradus polydactylus* n. sp.; Tappan & Loeblich Jr., p. 396, pl. 5, figs 1-7.

1973 *Multiplicisphaeridium monterrosae* (Cramer 1969) Eisenack *et al.*, p. 693-694.

1973 *Evittia monterrosa* (Cramer) nov. comb.; Thusu, p. 815, pl. 106, figs 2-7.

1981 *Dateriocradus monterrosae* (Cramer) n. comb.; Pöthé de Baldis, p. 238, pl. 3, fig. 5.

? 1989 *Oppilatala monterrosae* (Cramer) n. comb.; Le Hérissé, p. 176-177, pl. 23, figs 14-15, text-fig. 14:4

1990 *Dateriocradus monterrosae* (Cramer 1969b) Pöthé de Baldis 1981; Fensome *et al.*, p. 187 (no fig.).

Holotype. Cramer 1969a, pl. 70, fig. 5; slide F:006014A04.0871.433, specimen 645H10; from the Rose Hill Formation, upper Llandovery Series, Millerstown, Pennsylvania.

Diagnosis. (Cramer 1969a, p. 490). "Central portion of vesicle subtriangular, clearly differentiated from processes. The processes are located at the corners of the central portion of the vesicle. (see "Comments.") The processes are generally of the same length as or slightly longer than a side of the central portion; they are cylindrical but have a broad conical base which grades from the central portion of the vesicle into the process proper through a distance of about 1/10 of the process length. At the distal portion, pinnae and pinnulae (up to second order) are present; characteristically, there are three or four sets of pinnae. The splitting angle between pinnae and processes varies from 90 to 120 degrees; however, the configuration and complexity is a fairly constant morphologic character for the species. (A typical configuration is illustrated in Plate 70, figure 6.) The pinnulae of the last order tend to be split in a dichotomous fashion. The only branching is distal. The processes are entirely hollow as are the basal portions of the pinnae; the tops of the pinnae and pinnulae are solid. The process cavity and no complex unions between both morphographic units were seen. Characteristically, the central portion of the vesicle possesses a fracture (arrows in Pl. 70, figs. 5,7), which divides it in two almost equal parts. This fracture is interpreted as a straight split pylome, similar to that which is found in many species of *Veryhachium* and *Micrhystridium*. The processes and the central portion of the vesicle are unilayered and are apparently uniform; however, a consistent difference of colour was observed: all the processes are transparent (colorless to translucent (brown), whereas the central portion is always much darker (translucent to opaque). The vesicle wall is psilate and is about 1μ thick. No cysts were observed."

Description. Vesicle thin, laevigate, triangular in outline, with straight or slightly convex sides. Processes, laevigate, broad based, tapering, hollow, open to vesicle interior but with a distinct contact with the vesicle. Processes occur at each vesicle corner, commonly four processes, rarely three or five processes. Ramified branching of 1^{st}-3^{rd} order occurs $^1/_2$ to $^2/_3$ along process length at angles of 45°-120°. Excystment mechanism not observed.

Dimensions. V=15-18μm, PL=12.5-23μm, PØb=1.75-4μm, PN=3-5 (7 specimens measured).

Remarks. Forms recovered and described differ from the type material in two ways, they lack the highly ramified branching and can have processes that can branch from half way. These differences are not considered important enough to define a new species and forms recovered here are assigned to *D.* cf.

monterrosae. The processes of *Evittia* (now *Dateriocradus*) *tribrachiata* Lister (1970, pl. 5, fig. 5) are slightly broader, and the vesicle and process length slightly larger than those forms assigned to *D*. cf. *monterrosae* herein (V = 19-26μm, PL = 16-28μm). The overall morphology of *E. tribrachiata* is similar to *D*. cf. *monterrosae* herein and there is a possibility that it is a junior synonym, it is, however, retain as separate.

As stated by Le Hérissé (1989, p. 176-177), there is evidence to suggest that *monterrosae* belongs in *Oppilatala*, though the transfer proposed by Le Hérissé is questioned. The diagnosis of Cramer (1969a) states that the vesicle of *monterrosae* is darker than the processes, a common feature of *Oppilatala*. Also, the majority of those specimens figured by Cramer (1970a, pl. 8, figs 127, 129-132, 135) have plugged process bases and can be assigned to *Oppilatala*. The holotype of *monterrosae*, however, re-figured by Cramer (1970a, pl. 8, fig. 128) appears too dark for the internal nature of the processes to be ascertained. Until the holotype has been re-examined we must rely on the diagnosis of Cramer (1969a), which states that the "processes are entirely hollow." For this reason *monterrosae* is retained in *Dateriocradus* herein.

D. cf. *monterrosae* differs from *Dateriocradus* sp. A in having shorter processes (PL : V ratio this study; *D*. cf. *monterrosae* = 0.8-(1.3)-1.6, *D*. sp. A = 1.7-(2)-2.4). The holotypes of *D. monterrosae* and *D. polydactylus* have PL : V ratios of 0.8 and 1.4 respectively.

Occurrence. Tuscarora and Rose Hill formations, upper Llandovery Series, Pennsylvania (Cramer 1969a); San Pedro and Furada formations, Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer 1963, 1964b, 1970a, as *Baltisphaeridium molinum* Cramer 1963 ex Cramer 1964 and *D. monterrosae*); Silurian, Belgium (Martin 1967); Alger Formation, upper Llandovery Series; subsurface Florida (Llandovery-Prídolí series); Maplewood Formation, upper Llandovery Series; Neahga Formation, upper Llandovery Series, Ontario and New York; Red Mountain Formation, upper Llandovery Series, Georgia and Alabama; Crab Orchard and Osgood formations, upper Llandovery Series, Kentucky; Rose Hill Formation, Virginia (Cramer 1970a, Cramer & Diez 1970, 1972); Waldron Formation, Wenlock Series, Tunnel Mill, Indiana (Tappan & Loeblich Jr. 1971, as *D. polydactylus*); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Llandovery Series, Algeria (Jardiné *et al.* 1974); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); middle Buildwas Formation-Elton Group, Wenlock-Ludlow series, Welsh Borderland (Dorning 1981a, as *D. monterrosae* & *D. poldactylus*); lower Silurian, Ringerike, Norway (Dorning & Aldridge 1982); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983, as *D. polydactylus*); upper Wenlock Series, Wenlock type area (Swire 1993); Silurian, Argentina (Rubinstein 1993, as *D. polydactylus*); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995, as cf. *monterrosae* and *polydactylus*); rare over the Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road; sparse occurrences in the Middle Elton Formation (Goggin Road). Known range: Llandovery Series-Gedinnian Stage.

Dateriocradus sp. A Pl. 3, fig. 13.

Description. Vesicle laevigate, hollow, thin, triangular in outline with straight or slightly convex sides. Commonly there are four processes, rarely three or five; processes arise from the vesicle corners, with the fifth process being randomly positioned and generally reduced in size. Processes thin, hollow, slightly flexuous, tapering from a distinct contact with the vesicle to branched tips, rarely simple. Branching from 1st to 2nd order, rarely 3rd order, generally occurring at process tips, but occasionally from 1/2 way along the processes. Excystment by unornamented rupture of the vesicle wall between two processes.

Dimensions. V=11-22μm, PL=22-49μm, PØb=1.5-4μm, PN=3-5 (10 specimens measured).

Remarks. This taxon is distinguished from *D. monterrosae* by its longer processes (PL : V ratio this study; *D.* cf. *monterrosae* = 0.8-(1.3)-1.6, *D.* sp. A = 1.7-(2)-2.4); *Dateriocradus algerensis* (Cramer & Diez 1972) Dorning 1981a has a larger vesicle (V = 30-40μm) and longer processes. The processes of small, triangular, examples of the *Evittia remota* Group have digitate, not ramified branches.

Occurrence. Common over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), becoming rarer in the upper Lower Elton and Middle Elton formations (Goggin Road).

Genus **Dilatisphaera** Lister 1970

Type Species. By original designation, *Dilatisphaera laevigata* Lister 1970, p. 66, pl. 6, figs 10-12; Upper Elton Formation, Ludlow Series, Ludlow, Shropshire.

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. The general morphology of this genus has been likened to that of the dinoflagellates. Indeed, Martin (1966a) placed her new taxon *Hystrichosphaeridium* (now *Dilatisphaera*) *williereae* in the Dinophyceae. This genus was, however, not included in the *Cymbosphaeridium* clade of Colbath & Grenfell (1995), whose members were cited as possible candidates for Palaeozoic dinoflagellates (Colbath & Grenfell 1995, p. 310).

Dilatisphaera laevigata Lister 1970 Pl. 11, figs 3-5.

v* 1970 *Dilatisphaera laevigata* sp. nov.; Lister 1970, p. 66, pl. 6, figs 10-12, text-figs 18h, 20d.

1990 *Dilatisphaera laevigata* Lister 1970; Fensome *et al.*, p. 200 (no fig.)

Holotype. Lister 1970, pl. 6, fig. 10; MPK 125; Upper Elton Formation, Ludlow Series, MD6, NW of Upper Dinchope, Shropshire.

Diagnosis. (Lister 1970, p. 66). "Vesicle hollow, smooth, more or less spherical; processes few in number, variable in length from 0·4-1·5 times vesicle diameter, broad, thin-walled, smooth, hollow, tubiform and proximally closed; distally the processes may flare slightly and have a serrated margin or sometimes rounded terminations; the process tips are invariably open. Excystment suture conspicuous, apical, pentagonal in outline; operculum possesses a single plate-centred process."

Description. Vesicle spherical to subspherical, slightly thicker walled than the processes; vesicle ornament indeterminable under transmitted light, but with a SEM the vesicle appears laevigate, sparsely granulate or sparsely baculate. Processes very thin walled, columnar, hollow, closed to the vesicle cavity, open distally. With a SEM the processes appear smooth or possess a few randomly scattered grana along their length. Excystment occurs via a pylome.

Dimensions. V=13-18µm, PL=12-21µm, PØb=3-6µm, PN=5-7 (10 specimens measured).

Remarks. The laevigate nature of the vesicle was used by Lister (1970, p. 66) to separate *D. laevigata* from *Dilatisphaera williereae* (Martin 1966a) Lister 1970, which has a spinose-baculate vesicle. In the present study, however, SEM work has shown the vesicle ornament of *laevigata* to be variable between laevigate, sparsely granulate or sparsely baculate; the material is too poorly preserved for this ornament to be visible under transmitted light. The holotype of *laevigata* appears to possess an ornamented vesicle, which may suggest that *D. laevigata* and *D. williereae* are synonymous.

Occurrence. Much Wenlock Limestone-Upper Bringewood formations, Ludlow and Millichope areas, Shropshire (Lister 1970, Lister & Downie 1974); subsurface Florida (Llandovery-Prídolí series); Red Mountain Formation, lower-upper Llandovery Series; Rochester Formation, Wenlock Series, Pennsylvania and Virginia; Ross Brook Formation, Llandovery Series; Saint Clair Formation, upper Llandovery-lower Ludlow series; Waldron Formation, upper Wenlock Series, Kentucky (Cramer & Diez 1972); Llandovery Series, Llandovery type area (Hill 1974); upper Elton-middle Leintwardine groups, Ludlow Series, Welsh Borderland (Dorning 1981a); middle Wenlock Series, Austria (Priewalder 1987); lower Silurian, Ringerike, Norway (Smelror 1987); Hemse-Hamra formations, Ludlow Series, Gotland (Le Hérissé 1989); absent from Pitch Coppice Quarry; rare in the Lower and Middle Elton formations, increasing in abundance in the topmost Middle Elton Formation, Goggin Road. Known range: Llandovery-Prídolí series.

Genus **Dorsennidium** Wicander 1974 emend. Sarjeant & Stancliffe 1994

Type Species. By original designation, *Dorsennidium patulum* Wicander 1974, pl. 9, fig. 12; Chagrin Shale, Upper Devonian, Barberton test core 3, Ohio, USA.

Diagnosis. (Sarjeant & Stancliffe 1994, p. 39). "Acritarchs having a polygonal vesicle whose outline is determined by the number (4-10) and relative position of its spines. Eilyma single-layered or apparently so; surface laevigate to finely granular or shagreenate [*sic*]. The spines arise in more than one plane: proximally they merge so smoothly with the vesicle wall that no exact limit can be set to their bases; they are without linkage by ridges or crests to adjacent spines. Spines of relatively uniform size.

They are always hollow, the bases open to the vesicle interior, and without development of costae, striae or spinulets. The spines may have small pores in their wall, but are never branched and have tips that are always closed and pointed. A cryptosuture can be developed, but this is rarely observed."

Remarks. Sarjeant & Stancliffe (1994) used the plane, or planes, of process development to separate *Dorsennidium* and *Veryhachium*. Specimens with processes in a single plane were placed in *Veryhachium*, whilst those with processes in multiple planes were placed in *Dorsennidium* or *Micrhystridium*. Although practicable in the majority of cases, problems do occur. Some examples of *Dorsennidium rhomboidium* have four processes in a single plane, implying that they should be placed separately in *Veryhachium*, an impractical solution. It is apparent, therefore, that the rule on *Dorsennidium* possessing processes in multiple planes should be applied to the majority of specimens in any single species, allowing a small amount of leeway to encompass forms that do not comply.

The genus *Exilisphaeridium* Wicander, a junior synonym of *Micrhystridium* according to Eisenack *et al.* (1979a, p. 209), was considered to be a junior synonym of *Dorsennidium* by Sarjeant & Stancliffe (1994, p. 39). They stated that *Exilisphaeridium* no longer fell within the emended diagnosis of *Micrhystridium*; they did, however, also include *Exilisphaeridium* as a junior synonym of *Micrhystridium* (Sarjeant & Stancliffe 1994, p. 12). The only possible reason for exclusion from *Micrhystridium*, is the fact that vesicle width and process length are at the maximum of the range permissible under the emended diagnosis given by Sarjeant & Stancliffe (1994, p. 12). The type species *Exilisphaeridium simplex* Wicander 1974, is considered here to display the requisite characteristics of *Micrhystridium* and is considered a junior synonym.

Dorsennidium europaeum (Stockmans & Willière 1960) Sarjeant & Stancliffe 1994 emend.
Pl. 3, fig. 14.

1960 *Veryhachium europaeum* n. sp.; Stockmans & Willière, p. 3, pl. 2, fig. 25.

1962a *Veryhachium legrandi* n. sp.; Stockmans & Willière, p. 54, pl. 1, fig. 3, text-fig. 11a.

non. 1968 *Veryhachium legrandi* var. *pentapoda* nov. var.; Martinez-Macchiavello, p. 80, pl. 1, fig. 8, text-fig. 8.

1990 *Veryhachium europaeum* Stockmans & Willière 1960; Fensome *et al.*, p. 514-515 (no fig.).

1994 *Dorsennidium europaeum* (Stockmans & Willière 1960) comb. nov.; Sarjeant & Stancliffe, p. 40 (no fig.).

Holotype. Stockmans & Willière 1960, pl. 2, fig. 25; Frasnian Stage, borehole material, Belgium.

Original Diagnosis. (Translated from Stockmans & Willière, 1960, p. 3). "Form measuring from one edge to the base of the opposite point a length of about 18µ and adorned with four equal points of 25µ, three correspond with the angles of a triangle, the forth adorns one of the faces."

Emended Diagnosis. Vesicle laevigate, tetrahedral with straight to slightly convex sides. Processes hollow, open to vesicle interior, simple, straight or slightly flexuous; laevigate or faintly granulate. Excystment via unornamented rupture.

Dimensions. V=11-27μm, PL=15-32μm, PØb=2-4.5μm (10 specimens measured).

Remarks. The synonymy of *V. legrandi* var. *pentapoda*, proposed by Martin (1969, p. 92) and Wicander & Wood (1981, p. 64), is rejected as this taxon has five processes. The granulate ornament on the processes is visible under transmitted light on only the larger, thicker walled specimens. This species is very similar to *Dorsennidium wenlockianum*, which has a shorter fourth process, and *Dorsennidium formosum*, which has at least five processes.

Occurrence. This species has a wide geographic and stratigraphic distribution; a list of pre 1979 occurrences can be found in Eisenack *et al.* (1979b, p. 407). Siegenian-Emsian stages, Belgium (Vanguestaine 1979); Upper Visby-Högklint formations, lower Wenlock Series, Gotland (Cramer *et al.* 1979); Silica Formation, Givetian Stage, Ohio (Wicander & Wood 1981); Medina Group, lower Llandovery Series, New York (Miller & Eames 1982); Gedinnian-Siegenian stages, France (Moreau-Benoît & Poncet 1982); Haragan Formation, Lower Devonian, Oklahoma (Wicander 1986); lower Silurian, Ringerike, Norway (Smelror 1987); Llandovery-lower Wenlock series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Ordovician-Lower Jurassic.

Dorsennidium formosum (Stockmans & Willière 1960) Sarjeant & Stancliffe 1994

Pl. 3, fig. 15.

	1960	*Veryhachium formosum* n. sp.; Stockmans & Willière, p. 2, pl. 2, fig. 28.
p.	1970	*Veryhachium trapezionarion* n. sp.; Loeblich Jr., p. 743-744, fig. 38C (only).
	1975	*Goniosphaeridium formosum* (Stockmans & Willière 1960); Jux, p. 124.
	1984	*Michrystridium formosum* (Stockmans & Willière 1960); Amirie, p. 42.
	1987	*Veryhachium formosum* Stockmans & Willière 1960; Priewalder, p. 56, text-fig. 26.
	1990	*Veryhachium formosum* Stockmans & Willière 1960; Fensome *et al.*, p. 516 (no fig.).
	1994	*Dorsennidium formosum* (Stockmans & Willière 1960) comb. nov.; Sarjeant & Stancliffe, p. 40 (no fig.).

Holotype. Stockmans & Willière 1960, pl. 2, fig. 28; from the Frasnian Stage, borehole material, Belgium.

Diagnosis. (Translated from Stockmans & Willière 1960, p. 2). "Triangular form with corners extended into points situated in the same plane. Moreover, an expansion [=process] of the same type as these expansions is raised perpendicular to each of two faces in the middle. Supplementary processes are possible. Length measured from the middle of the edge to the start of the opposite point: 15μ. Length of arms: 22.5μ."

Description. Vesicle laevigate, triangular in outline with straight or slightly convex sides. Processes slender, tapering, straight or slightly flexuous, hollow, open to vesicle interior; laevigate or finely granulate under transmitted light (grana visible on thicker walled specimens only) and with a SEM. The processes are located at each corner of the vesicle and a further two processes arise from opposite sides of the vesicle; additional, shorter, accessory processes may also be randomly distributed over the vesicle. Generally, four of the processes are of equal length, with the fifth process sometimes being shorter; any further processes are generally reduced. Excystment by unornamented rupture.

Dimensions. V=12-25µm, PL=23-35µm, PØb=1.5-4µm, PN=5-6 (10 specimens measured).

Remarks. One of the paratypes of *V. trapezionarion* (Loeblich Jr. 1970, fig 38C), has a triangular vesicle with five processes and is included in synonymy with *D. formosum* herein; the other two specimens have been synonymised with *Dorsennidium rhomboidium* and *Dorsennidium pentagonale* herein. Number of processes and vesicle shape distinguish this species from several other similar taxa (*D. europaeum* = triangular with four processes; *D. rhomboidium* = rhomboidal, *Dorsennidium pentagonale* = polygonal, *Micrhystridium inflatum* = spherical to ellipsoidal).

There is strong evidence to suggest that *D. formosum*, *D. rhomboidium*, *D. pentagonale* and *M. inflatum* represent a morphological continuum of a single species. The general appearance and size range of these taxa are nearly identical, only differing from one another by process number and vesicle shape, which itself appears governed by the number of processes. In part, this morphological continuum is displayed by *V. trapezionarion* (Loeblich 1970, figs 38A-C), which has now been synonymised with three taxa of *Dorsennidium* within (see above). It was, however, decided to retain the taxa as separate until their relationships are analysed in detail.

Occurrence. Upper Devonian, Belgium (Stockmans & Willière 1960, 1962a, 1974); Permian, Britain (Wall & Downie 1963); Silurian, Belgium (Martin 1966a, 1969); Hettangian-upper Sinemurian stages, Lower Jurassic, England (Wall 1965); lower Dinantian Series, lower Carboniferous, Belgium (Stockmans & Willière 1966); Siegenian Stage, Belgium (Vanguestaine 1979, as part of *Veryhachium rhomboidium*); Ludlow Series, Austria (Priewalder 1987); lower Ludlow Series, England (Lister & Downie 1967); Llandovery Series, Libya (Hill & Molyneux 1988); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Silurian-Lower Jurassic.

Dorsennidium pentagonale (Stockmans & Willière 1963) comb. nov. Pl. 3, fig. 16.

	1963	*Micrhystridium pentagonale* nov. sp.; Stockmans & Willière, p. 470-471, pl. 3, fig. 18, text-fig. 32.
p.	1970	*Veryhachium trapezionarion* n. sp.; Loeblich Jr., p. 743-744, fig. 38A (only).
	1990	*Micrhystridium pentagonale* Stockmans & Willière 1963; Fensome *et al.*, p. 329 (no fig.).
	1994	*Micrhystridium*? *pentagonale* Stockmans & Willière 1963; Sarjeant & Stancliffe, p. 18 (no fig.).

Holotype. Stockmans & Willière 1963, pl. 3, fig. 18; preparation no' 1162; borehole material, Silurian, Belgium.

Diagnosis. (Stockmans & Willière 1963, p. 140; translation by Eisenack *et al.* 1979a, p. 479). "Organism of a pentagonal outline of which the angles are prolonged into relatively wide and long processes and with a surface that is ornamented by a few processes which are in everyway similar to each other and which have a greatly expanded base. Dimensions of the body 14.5µ; length of processes 9µ."

Description. Vesicle polygonal, laevigate, with a process arising from each corner. Processes laevigate or finely granulate, long, straight or flexuous, hollow, open to the vesicle interior and tapering to simple closed tips. Excystment by unornamented rupture.

Dimensions. V=14-27µm, PL=18-33µm, PØb=1.5-3µm, PN=6-10 (10 specimens measured).

Remarks. The holotype of this taxon appears damaged, though the polygonal shape of the vesicle is clearly discernible. Specimens recovered here have longer processes than the type material (14-27µm vs' 9µm), though poor preservation could account for this. The status of this species as a separate taxonomic identity was questioned by Sarjeant & Stancliffe (1994, p. 18). This species would be excluded from *Micrhystridium* under the present diagnosis of Sarjeant & Stancliffe (1994), as it has too few processes (6-10 vs' 9-35), and it has, therefore, been transferred to *Dorsennidium* herein.

This species is morphologically similar to several other species and is distinguished from them by the number of processes and shape of the vesicle (*D. rhomboidium* = rhomboidal , *D. formosum* = triangular, *M. inflatum* = spherical-ellipsoidal)(see *D. formosum*-Remarks above).

Occurrence. Silurian, Belgium (Stockmans & Willière 1963); Upper Visby Marl, lower Wenlock Series, Gotland (Cramer *et al.* 1979, as "*Micrhystridium stellatum*" Cramer *et al.* (herein), fig. 17A); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Silurian-Permian.

Dorsennidium rhomboidium (Downie 1959) Sarjeant & Stancliffe 1994 emend. Pl. 4, fig. 1.

v*	1959	*Veryhachium rhomboidium* sp. nov.; Downie, p. 62-63, pl. 12, fig. 10.
p	1970	*Veryhachium trapezionarion* n. sp.; Loeblich Jr., p. 743-744, fig. 38B (only).
non.	1984	*Veryhachium rhomboidium* Downie 1959 emend.; Turner, p. 145, pl. 11, figs 6,9.
	1990	*Veryhachium rhomboidium* Downie 1959 emend. Turner 1984; Fensome *et al.*, p. 523 (no fig.).
	1994	*Dorsennidium rhomboidium* (Downie 1959 emend. Turner 1984) comb. nov.; Sarjeant & Stancliffe p. 41 (no fig.).

Holotype. Downie 1959, pl. 12. fig. 10; Mik(P)21001; Wenlock Shales (= Coalbrookdale Formation), Wenlock Series, Silurian, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1959, p. 62-63). "Test rhomboidal, surface smooth, walls moderately thick, test size 16 to 23µ; processes, four or six, arising from the corners of the test, simple spines, length 50 to 100 per cent. of test size."

Emended Diagnosis. Vesicle square or rhomboidal, laevigate, with straight or slightly convex sides and 4-7 processes; processes hollow, tapering, simple, straight or flexuous, open to vesicle interior, laevigate or finely granulate. Excystment by unornamented rupture.

Dimensions. V=14-24µm, PL=18-32µm, PØb=1.5-4µm, PN=4-7 (18 specimens measured).

Remarks. The original diagnosis by Downie (1959, p. 62) included forms with four processes in a single plane; the emended diagnosis of Turner (1984, p. 145), which is not followed here, limited the number of processes to between five and nine. Those specimens from the Ordovician illustrated by Turner (1984) have considerably longer processes than those originally described and illustrated by Downie (1959) and are considered herein to represent a distinct species. The emended diagnosis takes into account the larger range in process numbers found in the present specimens and the results of SEM work. The fine grana on the processes are visible with transmitted light on only the larger, thicker walled specimens. The processes of the holotype (Downie 1959, pl. 12, fig. 10) appears laevigate when examined under transmitted light.

As with the type material, examples with four processes in a single plane have been found, which, if the present diagnosis of *Dorsennidium* were strictly followed, would not be placed in this genus. These forms have, however, been included in *D. rhomboidium*, as placing them in a separate species of *Veryhachium* is impractical (see *Dorsennidium*-Remarks above).

The synonymy of *V. trapezionarion* was proposed by Turner (1984); only the holotype of this taxon has been included here, however, as the two paratypes (Loeblich Jr. 1970, figs 38A, C) have been assigned to *D. formosum* and *D. pentagonale* herein.

The process number and vesicle shape distinguish *D. rhomboidium* from *Micrhystridium inflatum* (spherical-ellipsoidal), *D. formosum* (triangular) and *Dorsennidium pentagonale* (polygonal) (see also *D. formosum*-Remarks above). The processes of *Dorsennidium pertonense* (Dorning 1981a) Sarjeant & Stancliffe 1994, from the Ludlow Series of Ledbury Hill, Herefordshire, are faintly granulate, but is distinguished from *D. rhomboidium* by its slightly broader processes, though this variation may prove to be intraspecific.

Occurrence. Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959); British Permian (Wall & Downie 1963); Silurian, Belgium (Martin 1966a, 1969); Upper Devonian, Belgium (Stockmans & Willière 1974); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Ludlow Series, Algeria (Jardiné *et al.* 1974); Siegenian Stage, Belgium (Vanguestaine 1979); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); lower Silurian, Ringerike, Norway (Smelror 1987); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Llandovery-lower Wenlock Series, Gotland (Le Hérissé 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much

Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Llandovery Series-Permian.

Dorsennidium wenlockianum (Downie 1959 ex Wall & Downie 1963) comb. nov.

Pl. 4, fig. 2.

1959 *Veryhachium tetraëdron* var. *wenlockium* var. nov.; Downie, p. 62, pl. 12, figs 9,11 (invalid).

1962b *Veryhachium wenlockium* (Downie 1959); Stockmans & Willière, p. 29 (no fig.) (invalid).

1963 *Veryhachium europaeum* Stockmans & Willière var. *wenlockianum* var. nov.; Wall & Downie, p. 775 (no fig.).

1963 *Veryhachium europaeum* forma *wenlockianum* Downie 1959; Wall & Downie, p. 782 (no fig.).

1963 *Veryhachium europaeum* Stockmans & Willière var. *wenlockium* (Downie 1959); Downie, p. 636 (no fig.) (invalid).

1965 *Veryhachium wenlockium* Downie 1959 (as *V. tetraedron* var. *wenlockium*); Downie & Sarjeant, p. 153 (no fig.).

1990 *Veryhachium wenlockianum* (Downie 1959 ex Wall & Downie 1963) Downie & Sarjeant 1965; Fensome *et al.*, p. 527-528 (no fig.).

1994 *Veryhachium wenlockium* (Downie 1959) Downie & Sarjeant 1965; Sarjeant & Stancliffe, p. 35 (no fig.).

1994 *Dorsennidium europaeum* forma *wenlockium* (Downie 1959 *ex* Wall & Downie 1963) comb. nov.; Sarjeant & Stancliffe, p. 40 (no fig.).

Holotype. Downie 1959, pl. 12, fig. 9, Mik(P)23001; paratype, pl. 12, fig. 11, Mik(P)24001; Coalbrookdale Formation, Wenlock Series, Eaton Church, Wenlock Edge, Shropshire.

Original Diagnosis. (Downie 1959, p. 62). "The size of the test varies from 6 to 27 μ, the shape is always tetrahedral, the walls always smooth, yellow-green in colour. The processes range in length from 100 to nearly 500 per cent. of the test diameter."

Emended Diagnosis. Vesicle originally tetrahedral, laevigate, with straight or slightly convex sides. Three processes, which usually lie within the same plane, are of equal length, but the fourth process is reduced in size. Processes tapering, hollow, straight or slightly flexuous, open to the vesicle interior; laevigate or finely granulate. Excystment by unornamented rupture.

Dimensions. V=12-25μm, PL=9-50μm, PØb=1.5-3μ (10 specimens measured).

Remarks. The diagnosis of this taxon has been emended, using transmitted light and SEM studies, to clearly indicate the reduced nature of the fourth process. This species is commonly cited as being first legitimised by Wall & Downie (1963, p. 782) as *V. europaeum* forma *wenlockianum*; earlier in the paper (p. 775), however, it is clearly stated that *V. tetraëdron* var. *wenlockia* (a misspelling of *wenlockium*) was to be renamed *V. europaeum* var. *wenlockianum*, and this is the senior name. The spelling of the minor epithet as *wenlockianum* was considered to be an orthographic error by Sarjeant &

Stancliffe (1994, p. 35), who considered that the epithet should be spelt *wenlockium* as was originally intended by Downie (1959).

This species was both retained in, and transferred from, *Veryhachium* by Sarjeant & Stancliffe (1994, p. 35, 40). In both instances the authors referred to the same holotype and it must be considered that they made a simple mistake. The only clear emendation they made was to transfer the taxon to *Dorsennidium*, in so doing , however, they cited the basionym as *V. europaeum* forma *wenlockianum* (the epithet of which they spelt *wenlockium*), the junior synonym of *V. europaeum* var. *wenlockianum*.

As *V. europaeum* var. *wenlockianum* Downie 1959 ex Wall & Downie 1963 always has processes in more than a single plane it is herein transferred to *Dorsennidium* and raised to specific rank as *Dorsennidium wenlockianum*.

This taxon is similar to *D. europaeum* and *Veryhachium trisphaeridium*; four processes of equal length distinguishes *D. europaeum* and *V. trisphaeridium* has three process in a single plane.

Occurrence. Wenlock Series, England (Downie 1959, 1963); Silurian, Belgium (Martin 1966a, 1967); Klabava Shales, Arenig Series, Ordovician, Bohemia (Vavrdová 1965, 1972); lower Ludlow Series, England (Lister & Downie 1967); Devonian, Canada (Deunff 1967, specimen provisionally assigned to this species); Rochester Formation, Wenlock Series, Canada (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); lower Silurian, Ringerike, Norway (Dorning & Aldridge 1982); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Llandovery Series, Libya (Hill & Molyneux 1988); Upper Visby-lower Högklint formations, lower Wenlock Series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Arenig-Prídolí series, ? Devonian.

Dorsennidium sp. A — Pl. 5, figs 1, 3.

Description. Vesicle thin walled, square or rectangular, laevigate, hollow, often with a folded surface. There may be a single, linear, fold across the mid-section of the vesicle, or the folds may produce a square-rectangular or X-shaped pattern on the vesicle surface. Processes slender, straight or slightly flexuous, laevigate, tapering to simple tips, hollow, open to vesicle interior. Excystment mechanism not observed.

Dimensions. V=8-12µm, P =7-17µm, PØb=1-1.5µm, PN=6-8 (7 specimens measured).

Remarks. This species of *Dorsennidium* is much smaller than any of the other taxa of this genus recovered. In many respects (size and overall shape), it is similar to *Veryhachium leintwardinensis* Dorning 1981a, but differs in having more processes in more than a single plane. The thickenings/folds on the vesicle surface could suggest that this species should be placed in *Neoveryhachium*; not all of the processes, however, lie within a single plane and thus it is placed in *Dorsennidium* herein.

Occurrence. Uppermost Much Wenlock Limestone Formation (Goggin Road) and Much Wenlock Limestone-lowermost Lower Elton formation (Pitch Coppice Quarry).

Genus **Eisenackidium** Cramer & Diez 1968 ex Eisenack, Cramer & Diez 1973

Type Species. By original designation, *?Baltisphaeridium triplodermum* Cramer 1966a, p. 248-249, pl. 1, fig. 12, text-fig. 4:5; from the La Vid Formation, Emsian Stage, NW Spain (designated by Eisenack *et al.* 1973, p. 435).

Diagnosis. (Translated from Le Hérissé 1989, p. 120). "Acritarchs whose wall comprises two layers definitely separated (chambered structure). The two layers being composed of the endophragm, thick layer which delineates a spherical, triangular or polyhedric internal body, smooth or weakly ornamented; and the mesophragm, thin, transparent, often folded, which forms the processes. The form of the central body is a function of the number of processes. For certain species the endophragm develops a short, divaginate structure at the base of the processes. The 3 to 12 processes are cylindrical, hollow, simple or bifurcate; with process accessories, short and thin, sometimes present. The method of opening is unknown."

Remarks. The genus *Eisenackidium* was not validly published by Cramer & Diez (1968) as the proposed type species, *?Baltisphaeridium triplodermum* Cramer 1966a, had no designated holotype. The type species, and thus the genus, was validly published by Eisenack *et al.* (1973, p. 435, 445). *Eisenackidium* has incorrectly been considered the senior synonym of *Crameria* Lister 1970 (Eisenack *et al.* 1973, Martin 1981), which is considered, herein, a junior synonym of *Polyedrixium*; if *Eisenackidium* and *Crameria* were synonymous, *Crameria* would be the senior name (see Jardiné *et al.* 1972, p. 299).

The possibility that *Eisenackidium* and *Polyedrixium* are synonymous was raised by Playford (1977, p. 33), who felt that any reassignments should await re-examination of the type material. He questioned the nature of the central nerve-like structures reported in the processes of *E. triplodermum*, which, he noted, were present in some species of *Polyedrixium*, resulting from the junction of flaplike elements along the processes.

Eisenackidium wenlockense Dorning 1981a — Pl. 4, fig. 3.

p. 1970 *Baltisphaeridium dubitum* sp. nov.; Lister, p. 59, pl. 3, figs 2, 6 (only).
p. 1970 *Crameria* cf. *duplex* (Cramer 1964) comb. nov.; Lister, p. 62-63, pl. 5, figs 11-13, 15, ?16, text-fig. 17j (only).
1981a *Eisenackidium wenlockensis* n. sp.; Dorning, p. 188-189, pl. 2, fig. 12.
1990 *Eisenackidium wenlockense* Dorning 1981; Fensome *et al.*, p. 208 (no fig.).

Holotype. Dorning 1981a, pl. 2, fig. 12; WN28K, V38/4, MPK 2923; Much Wenlock Limestone Formation, Wenlock Series, Wrens Nest, Dudley, West Midlands (SO 935 917).

Diagnosis. (Dorning 1981a, p. 189). "Vesicle spherical to subspherical, 25-35µm in diameter, two layered wall; inner wall thick, rigid, laevigate, outer wall thin, flimsy, poorly attached to the inner wall; 3-6 processes, 14-20µm long, 4-12µm wide at base, formed of the same membrane as the outer vesicle wall, process base ill defined; processes simple or digitate, the 2-5 branches of one order; as preserved the processes are flattened, and often show longitudinal folds. Processes may be all simple or all branching, but often both will be found on the same specimen."

Description. An apparently double walled acritarch, with a moderately thick, laevigate, spherical to ellipsoidal vesicle, which appears to be encompassed by a thin membranous outer wall. The outer wall extends to form processes, which are broad based, tapering, generally simple with rounded tips, or rarely bi or trifurcate. Processes folded parallel or sub-parallel to the longest axis, giving the appearance of central nerve-like structures; rarely the processes are joined by low crests. Excystment by unornamented rupture.

Dimensions. V=16-25µm, PL=12-28µm, PØb=4.5-9µm, PN=3-5, W=1-1.5µm (8 specimens measured).

Remarks. This species appears similar to *Cymatiosphaera triangula* sp. nov. which lacks individual processes and has membranes that extend to sharp points; the junctions of these membranes can give the appearance of central nerve-like structures, similar to those seen on *E. wenlockense*.

Occurrence. Coalbrookdale-Lower Elton formation, middle Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Wenlock Series, Wenlock type area (Swire 1993); Common over the Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road; rare occurrences in the upper Lower Elton and Middle Elton formations. Known range: Sheinwoodian-lower Gorstian stages.

Eisenackidium sp. A Pl. 4, fig. 4.

Description. Acritarch which appears to have two walls. Vesicle subpolygonal, slightly thicker than processes, laevigate. The outer wall appears loosely attached to the central body and forms long, hollow, slender, laevigate processes that taper to simple tips, or are rarely bifurcate $^2/_3$rds along their length. Along the centre of the processes, parallel or sub-parallel to the longest axis, there are nerve-like structures, which extend to the process tips. Excystment mechanism not observed.

Dimensions. V=18-19µm, PL=20µm, PØb=3-4.5µm, PN=8-9 (2 specimens measured).

Remarks. This taxon is similar to *Polyedrixium pharaone* Deunff 1954a ex Deunff 1961, which differs in generally having a larger vesicle (20-25µm) and longer processes (40-50µm).

Occurrence. Much Wenlock Limestone Formation (Pitch Coppice Quarry); Much Wenlock Limestone-Lower Elton formation boundary, Goggin Road.

Genus **Estiastra** Eisenack 1959 emend. Sarjeant & Stancliffe 1994

Type Species. By original designation, *Estiastra magna* Eisenack 1959, p. 201-202, pl. 16, figs 17-20; from the Esthonus-Kalk, upper Gotlandium (Silurian), Kattentak, Estonia.

Diagnosis. (Sarjeant & Stancliffe 1994, p. 50). "Acritarchs of stellate aspect, composed of 4-10 processes arising in more than one plane. Processes very broad-based, conical to phalloid in outline; distally they may be acuminate, sometimes with a nipple-like prominence, or (rarely) briefly bifurcate, but they are never blunt or rounded and lack distinct branches. Central portion of vesicle formed by the confluence of process bases. Eilyma composed of one layer or of two layers in continuous contact; process tips may be solid or plugged. Surface psilate, punctate, granulate or pustulose, with or without striae on the processes, but not echinate and without systems of ridges connecting the process bases. Opening, where observed, by cryptosuture; when fully open, a section of the eilyma including one or two processes may be lost."

Remarks. The synonymy of *Rhiptosocherma* Loeblich Jr. & Tappan (1978) proposed by Sarjeant & Stancliffe (1994, p. 50) is rejected, as the type species, *Rhiptosocherma improcera* (Loeblich Jr. 1970) Loeblich Jr. & Tappan 1978, has blunt, rounded processes. *Estiastra* is similar to *Pulvinosphaeridium*, which differs in having blunt and rounded, not acuminate, processes; *Barbestriata* Sarjeant & Stancliffe 1994 has baculate-echinate processes; *Palacanthus* Wicander 1974 emend. Sarjeant & Stancliffe 1994 has all its processes in a single plane.

Estiastra granulata Downie 1963 — Pl. 4, fig. 8.

v*	1963	*Estiastra granulata* sp. nov.; Downie, p. 638, pl. 91, fig. 8.
cf	1965a	*Baltisphaeridium polygonale* (Eisenack 1931); Eisenack, p. 261-262, pl. 21, fig. 3.
	1965a	*Baltisphaeridium polygonale* Eis. 1931; Eisenack, pl. 24, figs 5-6.
vp.	1970	*Baltisphaeridium cantabricum* Cramer 1964 emend.; Lister, p. 58-59, pl. 3, fig. 7, pl. 4, figs 1, 4 (only).
	1977	*Goniosphaeridium polygonale* (Eisenack 1931); Eisenack, p. 30, 32, figs 18-20.
	1990	*Estiastra granulata* Downie 1963; Fensome *et al.*, p. 213 (no fig.).
	1994	*Estiastra granulata* Downie 1963; Sarjeant & Stancliffe, p. 51 (no fig.).

Holotype. Downie 1963, pl. 91, fig. 8; from Slide 9, position 120.615; WS/4a, Tickhill (=Tickwood) Beds, Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1963, p. 638). "A species of *Estiastra* 100 to 150 microns across with eight to twelve processes. The walls are thin, generally crumpled, and ornamented with a fine ornament of small closely spaced granules."

Description. Poorly preserved and often distorted by pyrite deformation. Vesicle hollow, irregular, ellipsoidal or polygonal, formed by the fusion of process bases, though on some specimens the processes appear distinct from the vesicle. Processes hollow, open to vesicle interior and tapering to simple, pointed, tips. Excystment mechanism not observed.

Dimensions. V=32-44μm, PL=40-78μm, PØb=8-16μm, PN=7-9 (7 specimens measured).

Remarks. The holotype of this taxon was reported to have an ornament of fine, closely spaced granules (Downie 1963, p. 638). On re-examination of the holotype, however, no such ornament could be seen and the roughened vesicle surface appears to be the result of preservation.

Those specimens assigned to *B. cantabricum* by Lister (1970) are divided herein into two separate taxa (*E. granulata* and *Pulvinosphaeridium dorningii* sp. nov.). Those specimens with thin walls and elongate, tapering, sharp tipped processes are assigned to this taxon; those thicker examples, often possessing a linear structure within the walls of the processes, which are broader based and taper to simple, noticeably rounded tips, are assigned to *P. dorningii* sp. nov.. Specimens from the Wenlock Series of Dudley, England, assigned to *Polygonium polygonale* by Eisenack (1965a, pl. 24, figs 5-6) are considered to belong in *E. granulata*; the holotype of *P. polygonale* has more numerous, shorter processes.

Occurrence. Coalbrookdale Formation, Wenlock Series, Shropshire (Downie 1963); Slite Formation, Wenlock Series, Gotland (Eisenack 1965a, as *B. polygonale*); Wenlock Series, Dudley, England (Eisenack 1965a, 1977, as *B. polygonale* and *G. polygonale*); Much Wenlock Limestone-Lower Elton formations, Ludlow and Millichope areas, Shropshire (Lister 1970, as *B. cantabrica*; Lister & Downie 1974, as *E. granulata* and *B. cantabricum*); upper Coalbrookdale-Lower Elton formations, Wenlock-Ludlow Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Pitch Coppice Quarry; Lower Elton Formation, Goggin Road. Known range: Sheinwoodian-lowermost Gorstian stages.

Eupoikilofusa Cramer 1970a

1973b *Moyeria*; Thusu, p. 141-142 (*nomen nudum*).

Type Species. By original designation, *Leiofusa striatifera* Cramer 1964a, p. 35-36, pl. 2, figs 9, 13 from the San Pedro Formation, probably lower Gedinnian Stage, Oblanca, NW Spain.

Diagnosis. (Cramer 1970a, p. 85). "Vesicle hollow, elongately fusiform three dimensionally to half moon shaped. A relatively short process may be present at each pole. These equivalent processes may attain up to ten percent of the length of the body proper but the length, and the presence or absence of these processes, are variable characters even in specimens from the same sample. Vesicle walls uniform, thin (0.5 micron) and psilate except for the sculptural elements. The wall is unilayered and, in general, uniform but has numerous longitudinally aligned thicker ribbles which apparently are bordered by areas of structural weakness and which cause numerous longitudinal wrinkles. Although the general appearance of this taxon is constant, the wrinkled striae which help to determine the aspect of the species are very variable indeed: not only in the length-but also in number, position and form of the wrinkles.

The longitudinal axis of the vesicle may be straight or may be curved. The species opens by a straight longitudinal split pylome situated at approximately the thickest portion of the vesicles."

Remarks. The name *Eupoikilofusa* was considered illegitimate (I.C.B.N. articles 63.1 and 63.2), and not legitimisable unless conserved, since the type species of *Dactylofusa* Brito & Santos 1965 and *Poikilofusa* Staplin *et al.* 1965 were not excluded when Cramer (1970a, p. 83) included the genera in synonymy with *Eupoikilofusa* (Fensome *et al.* 1990, p. 12). Thus, *Eupoikilofusa* was regarded as a junior synonym of *Dactylofusa* by Fensome *et al.* (1990, p. 179). Within the same publication, however, Cramer (1970a, p. 82, fig. 25b), separated, described and illustrated the type species of *Dactylofusa*, *Dactylofusa marahensis* Brito & Santos 1965. In remarks on the synonymy of *Dactylofusa*, Cramer (1970a, p. 80) indicated that he was erecting *Eupoikilofusa* to replace *Poikilofusa*; no species of *Dactylofusa* or *Poikilofusa* were transferred, however, to *Eupoikilofusa*. The author agrees with Dorning (1994) who considered *Eupoikilofusa* to be validly published and to display a distinct, characteristic striate ornament, which places it within a group of similar, fusiform acritarchs; *Leiofusa*-laevigate, *Eupoikilofusa*-striate, *Dactylofusa*-complex short processes often arranged in rows, *Poikilofusa*-small, simple processes, randomly distributed.

Eupoikilofusa filifera (Downie 1959) Dorning 1981a emend. Pl. 4, fig. 5; Pl. 10, fig. 14.

p.v*	1959	*Leiofusa filifera* sp. nov.; Downie, p. 65, pl. 11, fig. 7 (only).
	1981	*Eupoikilofusa filifera* n. comb.; Dorning, p. 181 (no fig.).
	.1989	*Eupoikilofusa striatifera typica* Cramer & Diez; Le Hérissé, p. 135-136, pl. 13, figs 9-15.
	1990	*Dactylofusa filifera* (Downie 1959) comb. nov.; Fensome *et al.*, p. 180 (no fig.).

Holotype. Downie 1959, pl. 11, fig. 7; Mik(P)10001; from the Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Original Diagnosis. (Downie 1959, p. 65). "A species of *Leiofusa* with the ends drawn out to form long hollow threads, body about one-third of total length, body width about one-quarter of its length."

Emended Diagnosis. Vesicle laevigate, hollow, thin, elongate, with striae along the length of the vesicle parallel to the longest axis. Striae result from longitudinal thickenings or folds in the vesicle wall, 3-5 per side, spaced 3-5μ apart at the widest point. At each pole, a thin, laevigate, hollow, elongate, straight or curved process is found, which lacks any striations; process-vesicle contact indistinct, processes open to the vesicle interior. Excystment by simple longitudinal rupture in the vesicle wall.

Dimensions. T=116-350μm, VL=58-132μm, VW=17-31μm (10 specimens measured).

Remarks. The second specimen assigned to this taxon by Downie (1959, pl. 11, fig. 6) does not belong in this species and is probably an example of *Leiofusa parvitartis*. The holotype of *Eupoikilofusa* *striatifera* Cramer 1964a (pl. 2, fig. 9), from the Silurian-Devonian of NW Spain, differs in having shorter processes with more longitudinal striations on the vesicle. Those specimens assigned to *Eupoikilofusa striatifera typica* (an invalid name, see Fensome *et al.*, p. 216) and illustrated by Le Hérissé (1989, pl. 13, figs 9-15) can be assigned to this *E. filifera*, as they have fewer striations and longer processes than the holotype of *E. striatifera*. Some forms illustrated by Cramer (1970a, pl. 3, fig. 51) as *E. striatifera* (age and locality unknown), are also similar to *E. filifera*, though are not included as the striae are weakly developed.

Occurrence. Coalbrookdale Formation, Wenlock Series, Shropshire (Downie 1959); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Silurian, Podolia (Kiryanov 1978); upper Llandovery Series-middle Elton Group, Ludlow Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley (Dorning 1983); Visby-Hamra formations, upper Llandovery-upper Ludlow series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road, being at its most abundant in the middle Lower Elton Formation (Goggin Road). Known range: upper Llandovery-Prídolí series.

Eupoikilofusa tenuistriata (Pöthé de Baldis 1975) Pöthé de Baldis 1981 Pl. 4, fig. 6; Pl. 11, fig. 6.

1975 *Leiofusa tenuistriata* n. sp.; Pöthé de Baldis, p. 494, pl. 3, fig. 6.

1981 *Eupoikilofusa* cf. *tenuistriata* (P. de Baldis) n. comb.; Pöthé de Baldis, p. 240, pl. 5, fig. 6.

1990 *Dactylofusa tenuistriata* (Pöthé de Baldis 1975a) comb. nov.; Fensome *et al.*, p. 182-183 (no fig.).

Holotype. Pöthé de Baldis 1975, pl. 3, fig. 6; 106.5/35.0; from the Los Espejos Formation, Wenlock Series, San Juan province, Argentina.

Diagnosis. (Translated from Pöthé de Baldis 1975, p. 494). "Vesicle of fusiform outline. Central body of elliptical outline and thin walled, with a very fine striate sculpture. The body ends abruptly, giving rise to processes which are short."

Description. Vesicle elongate, hollow; one edge almost straight, the other obviously inflated. Vesicle ornamented with fine costae (*c*. 0.3μm wide, spaced *c*. 0.05μm apart), costae run along the length of the vesicle parallel to the longest axis. Processes hollow, simple, laevigate, slightly thicker than the vesicle wall, displaced towards the straighter edge of the vesicle, with a distinct process-vesicle contact. Excystment mechanism not observed.

Dimensions. VL=40-56μm, VW=18-27μm, PL=29-41μm, PØb=2-5μm (8 specimens measured).

Remarks. This species was transferred to *Dactylofusa* by Fensome *et al.* (1990, p. 182), which they considered to be the senior synonym of *Eupoikilofusa*; the species is retained in *Eupoikilofusa*, which is considered validly published (see *Eupoikilofusa*-Remarks above).

Occurrence. Los Espejos Formation, Wenlock and Ludlow series, Argentina (Pöthé de Baldis 1975, 1981); Klinteberg (unit f), Hemse (units a, b, «marl top»), Eke (base) and Hamra (units a, b) formations, Ludlow Series, Gotland (Le Hérissé 1989); in low numbers from the upper Middle Elton Formation, Goggin Road. Known range: Wenlock-Ludlow series.

Genus **Evittia** Brito 1967 emend. Lister 1970

1966 *Evittia*; Brito, p. 78 (*nomen nudum*).
1967 *Evittia* Brito, new genus; Brito, p. 477.
1970 *Evittia* Brito 1967, mutatis characteribus; Lister, p. 66 (November).
1970 *Diexallophasis* Loeblich, n. gen.; Loeblich Jr., p. 714 (December).
1974 *Exochoderma* Wicander, n. gen.; Wicander, p. 24.

Type Species. By original designation, *Evittia sommeri* Brito 1967, p. 477, pl. 1, figs 9-12; from the Lower Devonian, Maranhão Basin, Brazil.

Diagnosis. (Lister 1970, p. 66). "Vesicle hollow, subspherical to polygonal, single walled; vesicle wall may be smooth or sculptured; processes are heteromorphic, hollow, invariably granular to echinate, communicating freely with the vesicle cavity. Excystment by cryptosuture, apical or near equatorial."

Remarks. The genus *Evittia*, as published by Brito 1966, was a *nomen nudum*, as type species, *E. sommeri*, had no designated holotype; the genus was validly published by Brito (1967, p. 477). In the original diagnosis of Brito (1966, p. 78), only the digitate nature of the process branching was mentioned and it was not until the emended diagnosis of Lister (1970, p. 66) that the granulate or echinate nature of the processes was expressed. This diagnosis of Lister (1970) encompasses those forms subsequently assigned to *Diexallophasis* by Loeblich Jr. (1970, p. 714) . The genera *Diexallophasis* and *Exochosphaeridium* , were considered junior synonyms of *Evittia* by Le Hérissé (1989, p. 125). He considered that these genera were described to encompass forms with similar morphologies to *Evittia* from the Silurian and Upper Devonian respectively, without evaluation of the intraspecific variation (Le Hérissé 1989, p. 125). In both cases, the authors did not compare their new genera to *Evittia.*

Evittia has been considered a junior synonym of *Baltisphaeridium* and *Multiplicisphaeridium* (see Fensome *et al.* 1990, p. 216), though it is now considered distinct. The digitate nature of branching and the presence of ornament on the vesicle and processes distinguishes *Evittia* from *Multiplicisphaeridium*; the processes of *Baltisphaeridium* are generally simple, though they may rarely branch, and the process cavities do not communicate with the vesicle interior.

Two species, from the Ludlow Series of NW Spain, are herein transferred to *Evittia.* Both *Multiplicisphaeridium aculeatum* and *Multiplicisphaeridium almarada* show ornamented vesicles and echinate processes, with *M. almarada* also displaying striations on the process bases. There is a possibility that these two taxa may be synonymous with other species of *Evittia* (e.g. *Evittia remota*), though no detailed synonymy is attempted herein.

Evittia aculeata (Diez & Cramer 1976) comb. nov. (= *Multiplicisphaeridium aculeatum* Diez & Cramer 1976, p. 126, pl. 3, figs 8, 10, text-fig. 3:5); *Evittia almarada* (Diez & Cramer 1976) comb. nov. (=*Multiplicisphaeridium almarada* Diez & Cramer 1976, p. 126-127, pl. 3, figs 13-14, text-fig. 3:6).

Evittia remota (Deunff 1955) Lister 1970 Group — Pl. 4, fig. 9; Pl. 11, figs 1-2.

	1955	*Veryhachium remotum* n. sp.; Deunff, p. 146, pl. 4, fig. 8.
	1963	*Baltisphaeridium denticulatum* nov. sp.; Stockmans & Willière, p. 458, pl. 1, fig. 4, text-fig. 13 (June).
	1963	*Baltisphaeridium granulatispinosum* sp. nov.; Downie, p. 640-641, pl. 91, figs 1, 7, text-fig. 3c (December).
	1969	*Baltisphaeridium furcatispinosum* n. nov.; Górka, p. 47-48, pl. 5, fig. 12 (illegitimate, see *B. denticulatum* in Fensome *et al.* 1990, p. 93-94).
	1970	*Evittia granulatispinosa* (Downie 1963) comb. nov.; Lister, p. 67-69, pl. 4, figs 2-3, 5-9, 12, pl. 5, fig. 2, text-fig. 17o, 20b.
p	1970	*Evittia remota* (Deunff 1955a) comb. nov.; Lister, p. 69-70, pl. 4, figs ?10, ?11, 13-15 (only) (November).
vp.	1970	*Multiplicisphaeridium fisherii* (Cramer 1968) comb. nov.; Lister, p. 86-87, pl. 10, fig. 18 (only).
	1970	*Diexallophasis denticulata* (Stockmans & Willière) n. comb.; Loeblich Jr., p. 715-716, figs 8 A-E, 9 A-C (December).
	1972	*Baltisphaeridium rojense*; Yankauskas & Vaiteunene, p. 121, pl. 17, figs 10-11, text-fig. 3.
	1973	*Multiplicisphaeridium denticulatum* (Stockmans & Willière 1963); Eisenack *et al.*, p. 587-591.
	1973	*Multiplicisphaeridium granulatispinosum* (Downie 1963); Eisenack *et al.*, p. 653.
	1973	*Multiplicisphaeridium remotum* (Deunff 1955); Eisenack *et al.*, p. 773.
	1974	*Diexallophasis granulatispinosa* (Downie) comb. nov.; Hill, p. 12 (no fig.).
	1974	*Peteinosphaeridium granulatispinosum* (Downie); Piskun, caption to pl. 12, fig. 12 (invalid combination).
	1977	*Diexallophasis remota* (Deunff) comb. nov., emend; Playford, p. 19-21, pl. 6, figs 12-14; pl. 7, figs 1-11, text-fig. 8.
	1989	*Evittia denticulata denticulata* (Cramer) comb. nov.; Le Hérissé, p. 126-127, pl. 11, figs 1-6.
	1990	*Diexallophasis remota* (Deunff 1955a) emend. Playford 1977; Fensome *et al.*, p. 198-199 (no fig.).
	1994	*Evittia remota* (Deunff 1955) Lister 1970; Sarjeant & Stancliffe, p. 55 (no fig.).

Holotype. Deunff 1955, p. 146, pl. 4, fig. 8; H-77, RU; from the matrix of a loose coral (*Favosites turbinata*), Onondaga Limestone, Devonian, Ontario, Canada.

Diagnosis. (Playford 1977 for *Diexallophasis remota*, p. 19-20). "Vesicle originally spherical or nearly so; outline variable-circular, subcircular, square, triangular, rectangular, or polygonal. Wall of vesicle single-layered, up to 1.5µm thick (average 0.7µm); almost smooth to faintly granulate or scabrate under light microscope; microgranulate, granulate, microgranulate to micropunctate, microrugulate, or microreticulate under scanning electron microscope. Long, slender, ± flexible processes distributed fairly regularly on vesicle; number variable, usually 4-12, average 6-7, rarely as many as 18-20. Processes heteromorphic or near heteromorphic, with essentially hollow interiors, and constituting drawn-out, basically subcylindrical extensions of vesicle wall, freely communicating with vesicle cavity. At proximal ends, processes have curved to angular contacts with wall of vesicle; distal extremities simple or, more typically, branched (bifurcate to first, second or rarely third order; or digitate). Branching often somewhat asymmetrical. Length of processes variable, from about 0.8 to 2.0 times vesicle diameter. Processes sculptured sparsely to moderately densely echinate to granulate elements, and in some specimens, with discontinuous, fine, subparallel (longitudinal) ridges that are usually developed proximally as a type of substriate subsidiary sculpture. Spines on processes up to 2 µm long, usually about 0.5- 1 µm. Excystment, rarely observed, is by simple rupture of vesicle wall."

Description. Vesicle thin walled, laevigate to faintly scabrate under transmitted light, with tetrahedral, rectangular, square, polygonal or spherical outline. With a SEM, the vesicle surface appears laevigate, granulate, microfoveolate, micropunctate or granoreticulate. Processes hollow, slender, straight or slightly flexuous, tapering to simple or digitate tips, rarely branched from half way along their length; processes slightly echinate or echinate under transmitted light, with a SEM the processes appear echinate, with the majority of their bases appearing striate; the striae just extend onto the vesicle surface. Excystment via rupture, which can be ornamented with large grana along its length.

Dimensions. V=13-40µm, PL=18-53µm, PØb=2.5-8.5µm, PN=4-10 (10 specimens measured).

Remarks. The diagnosis given above is the emended diagnosis proposed by Playford (1977) for *D. remota*, a junior synonym of *E. remota*. The species *Diexallophasis caperoradiola* Loeblich Jr. 1970 has a diagnosis that falls within the variation of the *E. remota* Group (as applied herein) and was considered a possible junior synonym of *E. remota* by Playford (1977, p. 21). The variation described in *D. remota* by Playford (1977) was considered too broad by Wicander & Wood (1981, p. 33), who separated forms possessing only simple processes into *Diexallophasis simplex* Wicander & Wood 1981.

Le Hérissé (1989), in describing specimens similar to those described here, used the name *E. denticulata*, considered a junior synonym of *E. remota* herein; he excluded *E. remota* from his synonymy, indicating that he considered it a distinct species. He also used vesicle ornament to subdivide *Evittia* into a number of species and subspecies (Le Hérissé 1989, p. 126-129, 131). Although the use of vesicle ornament has a use for subdivision, it is only practicable when using scanning electron microscopy. Specimens recovered in this study, which show a variety of vesicle ornament with a SEM (see Description above), have, therefore, been placed within an informal *E. remota* group.

Occurrence. This taxon has a very wide geographical and stratigraphical range, see Eisenack *et al.* (1973, p. 594, 596, 598, 600, 602, 604, 773) for a list of pre 1973 occurrences. Only the UK occurrences of this taxon are listed. Buildwas Formation, Wenlock Series, Shropshire (Downie 1963); Much Wenlock Limestone-Downton Castle Sandstone formations, upper Wenlock-Přídolí series, Shropshire (Lister 1970, Lister & Downie 1974); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Wenlock Series, Ayrshire (Dorning 1982); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Ashgill-Llandovery series, Libya (Hill & Molyneux 1988); Llandovery Series, type Llandovery area (Hill & Dorning 1984); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road. Known range (global): Silurian-Devonian.

Evittia robustispinosa (Downie 1959) Le Hérissé 1989 emend. Pl. 5, fig. 6; Pl. 10, figs 15-16.

v*	1959	*Baltisphaeridium robustispinosum* sp. nov.; Downie, p. 61, pl. 10, fig. 7.
	1973	*Tylotopalla robustispinosum* (Downie); Eisenack *et al.*, p. 1071-1072.
p	1978	*Tylotopalla tappanae* sp. nov.; Kiryanov, p. 87, pl. 13, fig. 7 (only).
	1989	*Evittia robustispinosa* (Downie) Lister; Le Hérissé, p. 129-130, pl. 12, figs 6-10.
	1990	*Tylotopalla robustispinosum* (Downie 1959) Eisenack *et al.* 1973; Fensome *et al.*, p. 500 (no fig.).

Holotype. Downie 1959, pl. 10, fig. 7; Mik(P)9002; from the Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Original diagnosis. (Downie 1959, p. 61). "A species of *Baltisphaeridium* with a more or less spherical test, diameter about 30μ, processes about 10μ, stout, 4μ wide at base, 10 to 15μ apart, about seven seen at circumference, surface of processes granular, terminated by a short hair, sometimes broken."

Emended diagnosis. Vesicle spherical to ellipsoidal, granulate under transmitted light, granoreticulate with a SEM. Processes short, broad based, echinate along their length, hollow and open to the vesicle interior. Under transmitted light the processes can appear simple, with pointed tips, or branched due to distal echinae. Excystment by rupture of the vesicle wall.

Dimensions. V=23-33μm, PL=8-17μm, PØb=3-8μm, PN=11-18 (7 specimens measured).

Remarks. The diagnosis has been emended to include new information from SEM work. The synonomy of *Tylotopalla wenlockia* Dorning 1981a, proposed by Le Hérissé (1989, p. 129), is rejected herein, as *T. wenlockia* has processes which are much more elongate than those of *E. robustispinosa.* The transfer of *robustispinosum* to *Evittia* was attributed to Lister (1970) by Le Hérissé (1989, p. 129). In his monograph, Lister indicated that *B. robustispinosum* should be transferred to *Evittia*; he did not, however, clearly use the name *E. robustispinosa* and the combination was not validly published.

Occurrence. Coalbrookdale Formation, Wenlock Series, Shropshire (Downie 1959); Ludlow Series, Shropshire (Lister & Downie 1967); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Ludlow Series, Podolia (Kiryanov 1978, as *T. tappanae*); Buildwas-Much Wenlock Limestone formations, Wenlock Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); upper Llandovery Series, Libya (Hill & Molyneux 1988); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Llandovery-Wenlock series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); very rare from the upper Lower Elton-Middle Elton formations, Goggin Road. Known range: Llandovery-lower Ludlow series.

Genus **Glyptosphaera** Kiryanov 1978

Type Species. By original designation, *Glyptosphaera speciosa* Kiryanov 1978, p. 53, pl. 4, figs 1-2; Ludlow Series, Podolia.

Diagnosis. (Translated from Kiryanov 1978, p. 52-53). "Vesicle spherical, single walled, relatively thick walled. The surface is covered by rather low crests or spines which create a characteristic pattern. Now and then the crests divide into short right angled branches or go basically parallel. Crests divide seldom so that it is impossible to pick out some of their separations. Specimen pattern has some tendency towards symmetry."

Remarks. The nature of the membranes differentiates *Glyptosphaera* from *Cymatiosphaera* and *Dictyotidium*, which have membranes or ridges that are joined, forming a closed series of fields. The large size range of individuals of the species assigned to *Glyptosphaera* herein may indicate that this genus is a prasinophyte alga. The presence of pylomes, not ruptures, in individuals of *Glyptosphaera speciosa* (see below), however, suggests its exclusion.

Glyptosphaera heltaskelta sp. nov. Pl. 4, fig. 10; Pl. 11, figs 15-16.

Name. Species name *heltaskelta*, after the fairground ride helta-skelta, in which a slide spirals around a central column.

Holotype. Pl. 11, fig. 15; TRENCH4/176-A (SEM)-L40; from the Middle Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle laevigate, spherical to ellipsoidal, single walled. Cristae, which may appear crenulate along their length, swirl around the vesicle, producing a distinctive concentric pattern. Excystment mechanism not observed.

Dimensions. V=16-56μm, C=up to 1.5μm, W=up to 4μm (9 specimens measured).

Remarks. The majority of specimens of this taxon have relatively thick walls (3-4μm) and large vesicles (35μ-56μm). One example (Pl. 11, fig. 16) is much smaller (V = 16μm) and has a thinner vesicle wall. It possesses, however, an identical arrangement of cristae and has been included in this taxon, which appears to display a similar range of sizes as *G. speciosa.* The large specimen illustrated by transmitted light (Pl. 4, fig. 10) has crenulate cristae, which sometimes appear to join, with rare central nodes being visible. This may suggest a close link between *G. heltaskelta* sp. nov. and the prasinophyte algal taxa *M. amydra.*

Forms assigned to *G. speciosa* by Le Hérissé (1989, p. 139, pl. 14, figs 18-20) appear superficially similar to *G. heltaskelta* sp. nov. in possessing generally unbranched cristae which swirl around the vesicle. The cristae on *G. heltaskelta* sp. nov. are, however, much more densely packed and have, on occasion, a crenulate appearance along their length. *G. heltaskelta* sp. nov. is differentiated from *G. speciosa* by its generally larger, thicker vesicle and characteristic swirling pattern of occasionally crenulate, unbranched, cristae.

Occurrence. Rare in the Lower Elton Formation, becoming more common in the Middle Elton Formation, Goggin Road.

Glyptosphaera speciosa Kiryanov 1978 Pl. 5, fig. 7; Pl. 11, figs 13-14.

1971 Example of cristate ornament; Tappan & Loeblich Jr., pl. 1, fig. 16.

1978 *Glyptosphaera speciosa* sp. nov.; Kiryanov, p. 53, 54, pl. 4, figs 1, 2.

1990 *Glyptosphaera speciosa* Kiryanov 1978; Fensome *et al.*, p. 232 (no fig.).

Holotype. Kiryanov 1978, pl. 4, fig.1; Ludlow Series, Podolia.

Diagnosis. (1978, p. 53-In Russian).

Description. Vesicle laevigate, spherical to ellipsoidal, single walled. Cristae generally branched, producing a characteristic labyrinth-like pattern; occasional small node-like structures may also be present. Excystment possibly by pylome.

Dimensions. V=15-48μm, C=0.2-0.5μm, W=0.75-1.5μm (19 specimens measured).

Remarks. This species was first figured as a scanning electron microphotograph by Tappan & Loeblich Jr. (1971, pl. 1, fig. 16), who used it as an example of cristate ornament. Some examples, illustrated and assigned to *G. speciosa* (Le Hérissé 1989, p. 139, pl. 14, figs 18-20) differ from the type material and specimens recovered here, in having cristae which do not branch to the same degree and form a swirl-like pattern on the vesicle, similar to that seen in *G. heltaskelta* sp. nov.; the placing of these examples into *G. speciosa* is questioned. One specimen (Le Hérissé 1989, pl. 14, fig. 17), however, shows cristae with a higher degree of branching and can be included in *G. speciosa.*

The size range of *G. speciosa* has been expanded to include very small, thin walled forms (pl. 11, fig. 14). These small specimens have an identical arrangement of cristae to their larger counterparts and a few specimens also show circular pylomes (diameter = 6μm).

This species differs from *G. heltaskelta* sp. nov. in being generally smaller, thinner walled, with less densely arranged, branched, cristae.

Occurrence. Silurian, Podolia (Kiryanov 1978); Högklint-Hamra formations, lower Wenlock-upper Ludlow series, Gotland, Le Hérissé 1989); rare over the much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), low abundances throughout the lower Elton Formation, becoming more common in the Middle Elton Formation, Goggin Road. Known range: Wenlock-Ludlow series.

Genus **Gorgonisphaeridium** Staplin, Jansonius & Pocock 1965

Type Species. By original designation, *Gorgonisphaeridium winslowii* Staplin, Jansonius & Pocock 1965, p. 193, pl. 19, figs 11, 18-20, text-fig. 4; Imperial Grassy Lake No. 3, 2-35-10-13-W4M, Southern Alberta; core, 3904', Banff Formation, Lower Mississippian, Carboniferous.

Diagnosis. (Staplin *et al.* 1965, p. 192). "Vesicles spherical; wall firm, relatively thick, smooth or with minute sculpture; spines numerous, solid, usually sinuous, slender or broad, of same material as vesicle wall. Tips simple or distally branched, flexible, bases may be slightly bulbous; vesicle size of known species relatively large."

Remarks. This genus differs from *Multiplicisphaeridium* in having processes which are solid, not hollow. Fensome *et al.* (1990, p. 238) considered the diagnosis of *Gorgonisphaeridium* to have been emended by Kiryanov (1978, p. 14-15). In the systematics section of his paper, however, there is no indication that any emendation was intended (Kiryanov 1978, p. 55).

Gorgonisphaeridium citrinum (Downie 1963) comb. nov. Pl. 5, fig. 4; Pl. 11, figs 11, 12.

v* 1963 *Lophosphaeridium citrinum* sp. nov.; Downie, p. 630-631, pl. 92, fig. 3.

1971 *Buedingiisphaeridium citrinum* (Downie 1963); Cramer, caption to pl. 3, fig. 13. (invalid combination, basionym not fully referenced).

1974 *Baltisphaeridium* aff. *citrinum* (Downie, Ch., 1963) nov. comb.; Stockmans & Willière, p. 12 (no fig.).

1990 *Baltisphaeridium citrinum* (Downie 1963) Stockmans & Willière 1974; Fensome *et al.*, p. 90 (no fig.).

Holotype. Downie 1963, pl. 92, fig. 3; Slide 5, WS/4a; from the Tickhill (=Tickwood) Beds, upper Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1963, p. 630-631) "Vesicle ellipsoidal, lemon yellow in colour. Ornament of capitate spine (pilae). Body size about 40 by 30 microns; spine length 1 to 2 microns, spacing 1 to 2 microns."

Description. Vesicle spherical to ellipsoidal, with a single, thin to moderately thick, laevigate wall. The vesicle is covered with numerous short, solid processes, which may be straight or flexuous, tapering or columnar, with simple or capitate tips. Excystment by unornamented rupture.

Dimensions. V= 6-29μm, PL=0.7-3μm, PØb=0.25-1μm (9 specimens measured).

Remarks. This species generally has a thinner vesicle wall than *G. succinum*, which also has fewer, longer processes, which are branched, not capitate. The diagnosis in Downie (1963) cites vesicle size as "40 by 30 microns", which is larger than those specimens recovered here. In his remarks, Downie (1963) states that most examples excyst via a pylome, the holotype shows no excystment structures; examples herein excyst via a rupture (Pl. 11, fig. 11).

The transfer of this taxon to *Baltisphaeridium* by Stockmans & Williere (1974) is rejected, as the holotype has a single wall and solid, simple or capitate processes.

Occurrence. Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1963); Much Wenlock Limestone-Lower Elton Formation, Pitch Coppice Quarry and Goggin Road; absent from the upper Lower Elton Formation, more common in the Middle Elton Formation, Goggin Road. Known range: Sheinwoodian-lower Gorstian stages.

Gorgonisphaeridium ? **listeri** sp. nov. Pl. 5, figs 10-11.

1970 *Gorgonisphaeridium* sp. nov.; Lister, p. 75, pl. 8, figs 5-7.

non. v* 1981a *Gorgonisphaeridium bringewoodensis* n. sp.; Dorning, p. 185-186, pl. 2, fig. 5.

Name. Species name *listeri*, after T. R. Lister who first described this taxon.

Holotype. Pl. 5, fig. 11; GOG12/302-A (2)-Q29/3; from the Middle Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. Vesicle ellipsoidal, subspherical, rarely subtriangular (convex sides), with a single, moderately thick wall. The vesicle has two distinct levels of ornament; a reticulate pattern (formed by the expanded, bulbous process bases) and processes. The processes are thin, solid, tapering, with generally simple tips, though some appear to possess small structures at their extremities. Excystment by unornamented rupture.

Dimensions. V=25-34μm, PL=1.5-6μm, W=0.75-1.5μm (8 specimens measured).

Remarks. Dorning (1981a, p. 185) included those specimens illustrated as *Gorgonisphaeridium* sp. nov. by Lister (1970) in synonymy with his new species *G. bringewoodensis*. The holotype of *G. bringewoodensis* lacks bulbous process bases, which produce the reticulate pattern on the vesicle of *G.* ? *listeri*, and is considered a distinct species. *G.* ? *listeri* appears very similar to *G.* ? *listeri* var. A, which has more processes and a smaller reticulate pattern on the vesicle.

Specimens recovered here are generally smaller than those recovered by Lister (1970, V = 31-40μm). This taxon, and the variant described below, have been provisionally included in *Gorgonisphaeridium* as they can appear subtriangular, raising the possibility that they are perhaps sporomorphs, though no other structures have been observed that would confirm this.

Occurrence. Upper Elton-Upper Bringewood formations, Ludlow Series, Ludlow and Millichope, Shropshire (Lister 1970); Middle Elton Formation, Goggin Road. Known range : Gorstian Stage.

Gorgonisphaeridium ? listeri var. A Pl. 5, figs 12-13.

Description. Vesicle single walled, generally subspherical or ellipsoidal, rarely subtriangular with convex sides. The vesicle has a dense covering of very thin, solid processes which taper to simple tips. The process bases are slightly bulbous, though this is difficult to observe on most specimens, and this produces a fine reticulate pattern on the vesicle surface. Excystment by simple, unornamented rupture.

Dimensions. V=22-31μm, PL=1-6μm, W=0.5-1μm (8 specimens measured).

Remarks. This taxon differs from *G. ? listeri* in possessing a much more dense arrangement of processes and a finer reticulate pattern on the vesicle (diameter = 0.5-1μm vs' 1.5-3μm). As stated above (*G. ? listeri*-Remarks) the subtriangular shape of some specimens may raise the possibility that this taxon is a sporomorph.

Occurrence. Much Wenlock Limestone-Lower Elton formation, Pitch Coppice Quarry and Goggin Road, Ludlow.

Gorgonisphaeridium ramosum Pöthé de Baldis 1981 Pl. 5, fig. 2; Pl. 11, figs 7-8.

1981 *Gorgonisphaeridium ramosum* n. sp.; Pöthé de Baldis, p. 243, pl. 4, fig. 4.

1990 *Gorgonisphaeridium ramosum* Pöthé de Baldis 1981; Fensome *et al.*, p. 239 (no fig.).

Holotype. Pöthé de Baldis 1981, pl. 4, fig. 4; Los Espejos Formation, lowest Ludlow Series, Los Azulejitos, San Juan Province, Argentina.

Diagnosis. (Translated from Pöthé de Baldis 1981, p. 243). "Vesicle of circular outline with a central body of membrane thin and smooth. Numerous, homomorphic, solid processes present, no connections with the interior of the central body, ramified evenly to third order at different stages along their length. The membrane of the central body and that of the processes is of the right type."

Description. Vesicle spherical to ellipsoidal, very thin walled, almost transparent; faintly scabrate under transmitted light, microrugulate with a SEM. Processes numerous, solid, noticeably thicker than vesicle wall, tapering slightly with irregularly branched tips (up to 3rd order). Excystment mechanism not observed

Dimensions. V=15-24μm, PL=4-8.5μm, PØb=1-2μm (6 specimens measured).

Remarks. This species resembles *Gorgonisphaeridium succinum*, but differs in having processes that are considerably thicker than the vesicle wall, which is thin and almost transparent.

Occurrence. Los Espejos Formation, lowest Ludlow Series, San Juan Province, Argentina (Pöthé de Baldis 1981); rare over the Much Wenlock Limestone-Lower Elton formation boundary and into the Lower Elton Formation, Pitch Coppice Quarry and Goggin Road. Known range: topmost Wenlock-lowermost Ludlow series.

Gorgonisphaeridium succinum Lister 1970 Pl. 5, fig. 8; Pl. 11, figs 9-10.

v* 1970 *Gorgonisphaeridium succinum* sp. nov.; Lister, p. 75, pl. 8, figs 1-4.
1973 *Multiplicisphaeridium succinum* (Lister 1970); Eisenack *et al.*, p. 805-806.
1978 *Gorgonisphaeridium succinum* Lister 1970; Kiryanov, p. 55, pl. 7, figs 7-9a, b.
1990 *Gorgonisphaeridium succinum* Lister 1970; Fensome *et al.*, p. 240 (no fig.).

Holotype. Lister 1970, pl. 8, fig. 1; Lower Elton Formation, Ludlow Series, LD3, Pitch Coppice Quarry, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 75). "Vesicle hollow, spherical, thick-walled (one layer), smooth to minutely verrucate; numerous closely spaced processes, less than $^1/_3$ of vesicle diameter in length; processes appear as solid outgrowths of vesicle wall, tapering only very slightly distally and branching irregularly. Excystment by cryptosuture; no dehiscent specimens have so far been found."

Description. Vesicle ellipsoidal to spherical, thin to moderately thick walled, laevigate or granulate. Processes numerous, solid, slightly tapering along their length, branching irregularly (up to 3rd order). Excystment by unornamented rupture.

Dimensions. V=16-24µm, PL=3.5-11µm, PØb=0.7-2µm, W=0.5-1.5µm (11 specimens measured).

Remarks. The very thin vesicle and thicker processes of *G. ramosum* separate it from *G. succinum*. The vesicle of the holotye is laevigate.

Occurrence. Common in the Much Wenlock Limestone and Lower Elton formations, Ludlow and Millichope areas; rare in the Upper Coalbrookdale, Upper Elton and Lower Whitcliffe formations, middle Wenlock-Ludlow series, Ludlow type area, Shropshire (Lister 1970, Lister & Downie 1974); Silurian, Podolia (Kiryanov 1978); Slite (unit f, marl of NW), Slite-Sundre formations, middle Wenlock-Pŕídolí series (Le Hérissé 1989); Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road, becoming less common through the Lower Elton Formation, then more common in the Middle Elton Formation (Goggin Road). Known range: Sheinwoodian Stage-Pŕídolí Series.

Gorgonisphaeridium sp. A Pl. 5, fig. 5.

Description. Vesicle laevigate, subspherical to subtriangular, with a single moderately thick wall. The processes are numerous, straight, solid, long, thin, columnar with simple or branched tips. Excystment mechanism not observed.

Dimensions. V=18-20µm, PL=2-2.5µm, PØb=0.2µm, W=1-1.5µm (6 specimens measured).

Remarks. This species differs from *G. succinum* in being smaller, with a subspherical to subtriangular vesicle and has much thinner, columnar processes; the processes of *G. citrinum* are broader and shorter.

Occurrence. Much Wenlock Limestone-Middle Elton Formation, Pitch Coppice Quarry and Goggin Road.

Gorgonisphaeridium sp. B Pl. 5, fig. 9.

Description. Vesicle ellipsoidal or spherical, with a single, moderately thick wall. Processes short, solid, broad based, columnar or slightly tapering, simple or commonly bifurcate, occasionally further subdivided.

Dimensions. V=23-28μm, PL=3-8μm, PØb=1.5-4μm, W=0.75-1μm, PN=28-37 (3 specimens measured).

Remarks. This taxon, which has been recovered in only a few samples, has been placed in *Gorgonisphaeridium* because it possesses a single wall, from which solid processes arise.

Occurrence. Very rare, being recovered from the Much Wenlock Limestone Formation, Pitch Coppice Quarry and Lower Elton Formation, Goggin Road.

Genus **Hapsidopalla** Playford 1977 emend. Wicander & Wood 1981

Type Species. By original designation, *Micrhystridium sannemanni* Deunff 1957, p. 6; p. 13, fig. 1; p. 14, figs 5-9; Devonian, l'Amerique du Nord, France.

Diagnosis. (Playford 1977, p. 25). "Vesicle hollow, apparently single-layered, originally spherical to ellipsoidal; outline circular to subcircular or oval, clearly differentiated from processes. Numerous, ± evenly spaced, hollow, essentially homomorphic and smooth processes project from vesicle wall and branch distally; tips closed. Though discrete from one another, adjacent processes are interconnected proximally by muri that form a distinct ± uniform reticulum sculpturing the vesicle surface; processes characteristically project from junctions of muri, never from lacunae. Lacunae typically triangular to polygonal. Interior of processes in free communication with vesicle cavity. Excystment by splitting of vesicle wall."

Emended Diagnosis. (Wicander & Wood 1981, p. 42-43). " This genus is emended here to include those forms with rosette-like vesicle sculpture and acuminate processes."

Remarks. The vesicle ornament, process nature and method of excystment separate this genus from several others. *Ammonidium* and *Helosphaeridium* do not possess the low ridges that join the processes together, and the presence of a pylome, not a rupture, separates *Stelliferidium* Deunff, Górka & Rauscher 1974.

Histopalla Playford in Playford & Dring 1981 is very similar to *Hapsidopalla* and is distinguished by its unbranched, solid processes. Both taxa have vesicles ornamented by low ridges which radiate from the base of the processes; this could be used to suggest that the difference in process nature should be considered of interspecific, not intergeneric importance.

Hapsidopalla jeandeunffii Le Hérissé 1989 Pl. 5, fig. 14; Pl. 11, figs 17-18.

1989 *Hapsidopalla jeandeunffii* n. sp.; Le Hérissé, p. 142-143, pl. 17, figs 5-6.

Holotype. Le Hérissé 1989, pl. 17, figs 5-6; marl of the Hemse Formation, Ludfordian Stage, Ludlow Series, Gotland.

Diagnosis. (Translated from Le Hérissé 1989, p. 142). "A species of the genus *Hapsidopalla* with a spherical vesicle ornamented with numerous processes, very short, homomorphic, conical, terminating with a rosette of four filamentous spines; the processes are equidistant, linked by crests which delineate a regular network with rosace pattern; the walls have a simple pattern, with cylindrical section; the processes are hollow and communicate with the vesicle cavity; opening type simple split."

Description. Vesicle spherical to ellipsoidal, with a single, thin, laevigate wall. Processes numerous, evenly spaced over vesicle surface, short, columnar or slightly tapering with expanded bases. The tips of the processes appear capitate under transmitted light, with a SEM they appear capitate or branched; branches short, 2-4 in number, arranged around the tip in a rosette. The bases of the processes are joined by low ridges. Excystment by large, unornamented rupture.

Dimensions. V=18-29µm, PL=1-2.5µm (12 specimens measured).

Remarks. H. jeandeunffii appears similar to *Histopalla margarita* Le Hérissé 1989, which has simple, solid, processes whose bases are joined by more numerous ridges (10-12 vs' 5-6).

Occurrence. Upper part of the Mulde, Klinteberg (unit f), Hemse and basal Eke formations, Homerian-Ludfordian stages, Wenlock-Ludlow series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road, particularly common in the Middle Elton Formation, Goggin Road. Known range: Homerian-Ludfordian stages.

Genus **Helosphaeridium** Lister 1970

Type Species. By original designation, *Helosphaeridium clavispinulosum* Lister 1970, p. 76, pl. 8, figs 8,12,16, text-figs 18g,27b; Lower Elton Formation, Ludlow Series, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 76). "Vesicle single-walled, hollow, spherical to ellipsoidal with ornament of small, numerous, evenly spaced, solid or hollow processes flaring distally in a claviform fashion. Excystment by cryptosuture."

Remarks. Processes which expand distally separate this genus from *Lophosphaeridium*, which has an ornament of solid tubercles, which are not capitate distally.

Helosphaeridium clavispinulosum Lister 1970 Pl. 5, fig. 15; Pl. 11, fig. 19; Pl. 12, fig. 1.

v* 1970 *Helosphaeridium clavispinulosum* sp. nov.; Lister, p. 76, pl. 8, figs 8, 12, 16, text-figs 18g, 27b.

1990 *Helosphaeridium clavispinulosum* Lister 1970; Fensome *et al.*, p. 246 (no fig.).

Holotype. Lister 1970, pl. 8, fig. 12; MPK 156, L1; Lower Elton Formation, Ludlow Series, Ledbury, Herefordshire, UK.

Diagnosis. (Lister 1970, p. 76). "Ellipsoidal, hollow, thin-walled vesicle with ornament of small cones or tubes with capitate tips. Size of the ornament varies from 1-1.5μ, spacing is variable from 1.7-3μ, but within a given individual spacing and size are constant. Excystment by near-equatorial cryptosuture producing hemicysts."

Description. Vesicle laevigate, ellipsoidal, hollow, with a thin, single wall. The vesicle is covered with an ornament of numerous, short, columnar processes, that have a sharp contact with the vesicle. The processes appear solid, most have capitate tips, though with a SEM some are seen to possess a rosette arrangement of bumps, which appears to be the start of branching. Excystment by large, unornamented rupture, which almost divides the vesicle into two equal halves.

Dimensions. V=24-34μm, PL=1.5μm (3 specimens measured).

Remarks. This species closely resembles *H. jeandeunffii*, which differs in having processes that are joined by low ridges. Specimens recovered in the present study are smaller than those recorded by Lister (1970) (V = 24-34μm (herein) compared to VL = 38-58μm, VW = 21-35μm)

Occurrence. Lower-Upper Elton formations, Ludlow Series, Ludlow and Millichope areas, Shropshire (Lister 1970, Lister & Downie 1974); lower Silurian, Ringerike, Norway (Smelror 1987); Silurian, Argentina (Rubinstein 1993, as *H.* cf. *clavispinulosum*); very rare from the Much Wenlock Limestone and Lower Elton formations, Goggin Road. Known range: Llandovery-Ludlow series.

Helosphaeridium latispinosum Lister 1970 Pl. 5, fig. 16.

v* 1970 *Helosphaeridium latispinosum* sp. nov.; Lister, p. 77, pl. 8, figs 15, 18-19, text-fig. 27c.

non. 1973b *Helosphaeridium latispinosum* Lister 1970; Thusu, p. 138, pl. 1, figs 21-23.

1990 *Helosphaeridium latispinosum* Lister 1970, Fensome *et al.*, p. 246 (no fig.).

Holotype. Lister 1970, pl. 8, fig. 19; MPK163, MD6; Upper Elton Formation, Ludlow Series, NW of Dinchope, Shropshire, UK.

Diagnosis. (Lister 1970, p. 77). "Vesicle hollow, more or less ellipsoidal, relatively thin-walled. Processes numerous, evenly spaced, uniform, small (c. 0.8μ), parallel sided (c. 0.9μ wide), with dilated terminations. Excystment by cryptosuture producing hemicysts."

Description. Vesicle spherical to ellipsoidal, thin, hollow, covered with a dense arrangement of short processes. Processes appear solid, with expanded tips; on some well preserved specimens the tips seem to join, giving the appearance of an outer sheath. Excystment by large, unornamented rupture, which almost divides the vesicle in two.

Dimensions. V=29-38µm, PL=0.25-1µm (8 specimens measured).

Remarks. Width of processes was originally used to separate this species from *Helosphaeridium pseudodictyum*, which possesses narrower processes (Lister 1970). As with *H. pseudodictyum*, this species closely resembles *Percultisphaera stiphrospinata*, which differs in possessing a second ornament of thin, solid, wiry processes. As their morphologies are so similar, *H. pseudodictyum* and *H. latispinosum* could be considered to represent the end members of an intraspecific variation within a single species. Examples of *P. stiphrospinata* show a similar variation with forms possessing both broad and narrow first order ornament.

Occurrence. Upper Elton-Lower Leintwardine formations, Ludlow Series, Ludlow and Millichope areas, Shropshire (Lister 1970, Lister & Downie 1974); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); upper Middle Elton Formation, Goggin Road. Known range: Sheinwoodian-Ludfordian stages.

Helosphaeridium pseudodictyum Lister 1970 Pl. 5, fig. 18.

v* 1970 *Helosphaeridium pseudodictyum* Lister, p. 76, 77, pl. 8, figs 9-11, 13, 14, 17, text-figs 18d, 18e, 27a.

.1973b *Helosphaeridium latispinosum* Lister 1970; Thusu, p. 138, pl. 1, figs 21-23.

1990 *Helosphaeridium pseudodictyum* Lister 1970; Fensome *et al.*, p. 246 (no fig.).

Holotype. Lister 1970, pl. 8, fig. 10, text-fig. 18d; MPK 154; Lower Elton Formation, Ludlow Series, LD54A, Eaton Lane, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 76). "Vesicle more or less ovoid, moderately thin-walled; ornament of numerous, evenly-spaced, small, parallel-sided outgrowths which flare distally (as shown in Text-fig. 27a), frequently making contact with those adjacent. Excystment by cryptosuture."

Description. Vesicle thin, hollow, ellipsoidal, rarely spherical, with in a dense arrangement of short processes. Processes appear solid, with expanded tips; on well preserved specimens the tips seem to join, giving the appearance of an outer sheath. Excystment by large, unornamented rupture, which almost splits the vesicle in two.

Dimensions. V=28-37µm, PL= <0.5µm (10 specimens measured).

Remarks. This species is similar to *H. latispinosum* and *P. stiphrospinata* (see *H. latispinosum*-Remarks above).

Occurrence. Wenlock Shales, Millichope; Much Wenlock Limestone-Upper Bringewood formations, Ludlow and Millichope areas; Lower-Upper Leintwardine formations, Ludlow area, Shropshire (Lister 1970); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b, as *H. latispinosum*); Much Wenlock Limestone-Upper Leintwardine formation, Wenlock-Ludlow series, Ludlow (Lister & Downie 1974); Buildwas -Whitcliffe formation, Wenlock-Ludlow series, Welsh Borderland (Dorning 1981a); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Visby, Högklint and Slite formations, upper Llandovery-Wenlock series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993, as *H.* cf. *pseudodictyum*); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: upper Llandovery-Ludlow series.

Helosphaeridium sp. A Pl. 5, fig. 19.

Description. Vesicle ellipsoidal, single walled, covered in an ornament of short, solid, projections, that are regularly distributed over the vesicle; under transmitted light these projections appear capitate or rounded. Excystment mechanism not observed.

Dimensions. VL=34-39μm, VW=22-26μm, Ornament=0.5-1μm high (3 specimens measured).

Remarks. This taxon is separated from *H. pseudodictyum* and *H. latispinosum* by its ornament of fewer, larger, processes.

Occurrence. Uppermost Lower Elton Formation, Goggin Road.

Helosphaeridium sp. B Pl. 5, figs 17, 21.

Description. Vesicle spherical to ellipsoidal, moderately thick walled, laevigate. The vesicle has an ornament of apparently solid, short, bulbous, baculate or capitate processes. Excystment structures rarely seen, though several specimens show small, unornamented, ruptures.

Dimensions. V=20-27μm, PL=upto 2μm, W=0.5-1.5μm (10 specimens measured).

Remarks. The height of the ornament separates this species from *Helosphaeridium* ? sp. C, which possesses an ornament of shorter capitate processes, spines or grana.

Occurrence. Uppermost Middle Elton Formation, Goggin Road.

Helosphaeridium ? sp. C Pl. 5, fig. 20.

Description. Vesicle spherical to ellipsoidal, laevigate under transmitted light, laevigate or rarely punctate with a SEM, thin to moderately thick walled. The vesicle has a homomorphic or heteromorphic ornament of very short capitate processes, spines or grana, which appear solid. Excystment mechanism not observed.

Dimensions. V=20-32μm, PL= <0.6μm, W=0.5-1μm (9 specimens measured).

Remarks. In general morphology this taxon closely resembles *Helosphaeridium* sp. B, which differs in having a thicker wall and ornament of larger, bulbous or capitate processes. This taxon may possibly belong in *Lophosphaeridium* as it is difficult to clearly ascertain the true nature of the ornament.

Occurrence. Much Wenlock Limestone-Middle Elton Formation, Goggin Road; particularly common from the middle Lower Elton Formation.

Genus **Hoegklintia** Dorning 1981a

Type Species. By original designation, *Baltisphaeridium visbyense* Eisenack, 1959, p. 200-201, pl. 16, figs 12-14, text-fig. 7; Högklint limestone, Wenlock Series, Högklint, Gotland, Sweden.

Diagnosis. (Dorning 1981a, p. 192). "Vesicle subspherical to subpolygonal in outline, large, ill defined from processes, wall thin, laevigate; three to several processes, thin walled, broad ill defined base, distally branched, bifurcate to multifurcate in one to three orders; the distal termination is sharp to somewhat blunt, often with some darkening of the process wall at the tip."

Remarks. Vesicle size distinguishes this genus from *Multiplicisphaeridium*, which are generally smaller and thicker walled. Both *Estiastra* and *Polygonium* Vavrdová 1966 are similar in size and general appearance, but have generally simple processes.

Hoegklintia cf. **corallina** (Eisenack 1959) Le Hérissé 1989 Pl. 6, fig. 1.

cf	1959	*Baltisphaeridium corallinum* n. sp.; Eisenack, p. 201, pl. 16, figs 15-16.
	1965a	*Baltisphaeridium corallinum* Eisenack 1959; Eisenack, pl. 24, fig. 7.
cf	1965a	*Baltisphaeridium* cf. *corallinum*; Eisenack, pl. 24, fig. 8.
cf	1969	*Multiplicisphaeridium corallinum* (Eisenack 1959); Eisenack, p. 259-260 (no fig.).
	1970	*Multiplicisphaeridium corallinum* (Eisenack 1959) comb. nov.; Lister, p. 88-89, pl. 12, figs 5, 6, 8 (already validly transferred by Eisenack 1969).
cf	1989	*Hogklintia corallina* (Eisenack) n. comb.; Le Hérissé, p. 146-147, pl. 15, figs 1-6.
	1990	*Multiplicisphaeridium corallinum* (Eisenack 1959a) Eisenack 1969a; Fensome *et al.*, p. 343 (no fig.).

Holotype. Eisenack 1959, pl. 16, fig. 15; preparation E1, Gotl. 2 Nr.10; from the Slite Formation, Wenlock Series, Slite, Gotland.

Diagnosis. (Eisenack 1959, p. 201-In German).

Description. Vesicle irregular or polygonal, hollow, poorly preserved. Processes hollow, open to vesicle interior, columnar or slightly tapering, with a characteristic ramified branching. Excystment mechanism not observed.

Dimensions. V=37-60µm, PL=35-59µm, PØb=11-18µm, PN=6-9 (5 specimens measured).

Remarks. The holotype of *H. corallina* has more numerous, shorter processes, though the style of branching is similar to specimens recovered here. Examples recovered from the Wenlock Series of Dudley by Eisenack (1965a, 1977) are similar to the material recovered here and to that illustrated by Lister (1970). As with *H.* cf. *digitata* (see below), there appear to be subtle differences between specimens from the UK and the Baltic; this was also noted by Lister (1970, p. 88). The material from the UK differs from the type material of Eisenack (1959) in having fewer, longer, processes and smaller vesicles. For this reason, specimens recovered in the present study have been assigned to *H.* cf. *corallina.*

Occurrence. Wenlock-Ludlow series, Gotland (Eisenack 1959, 1965a); Gotlandian (Silurian), Alabama (Cramer 1968b); Silurian, Belgium (Martin 1967, 1969); Högklint Formation, basal Wenlock Series (Cramer *et al.* 1979); Wenlock Series, Dudley, West Midlands (Eisenack 1965a, 1977); Much Wenlock Limestone Formation (Wenlock Series), Ludlow and Millichope areas; Lower Elton Formation (Ludlow Series), Ludlow area, Shropshire (Lister 1970, Lister & Downie 1974); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974); Jupiter and Gun River formations, middle-upper Llandovery Series, Anticosti Island; Rochester Formation, Wenlock Series, New York, Ontario, Pennsylvania; Dayton Limestone, upper Llandovery Series, Ohio; Osgood and Alger formations, upper Llandovery Series, Indiana, Kentucky, Ohio; Quoddy Formation, upper Llandovery Series; Red Mountain Formation, upper Llandovery Series, Georgia (Cramer 1970a, Cramer & Diez 1972); upper Visby-Eke formations, lower Wenlock-Ludlow series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Lower Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: middle Llandovery-Ludlow series.

Hoegklintia cf. **digitata** (Eisenack 1938) Dorning 1981a — Pl. 6, fig. 2.

cf	1938	*Hystrichosphaeridium digitatum* n. sp.; Eisenack, p. 20, 22, pl. 4, figs 3-5, text-fig. 7.
non.	1958	*H.* cf. *digitatum* Eisenack, 1938; Downie, p. 337-338, pl. 16, fig. 9, text-fig. 2c.
cf	1959	*Baltisphaeridium digitatum* (Eisenack 1938); Eisenack, p. 200, pl. 16, figs 10-11.
cfp	1965a	*Baltisphaeridium visbyense* Eisenack 1959; Eisenack, p. 262-263, pl. 21, fig. 5 (only).
cf	1969	*Multiplicisphaeridium digitatum* (Eisenack 1938); Eisenack, p. 259 (no fig.).
	1970	*Multiplicisphaeridium visbyense* (Eisenack 1959) comb. nov.; Lister, p. 95-96, pl. 12, fig. 7.
cf	1970	*Multiplicisphaeridium radicosum* n. sp.; Loeblich Jr., p. 730, figs 23A-E.
p.	1977	*Multiplicisphaeridium digitatum* (Eisenack 1938); Eisenack, p. 32, figs 21-22 (only).
cf	1981a	*Hogklintia digitata* n. comb.; Dorning, p. 192 (no fig.).
cf	1985	*Hogklintia radicosum*; Jacobson & Achab, p. 183.
cf	1989	*Hogklintia digitata* (Eisenack) n. comb.; Le Hérissé, p. 147, pl. 15, figs 7, 9, 10 (combination already validly published by Dorning 1981a).
cf	1990	*Hoegklintia digitata* (Eisenack 1938a) Dorning 1981a; Fensome *et al.*, p. 248 (no fig.).

Holotype. Eisenack 1938, pl. 4, fig. 3; from the Baltic Silurian. Holotype lost (Eisenack 1959, p. 200), neotype designated (Eisenack 1959, p. 200, pl. 16, fig. 11. *Baltisphaeridium digitatum*); preparation E1, F1, 1 Nr.4; Lyckholmer Stage (F1), upper Ordovician, Pastorat Haggers (Haggeri), Estonia.

Diagnosis. (Eisenack 1959, p. 200-In German).

Description. Vesicle hollow, irregular, ellipsoidal or polygonal. Processes hollow, open to vesicle interior, distinct from vesicle, tapering to simple, rounded, or, more commonly, branched tips (1st-2nd order). Excystment mechanism not observed.

Dimensions. V=27-58µm, PL=48-66µm, PØb=8-18µm, PN=6-11 (7 specimens measured).

Remarks. The Baltic holotype and neotype of *H. digitata* (Eisenack 1938, pl. 4, fig. 3; Eisenack 1959, pl. 16, fig. 11) have shorter, broader based, processes, with longer branches, which appear more stunted than specimens from the UK (this study, Lister 1970, Eisenack 1977). As with *H.* cf. *corallina* (see above), there is a possibility that British specimens should be placed within a separate species to those from the Baltic, which appear subtly different. The type material of Eisenack (1959) has larger vesicles and more numerous processes. Specimens recovered herein have, however, been assigned to *H.* cf. *digitata* as they are similar to one form illustrated by Eisenack (1965a, pl. 21, fig. 5), from the Högklint Limestone of Gotland.

H. digitata is similar to several other large acritarchs, *E. granulata* has simple processes; *H. corallina* has more complexly branched processes; *Hoegklintia visbyensis* (Eisenack 1959) Dorning 1981 has an overall triangular shape and the processes of *Hoegklintia ancyrea* (Cramer & Diez 1972) Dorning 1981a are always distinct from the vesicle.

Occurrence. Silurian, Estonia (Eisenack 1938); Visby, Högklint Formations, upper Llandovery-Wenlock series, Gotland (Eisenack 1938, 1962, 1965a, b); Baltic, upper Ordovician (Eisenack 1959); Wenlock Series, England (Downie 1953, 1963; Eisenack 1977); Silurian, Belgium (Martin 1967, 1969); Gotlandian (Silurian), Alabama (Cramer 1968b); middle-upper Silurian, N Spain (Cramer & Diez 1968); Ludlow Series-Gedinnian Stage, NW Spain (Cramer 1969b); upper Arenig Series, Ordovician and Ordovician erratics, Poland (Górka 1969); Much Wenlock Limestone-Lower Elton formations, Ludlow, Shropshire (Lister 1970); middle Ordovician, borehole material, Gotland (Kjellström 1971); Ashgill Series, Ordovician, Oklahoma (Loeblich Jr. 1970, as *M. radicosum*); uppermost Red Mountain Formation, upper Llandovery Series, Georgia and Alabama; Gun River and Jupiter formations, middle-upper Llandovery Series, Anticosti Island; Rochester Formation, Wenlock Series, New York, Ontario, Pennsylvania; Osgood and Alger formations, upper Llandovery Series, Indiana, Kentucky, Ohio; Crab Orchard Formation, upper Llandovery Series, Kentucky; Dayton and Laurel limestones, upper Llandovery Series, Ohio; Rose Hill Formation, upper Llandovery Series, Pennsylvania (Cramer 1970a, Cramer & Diez 1972); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974); Caradoc Series, Ordovician, Canada (Martin 1983, as *M. radicosum*); Llandovery-middle Wenlock series, Welsh Borderland (Dorning 1981a); Ashgill Series, Ordovician, Anticosti Island (Jacobson & Achab 1985, as *H. radicosa*); lower Silurian, Ringerike, Norway (Smelror 1987); Ordovician-Silurian boundary, Visby, Slite, Mulde and Burgsvik formations, Ordovician-Ludlow Series, Silurian, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Lower Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Arenig Series-Gedinnian Stage.

Genus **Leiofusa** Eisenack 1938 emend. Eisenack 1965b emend. Combaz, Lange & Pansart 1967 emend. Cramer 1970a

Type Species. By original designation, *Ovum hispidum fusiformis* Eisenack 1934, p. 65-66, pl. 4, fig. 19; probably Ordovician erratic limestone (inc. graptolites), Baltic region. Holotype lost (Eisenack *et al.*, 1976, p. 365).

Diagnosis. (Cramer 1970a, p. 71). "Vesicle hollow, fusiform with simple pointed processes at each pole. Processes varying in length from less than one tenth to as much as 5 times the length of the body. Vesicle wall unilayered, psilate to microgranulate. Sculptural elements not arranged in longitudinal rows. The long axis of the vesicle coincides with the longitudinal vesicles symmetry axis. Vesicle symmetry longitudinal, holomorphic. Longitudinal axis straight or essentially so. Pylome circular, slit shaped, or formed by equatorial splitting."

Remarks. This genus is similar to *Eupoikilofusa*, *Poikilofusa* and *Dactylofusa* in possessing a fusiform vesicle. It is the ornament on the vesicle that separates the four genera. Leiofusids are generally laevigate, poikilofusids have a randomly arranged ornament of short processes, dactylofusids have a ornament of short processes in longitudinal rows and eupoikilofusids are usually striate.

Leiofusa estrecha Cramer 1964a — Pl. 4, fig. 7.

1964a *Leiofusa estrecha* n. sp.; Cramer, p. 36, figs 8, 11.

1964b *Leiofusa elenae* n. sp.; Cramer, p. 323, text-fig. 33:12.

1965 *Leiofusa communis*; Brito & Santos, p. 9, pl. 1, fig. 10 (according to Cramer 1970a, p. 77; Eisenack *et al.* 1976, p. 353, 359; junior synonym of *Leiofusa fusiformis* Eisenack 1934 according to Moreau-Benoît 1974, p. 128).

1990 *Leiofusa estrecha* Cramer 1964a; Fensome *et al.*, p. 263 (no fig.).

Holotype. Cramer 1964a, fig. 11; probably lower Gedinnian Stage, Oblanca, Cantabric Mountains, León, NW Spain.

Diagnosis. (Cramer 1964a, p. 36). "Species of *Leiofusa* with hollow body having form of a thick needle, there is a gradual transition from the test to the spines at each pole. The wall is psilate, consists of one layer and is not transparent. The spines at the poles are usually broken."

Description. Wall thin and semi-transparent or moderately thick; vesicle hollow, laevigate, elongate, fusiform, with two polar processes. Processes laevigate, tapering, straight or flexuous, commonly broken, simple, hollow, open to vesicle; rarely distinct from the vesicle. Excystment mechanism not observed.

Dimensions. VL=124-175μm, VW=23-32μm, PL=116-126μm (often broken) (7 specimens measured).

Remarks. The species *L. communis* and *L. elenae* have been considered junior synonyms by Cramer (1970a, p. 77) and Le Hérissé (1989, p. 149-150) respectively, though the former has also been regarded as a junior synonym of *Leiofusa fusiformis* Eisenack 1934 by Moreau-Benoît (1974, p. 128). *Leiofusa tanaocyta* Loeblich Jr. 1970 is also very similar to this species, but appears to have shorter processes, though the two taxa may be synonymous.

Occurrence. Uppermost Formigoso Formation (Llandovery-Wenlock series) and San Pedro Formation, Ludlow Series, Silurian-lower Gedinnian Stage, NW Spain (Cramer 1964 a & b, 1966b, 1969b); Silurian, Alabama (Cramer 1968b); Lower Devonian, Brazil (Brito 1967, Brito & Santos 1965); Llandovery-lower Ludlow Series, USA (Cramer & Diez 1972); Silurian, France (Moreau-Benoît 1969); Llanvirn Series, middle Ordovician, Britain (Paris & Deunff 1970); Silurian-Devonian, Germany (Eisenack 1971); subsurface Florida (Llandovery-Prídolí series); Red Mountain Formation, lower-upper Llandovery Series; St. Clair Formation, upper Llandovery-lower Ludlow series (Cramer 1970a, Cramer & Diez 1972); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Llandovery Series-Gedinnian Stage, Sahara (Jardiné & Yapaudjian 1968); Tanezzuft and Acacus formations, Wenlock-Ludlow series, Libya (Richardson & Ioannides 1973); ?upper Ordovician-Gedinnian Stage, Algeria (Jardiné *et al.* 1974); upper Ordovician-Silurian (Moreau-Benoît 1974); Ordovician (post Arenig Series) and Silurian-Devonian, France (Rauscher 1973); upper Llandovery Series, Canada (Achab 1976); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); Leintwardine-Whitcliffe groups, Ludlow Series, Welsh Borderland (Dorning 1981a); upper Ordovician-lower Silurian, Anticosti Island (Duffield & Legault 1981); Haragan Formation, Lower Devonian, Oklahoma (Wicander 1986); Llandovery-Wenlock series, Gotland (Le Hérissé 1989); upper Wenlock Series, Wenlock type area (Swire 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995, as cf. *estrecha*); rare in the Lower Elton Formation, Goggin Road. Known range: post Arenig Series-Lower Devonian.

Leiofusa parvitatis Loeblich Jr. 1970 Pl. 6, fig. 9.

1970 *Leiofusa parvitatis* n. sp.; Loeblich Jr., p. 724-725, figs 18F-G.

1990 *Leiofusa parvitatis* Loeblich Jr. 1970a; Fensome *et al.*, p. 264 (no fig.).

Holotype. Loeblich Jr. 1970, fig. 18G, paratype, fig. 18F; holotype 69-152(2) 32.7-109.2, paratype 69-150(6) 39.2-98; Maplewood Formation, upper Llandovery Series, access road to Rochester Gas & Electric Corporation plant, Genesee River, Rochester, New York, USA.

Diagnosis. (Loeblich Jr. 1970, p. 724-725). "Central body fusiform in outline, with a long hollow process at each pole, processes become solid near the distal end; wall smooth, less than 1μ in thickness; on one specimen (fig. 18F) a small subcircular portion of the wall is broken out but remains attached; this may be the operculum covering the pylome."

Description. Vesicle elongate, fusiform, thin, laevigate, hollow, with two polar processes. Processes long, slender, laevigate, hollow, open to vesicle interior, flexuous, displaying an indistinct contact with the vesicle. Excystment mechanism not observed.

Dimensions. VL=19-35.5μm, VW=6-12μm, PL=29-49μm (10 specimens measured).

Remarks. This species closely resembles *Leiofusa tumida*, but differs in having an elongate vesicle with processes that have no distinct bases.

Occurrence. Maplewood Formation, upper Llandovery Series, New York (Loeblich Jr. 1970); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); middle-upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); upper Llandovery Series, Libya (Hill & Molyneux 1988); upper Llandovery-upper Ludlow series (? Prídolí Series), Gotland (Le Hérissé 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road. Known range: upper Llandovery-Ludlow (?Prídolí) series.

Genus **Leiosphaeridia** Eisenack 1958a emend. Downie & Sarjeant 1963 emend. Turner 1984

Type Species. By original designation, *Leiosphaeridia baltica* Eisenack 1958a, p. 8, pl. 2, fig. 5; erratic pebble, Baltic region, Ostsee-Kalk, approximately Lyckholm Stage, Ashgill Series, upper Ordovician.

Diagnosis. (Turner 1984, p. 116). "Spherical to ellipsoidal bodies without processes, often collapsed or folded, with or without pylomes. Walls granular, or unornamented, thin or thick, without divisions into fields and transverse or longitudinal furrows or girdles."

Remarks. No attempt was made to speciate specimens of *Leiosphaeridia* found in this study. They were, however, divided into eight groups on vesicle size (<46μm, 46-85μm, 85-132μm, 132μm+) and wall thickness (<3μm, >3μm). A comprehensive list of genera that are, or have been, considered junior synonyms of this taxon can be found in Fensome *et al.* (1990, p. 271-272).

Genus **Leptobrachion** Dorning 1981a

Type Species. By original designation, *Baltisphaeridium arbusculiferum* Downie 1963, p. 644, pl. 91, fig. 5, text-fig. 3d; sample WS/4b, Wenlock Shales, Tickhill [*sic* = Tickwood] Beds, Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Dorning 1981a, p. 193). "Vesicle subspherical, double walled; inner wall thick, outer wall thin and continuous with processes; processes few to several thin, tapering, some or all branching up to fifth order, processes often preserved flattened. Excystment by a straight split in the vesicle wall."

Remarks. Excystment mechanism, wall structure and process nature were used to separate this genus from other similar genera (Dorning 1981a, p. 193). *Baltisphaeridium* have pylomes and rarely branched processes; *Multiplicisphaeridium* are single walled; *Oppilatala* have processes that are plugged proximally and *Eisenackidium* have generally simple processes.

Leptobrachion arbusculiferum (Downie 1963) Dorning 1981a Pl. 6, fig. 4.

v*	1963	*Baltisphaeridium arbusculiferum* sp. nov.; Downie, p. 644, pl. 91, fig. 5, text-fig. 3d.
	1965	*Multiplicisphaeridium arbusculiferum* (Downie) comb. nov.; Staplin *et al.* p. 181.
v*p.	1970	*Baltisphaeridium dubitum* sp. nov.; Lister, p. 59, pl. 3, fig 5, text-fig. 20a (only).
non.	1970	*Multiplicisphaeridium arbusculiferum* (Downie 1963) Staplin, Jansonius & Pocock 1965; Lister, 1970, pl. 10, fig. 14-17, 19, pl. 11, figs 1-2.
non.	1973	*Multiplicisphaeridium arbusculiferum* (Downie 1963); Eisenack *et al.*, p. 525-527.
	1973	*Multiplicisphaeridium dubitum* (Lister 1970); Eisenack *et al.*, p. 613-614.
	1974	*Peteinosphaeridium arbusculiferum* (Downie 1963); Piskun, pl. 12, figs 6,7.
	1981a	*Leptobrachion arbusculiferum* n. comb.; Dorning, p. 193 (no fig.).
	1990	*Leptobrachion arbusculiferum* (Downie 1963) Dorning, 1981a; Fensome *et al.*, p. 290 (no fig.).

Holotype. Downie 1963, pl. 91, fig. 5; slide 2, position, 010.560; WS/4b, Wenlock Shales, Tickhill [*sic* = Tickwood] Beds, Coalbrookdale Formation, Wenlock Series, near Eaton Church, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1963, p. 644). "Test subspherical to subpolygonal, processes long broad tapering, forking irregular at a moderate angle, branches often long and broad; forking usually bifurcate up to fourth order."

Description. An apparently double walled acritarch, with a spherical, moderately thick, laevigate wall. Processes thin, almost transparent, circular in cross section, hollow, closed to vesicle interior, columnar or tapering, simple or more commonly branched to 3rd order. Excystment mechanism not observed.

Dimensions. V=14-22μm, PL=16-22μm, PØb=1.5-3μm, PN=7-12, W=0.5-1μm (8 specimens measured).

Remarks. The holotype of this taxon appears to possess two walls, with a thicker vesicle and thinner, almost transparent processes. Several authors have assigned morphologically similar acritarchs, with a single wall, to this species; some of these should be assigned to *Multiplicisphaeridium arbusculum*. Only a single specimen from those examples illustrated as *B. dubitum* and *M. arbusculiferum* by Lister (1970) is clearly assignable to *L. arbusculiferum*, the others being considered to be assignable to the following taxa:

B. dubitum, pl. 3, figs 1, ?4 & text-fig. 17n, ?19l = *Leptobrachion* sp. A.

M. arbusculiferum, pl. 10, figs 14, 15 = *M. arbusculum*; pl. 10, fig. 19 = *Leptobrachion* sp; pl. 11, figs 1-2 = *M. arbusculum*; pl. 10, figs 16, 17 = *Multiplicisphaeridium arbusculum* var. A.

Occurrence. Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1963); Much Wenlock Limestone-Middle Elton formations, Wenlock-Ludlow Series, Ludlow and Millichope areas, Shropshire (Lister 1970, *B. dubitum*); Coalbrookdale Formation-Elton Group, middle

Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Slite-Eke formations, Wenlock-Ludlow series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road, becoming rarer in the Lower Elton Formation, with a single occurrence in the Middle Elton Formation (Goggin Road). Known range: Wenlock-Ludlow series.

Leptobrachion digitatum sp. nov. Pl. 6, fig. 5; Pl. 12, fig. 2.

vp. 1970 *Baltisphaeridium* sp. nov.; Lister, p. 59, pl. 2, figs 14, ?16 (only).

Name. Species name *digitatum*, after the latin *digitus* = finger, refering to the finger-like nature of the processes.

Holotype. Pl. 6, fig. 5, TRENCH1/11-A (1)-N40/4, from the Lower Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Diagnosis. An apparently double walled acritarch, possessing a laevigate, spherical to ellipsoidal, thin or more commonly, moderately thick walled vesicle. Processes hollow, laevigate, thin, almost transparent, closed to vesicle interior; most processes taper to simple tips, though some, which tend to be much broader, have characteristic bifurcate or trifurcate branching. Excystment by unornamented rupture.

Dimensions. V=15-27µm, PL=12-19.5µm, PØb=1.5-7.6µm, PN=6-16, W=0.25-1µm (10 specimens measured).

Remarks. This species differs from *L. arbusculiferum* in possessing mainly simple processes, having only a few with characteristic bifurcate or trifurcate branching, whereas the branching of *L. arbusculiferum* tends to be ramified. *Leptobrachion malvernia* Dorning 1981a, from the Coalbrookdale Formation (Wenlock Series, Herefordshire), has similar processes which differ in having a more complex multifurcate style of branching (up to fifth order).

Occurrence. Lower Elton formation, Ludlow Series, Ludlow, Shropshire (Lister 1970); Much Wenlock limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), becoming rarer through the Lower Elton Formation, with rare occurrences in the Middle Elton Formation. Known range: uppermost Homerian-lower Gorstian stages.

Leptobrachion sp. A Pl. 6, fig. 3.

vp. 1970 *Baltisphaeridium dubitum* sp. nov.; Lister, pl. 3, figs 1, ?4, text-fig. 17n, ?19l (only).

Description. An apparently double walled acritarch, vesicle spherical to ellipsoidal, moderately thick walled, laevigate. Processes thin, almost transparent, hollow, closed to vesicle interior, long and slender, tapering to simple or branched tips; branching of 1st order. Excystment by unornamented rupture.

Dimensions. V=14-22µm, PL=19-32µm, PØb=1-6µm, PN=6-8 (10 specimens measured).

Remarks. This species differs from *L. arbusculiferum* in having generally fewer processes that are longer and more simply branched; *L. digitatum* sp. nov. has generally more numerous, shorter, processes which may have characteristic bifurcate or trifurcate branching.

Occurrence. Lower Elton-Upper Elton formations, Ludlow Series, Ludlow, Shropshire (Lister 1970); Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), rare in the Lower and Middle Elton formations of Goggin Road. Known range: upper Homerian-lower Gorstian stages.

Leptobrachion sp. B Pl. 6, fig. 8.

Description. An apparently double walled acritarch; vesicle ellipsoidal, laevigate, moderately thick walled with thin, almost transparent processes. Processes hollow, laevigate, tapering, with tips that branch to 2nd or 3rd order or are bifurcate. Excystment mechanism not observed.

Dimensions. V=11-18µm, PL=6-18µm, PØb=1.5-3.5µm, PN=6-8 (6 specimens measured).

Remarks. In general appearance this taxon closely resembles *L. arbusculiferum*, but is distinguished by its smaller overall size.

Occurrence. Rare in the Middle Elton Formation, Goggin Road.

Leptobrachion sp. C Pl. 6, fig. 7.

Description. An apparently double walled acritarch. Vesicle ellipsoidal, moderately thick walled, granulate. Processes thin, almost transparent, hollow, tapering or columnar, cylindrical with multifurcate tips. Excystment mechanism not observed.

Dimensions. V=21 x 24µm, PL=8µm, PØb=4.5µm, PN=10 (1 specimen measured).

Remarks. This taxon is very distinctive and the granulate vesicle, with broad, cylindrical, multifurcate processes, distinguishes it from any other species of *Leptobrachion* recovered in this study.

Occurrence. From a single sample, Lower Elton Formation, Pitch Coppice Quarry.

Genus **Lophosphaeridium** Timofeev 1959 ex Downie 1963 emend. Lister 1970

Type Species. By original designation, *Lophosphaeridium rarum* Timofeev 1959, p. 29, pl. 2, fig. 5; from the lower Ordovician, Russia.

Diagnosis. (Lister 1970, p. 61). "Vesicle hollow, single-walled with ornament of solid tubercles. Excystment is by cryptosuture."

Remarks. This genus is very similar to *Helosphaeridium* (capitate or bulbous projections) and *Buedingiisphaeridium* (see *Buedingiisphaeridium*-Remarks above).

Lophosphaeridium sp. A Pl. 6, fig. 10.

Description. Vesicle spherical, semi-transparent, yellow-orange in colour, with a dense ornament of solid grana. Excystment by unornamented rupture.

Dimensions. V=24-30μm, W=0.5-1μm (4 specimens measured).

Remarks. It was decided to retain this species in open nomenclature as it would be difficult to distinguish it from the numerous, other species of *Lophosphaeridium* described (73 in Fensome *et al.* 1990).

Occurrence. Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road.

Genus **Micrhystridium** Deflandre 1937 emend. Sarjeant & Stancliffe 1994

1965 *Solisphaeridium* Staplin, Jansonius & Pocock, p. 183-184
1974 *Exilisphaeridium* Wicander, p. 24.

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

Diagnosis. (Sarjeant & 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 μm; larger species very rarely range above 27 μm 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 μm to greater than the vesicle diameter. Release of vesicle contents occurs by formation of a linear slit or a cresentic to horseshoe-shaped opening (epityche) or by opening of a cryptosuture, causing loss of an irregularly shaped portion of one surface: regularly formed circular to polygonal openings (pylomes) are not developed."

Remarks. The diagnosis of *Micrhystridium* has been revised by many authors (see Sarjeant and Stancliffe 1994, p. 12), and numerous have been considered synonymous (see Eisenack *et al.* 1979a, Sarjeant & Stancliffe 1994).

Many of the genera listed as synonymous do not truly conform to the latest emended diagnosis. For example *Ecmelostoiba* Wicander 1974 has too few processes; the type species has 5-7, whereas the present diagnosis stipulates 9-35. The vesicle diameters of the type species of several other genera listed exceed the general maximum of 20μ stated in the diagnosis, though it was noted that the vesicle diameter can rarely exceed 27μm. Genera like *Ephelopalla* Wicander 1974 (V = 29-42μm) and *Pustulisphaeridium* Wicander 1974 (V = 35-40μm) are clearly outside the present diagnosis of *Micrhystridium.* Other genera, *Ecthymabrachion* Wicander 1974 (V = 28-32µm) and *Uncinisphaera* Wicander 1974 (V = 22-30µm), could possibly be included in *Micrhystridium*. Only *Exilisphaeridium* Wicander 1974 (V = 21µm), which was also included in synonymy with *Dorsennidium* (Sarjeant & Stancliffe 1994, p. 39), and *Guttatisphaeridium* Wicander 1974 (V = 21-27µm) fall within the maximum accepted size range. The genera *Ephelopalla* Wicander 1974, *Guttatisphaeridium* and *Pustulisphaeridium* Wicander 1974 also have what were described as having secondary deposits, which either partly or completely constricted the processes. Without examination of the holotypes, the true nature of these deposits is unknown; for these reasons only *Exilisphaeridium* and *Solisphaeridium* are included in synonymy.

Several genera of very small Cretaceous acritarchs, erected on the basis of SEM work (Habib & Knapp 1982), were lowered in rank and considered subgenera of *Micrhystridium* by Sarjeant & Stancliffe (1994, p. 12-14). As these genera were described using a SEM , not a light microscope, it was considered that the "preferable taxonomic procedure is to give such taxa the status of subgenera" (Sarjeant & Stancliffe 1994, p. 11).

Micrhystridium inflatum (Downie 1959) Lister 1970 Pl. 6, figs 13-14.

v* 1959 *Micrhystridium stellatum* var. *inflatum* var. nov.; Downie, p. 61, pl. 11, fig. 12.
1963 *Baltisphaeridium longispinosum* (Eisenack) var. *parvum* var. nov.; Downie, p. 639, pl. 91, fig. 2.
p. 1970 *Micrhystridium inflatum* Downie 1959 emend.; Lister, p. 79-80, pl. 10, figs 2-4,6; text-fig. 19a (only).
1979a *Micrhystridium stellatum inflatum* Downie 1959; Eisenack *et al.*, p. 507.
1990 *Micrhystridium stellatum* var. *inflatum* Downie 1963; Fensome *et al.*, p. 333 (no fig.).
1994 *Dorsennidium inflatum* (Downie 1959 emend Lister 1970) comb. nov.; Sarjeant & Stancliffe, p. 40 (no fig.).

Holotype. Downie 1959, pl. 11, fig. 12; Mik(P) 14002; Wenlock Shales (=Coalbrookdale Formation), Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Lister 1970, p. 79). "Vesicle hollow, subspherical to polygonal, smooth, single-walled; vesicle diameter 14-35µ; processes smooth, slender, flexuous, tapering to a fine point, equal to or greater than the vesicle diameter in length. Excystment by cryptosuture, apical or near-equatorial in position."

Description. Vesicle spherical to ellipsoidal, laevigate under transmitted light, bearing several long, slender, straight or flexuous processes. Processes simple, hollow, open to vesicle interior. Excystment by unornamented rupture.

Dimensions. V=15-23µm, PL=16-39µm, PØb=1.5-3µm, PN=6-9 (16 specimens measured).

Remarks. Sarjeant & Stancliffe (1994, p. 40) transferred this species from *Micrhystridium* to *Dorsennidium* on the basis that "the small number of spines dictates the polygonal body shape." The holotype (Downie 1959, pl. 11, fig. 12), however, clearly has a spherical vesicle. This species does not belong in *Dorsennidium* and also has too few processes (6-9 not 9-35) to be placed in *Micrhystridium* under the present diagnosis. It has been included in this genus, however, because of its spherical-ellipsoidal vesicle.

M. inflatum is morphologically akin to several other taxa, which may represent a morphological continuum of a single species (see *D. formosum*-Remarks above), and is distinguished by its spherical-ellipsoidal vesicle (*D. formosum* = triangular, *D. rhomboidium* = rhomboidal, *D. pentagonale* = polygonal).

Occurrence. Buildwas and Coalbrookdale formations, Wenlock Edge, Shropshire (Downie 1959, 1963); Visby Marl, Wenlock Series, Gotland (Eisenack 1965a); Lower Devonian, Brazil (Brito 1965, 1967); Llandovery-basal Wenlock series (Martin 1966b, 1967); Lower Devonian, France (Moreau Benoît 1967); Ludlow Series, Ludlow and Millichope, Shropshire (Lister 1970); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Siegenian Stage, Belgium (Vanguestaine 1979); Much Wenlock Limestone Formation, Dudley, UK (Dorning 1983); middle Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Visby, Slite, Mulde and Eke formations, Llandovery-Ludlow series, Gotland (Le Hérissé 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Llandovery Series-Lower Devonian.

Micrhystridium intonsurans (Lister 1970) Dorning 1981a — Pl. 6, fig. 12; Pl. 12, fig. 7.

1970 *Micrhystridium stellatum* var. *intonsurans* var. nov.; Lister, p. 82-83, pl. 9, figs 18-20; pl. 10, fig. 1, text-fig. 24a.

1981a *Micrhystridium intonsurans* n. stat.; Dorning, p. 194 (no fig.).

1990 *Micrhystridium intonsurans* (Lister 1970) Dorning, 1981; Fensome *et al.*, p. 324 (no fig.).

1994 *Multiplicisphaeridium intonsurans* (Lister 1970) comb. nov.; Sarjeant & Stancliffe, p. 32 (no fig.).

Holotype. Lister 1970, pl. 9, fig. 18; MPK 181; Lower Elton Formation, Ludlow Series, LD54A, Elton Lane, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 83). "A polygonal variety of *M. stellatum* with short rigid processes; processes barbed along their median portions and at their distal extremities."

Description. Vesicle commonly polygonal, rarely spherical, laevigate, thin walled, with short, slender, tapering, straight or flexuous, hollow processes; process cavities open to the vesicle interior.

The processes are ornamented along their length with short spines, which are particularly concentrated at the tips. Excystment by unornamented rupture.

Dimensions. V=8-15µm, PL=4-7µm, PØb=0.8-1.5µm, PN=17-26 (10 specimens measured).

Remarks. Sarjeant & Stancliffe (1994, p. 32) cited the branched nature of the processes as the reason for transferring this species to *Multiplicisphaeridium*. The processes, which have slightly rounded tips, are not branched, but have small spines along their length and especially at their process tips. This species is similar to *Nanonobarbophora* (now *Micrhystridium* subgenus *Nanonobarbophora*) *barbata* (Habib & Knapp 1982) Sarjeant & Stancliffe 1994 which has an ornament of short spines along the length of its processes; the spines, however, are not concentrated at the process tips, which do not appear branched.

The spinose ornament on the processes of *M. intonsurans* is only clearly visible with a SEM; under transmitted light the processes appear granulate and the tips seem slightly bulbous. Since under transmitted light the true nature of the process tips cannot be seen, and also because of the close morphological similarities between *M. intonsurans* and some forms of *M. stellatum*, this taxon is retained in *Micrhystridium*.

Occurrence. Ludlow Series (especially the Lower Elton and Lower Whitcliffe formations), Ludlow and Millichope, Shropshire (Lister 1970); Siegenian-Emsian stages, Belgium (Vanguestaine 1979); Wenlock Series, Ayrshire (Dorning 1982); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock Series-Emsian Stage.

Micrhystridium stellatum Deflandre 1945 Pl. 6, fig. 11; Pl. 12, fig. 6.

1942 *Micrhystridium stellatum*; Deflandre, p. 476, figs 7,8 (*nomen nudum*).
1945 *Micrhystridium stellatum* Deflandre; Deflandre, p. 65, pl. 3, figs 16-19.
1974b *Veryhachium stellatum* (Deflandre 1945a); Pöthé de Baldis, p. 371-372.
1975 *Micrhystridium stellatum* Deflandre; Pöthé de Baldis, p. 492, pl. 5, fig. 18.
1990 *Micrhystridium stellatum* Deflandre 1945a; Fensome *et al.*, p. 333 (no fig.).
1994 *Micrhystridium stellatum* Deflandre 1945; Sarjeant & Stancliffe, p. 18 (no fig.).

Holotype. Deflandre 1945, pl. 3, fig. 16-18; AY14, Calcaire de la Roquemaillère (Wenlock Series), Montage Noire; sample no' 421.

Diagnosis. (Deflandre 1945, p. 65, translation by Eisenack *et al.* 1979a, p. 505). "The globular central body, tending to be somewhat polyhedral bears strong simple spines which are straight or slightly curved, of length greater than half the diameter of the central body. These spines are not very numerous: a dozen or a few more; they are more or less strongly developed, according to the specimens in question; the polyhedral aspect coincides with the reduction in the number of processes. The body wall is a reddish brown or is very dark yellowish brown, the spines are almost black. The diameter of the organism, without spines, is from 11 to 16µ; it attains 25 to 28µ, spines included."

Description. Vesicle commonly polygonal, rarely spherical, laevigate, thin walled. Processes laevigate, slender, tapering to simple tips, hollow and open to the vesicle interior. Excystment by unornamented rupture.

Dimensions. V=11-20µm, PL=5-16µm, PØb=1-2µm, PN=10-23 (11 specimens measured).

Remarks. In general morphology this species closely resembles *M. intonsurans*, which differs in having slightly shorter processes, along which a distinctive ornament of small spines occurs. *M. inflatum* has a larger vesicle and fewer, longer processes; *Micrhystridium* sp. A has a sparse and irregular covering of fewer, shorter, flexuous, solid processes.

Occurrence. This species has a widespread geographical and stratigraphical occurrence (see Eisenack *et al.* 1979a, p. 505-506). The UK occurrences of this species are:

Tremadoc Series, Great Britain (Downie 1958); Oxford Clay, Upper Jurassic (Sarjeant 1961); Lower Permian, Yorkshire (Wall & Downie 1962); Wenlock Series, Shropshire (Downie 1959, 1963); Hettangian-Sinemurian stages, Lower Jurassic (Wall 1965); lower Ludlow Series, England (Lister & Downie 1967); Wenlock-Prídolí series, Shropshire (Lister 1970); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Ordovician-Jurassic.

Micrhystridium sp. A — Pl. 6, fig. 15.

Description. Vesicle ellipsoidal, laevigate, hollow, with a sparse and irregular covering of short, flexuous processes, which taper to simple tips and are apparently solid. No excystment structures observed.

Dimensions. V=22-24µm, PL=4-9µm, PØb=1-2µm, PN=13-14, W=0.5µm (2 specimens measured).

Remarks. Only a few specimens of this taxon were recovered and it is thus placed in open nomenclature. The sparse, irregular, covering of simple, solid, processes distinguishes this taxon from *M. stellatum*, which is thinner walled and has longer, hollow processes.

Occurrence. Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road, with rare occurrences in the Middle Elton Formation, Goggin Road.

Micrhystridium ? sp. B Pl. 6, figs 6, 16.

Description. Vesicle laevigate, ellipsoidal to spherical, moderately thick walled. The vesicle surface is covered with numerous short processes, which taper to simple points. The processes can be straight or flexuous, hollow or apparently solid and some appear to be finely granulate along their lengths, though most appear laevigate. Excystment mechanism not observed.

Dimensions. V=25-32µm, PL=4-12µm, PØb=2-3µm, PN=22-32, W=0.5µm (5 specimens measured).

Remarks. This taxon is only provisionally placed in *Micrhystridium* because of the vesicle size (22-32µm), which exceeds the general maximum of 20µm of the generic diagnosis (Sarjeant & Stancliffe 1994). There is provision in the diagnosis, however, that allows the inclusion of forms which have vesicle diameters which rarely exceed 27µm.

This taxon is quite distinct from the other specimens recovered and assigned to *Micrhystridium*. The vesicles of *M. intonsurans* and *M. stellatum* are smaller and thinner walled; *M. inflatum* has fewer, longer, flexuous processes and *Micrhystridium* sp. A is smaller and has an irregular covering of short, solid processes.

Occurrence. Rare in the Middle Elton Formation, Goggin Road.

Genus **Multiplicisphaeridium** Staplin 1961 emend. Staplin, Jansonius & Pocock 1965 emend. Eisenack 1969 emend. Lister 1970

Type Species. By original designation, *Multiplcisphaeridium ramispinosum* Staplin 1961, p. 411, pl. 48, fig. 24, text-figs 9g, h; Woodbend Formation, Upper Devonian, Alberta, Canada.

Diagnosis. (Lister 1970, p. 83). "Vesicle hollow, spherical to ellipsoidal, single-walled; processes with closed tips, heteromorphic simple or compound branching, wall smooth or with minor ornamentation; no differentiation between vesicle wall and processes; process cavity in open connection with vesicle interior. Excystment by cryptosuture, apical or near-equatorial."

Remarks. A full discussion of the taxa that have been considered synonymous with *Multiplicisphaeridium* can be found in Fensome *et al.* (1990, p. 338-339), who incorrectly cited the last emendation as being by Turner (1984) who only listed the emended diagnosis of Lister (1970). This genus is similar to several other genera; *Micrhystridium* have generally simple processes that rarely branch; *Leptobrachion* have two walls; *Cymbosphaeridium* appear double walled and have a pylome; *Evittia* have ornament on the vesicle and processes and a distinctive digitate style of branching; *Dateriocradus* have triangular vesicles; *Hoegklintia* are much larger and *Baltisphaeridium* appear to have two walls and generally simple processes, which are closed to the vesicle interior.

Multiplicisphaeridium arbusculum Dorning 1981a Pl. 7, fig. 1.

p. 1970 *Multiplicisphaeridium arbusculiferum* (Downie 1963) Staplin, Jansonius & Pocock 1965; Lister, p. 86-87, pl. 10, figs 14-15, pl. 11, figs 1-2, text-fig. 25c (only).

v* 1981a *Multiplicisphaeridium arbusculum* n. sp.; Dorning, p. 194-195, pl. 1, fig. 7.

1981a *Multiplicisphaeridium arbusculatum*; Dorning, table 1 (*nomen nudum*).

1990 *Multiplicisphaeridium arbusculum* Dorning 1981; Fensome *et al.*, p. 340 (no fig.).

Holotype. Dorning 1981a, pl. 1, fig. 7; WN28K, U41/4, MPK 2905; Much Wenlock Limestone Formation, Wenlock Series, Wrens Nest Inlier, Dudley, West Midlands (SO 9350 9175).

Diagnosis. (Dorning 1981a, p. 195). "Vesicle subspherical, 15-25µm in diameter, laevigate; 6-12 laevigate processes, 18-30 µm long, base about 3µm wide, tapering to sharp points; branching is irregular up to fourth order, and irregular within the processes of an individual; the first order of branching often occurs about one third to one half of the length of the process. Branching angle 30-40°."

Description. Vesicle spherical to ellipsoidal, laevigate, bearing long, tapering processes which may be simple or are more commonly branched (upto 3rd order) at $^{2}/_{3}$rds along their length. The processes, including some of the branches, are hollow and open to the vesicle interior. Excystment mechanism not observed.

Dimensions. V=15-23µm, PL=15-29µm, PØb=1.5-5µm, PN=5-11 (20 specimens measured).

Remarks. The processes on *Multiplicisphaeridium variabile* tend to be more numerous, and the vesicle is polygonal (usually hexagonal), not spherical or ellipsoidal. *Multiplicisphaeridium eltonense* is generally smaller, with more numerous, narrower, shorter processes. The spherical-ellipsoidal vesicle distinguishes this species from *Multiplicisphaeridium arbusculum* var. A, which appears identical, but possesses a rhomboidal-polygonal vesicle. The two taxa have been separated as their stratigraphic ranges are slightly different.

This species was erected by Dorning (1981a) to accommodate forms with a single wall which had been assigned to *Multiplicisphaeridium* (now *Leptobrachion*) *arbusculiferum*. The epithet was incorrectly spelt as *arbusculatum* by Dorning (1981a, Table 1, p. 179).

Occurrence. Lower Elton Formation, Ludlow Series, Ludlow (Lister 1970 as *M. fisherii*); upper Wenlock Series-lower Ludlow Series, Ludlow and Millichope, Shropshire (Lister 1970, as *M. arbusculiferum*); Coalbrookdale Formation-Elton Group, middle Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); middle-upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); lower Wenlock Series, Austria (Priewalder 1987); lower Silurian, Ringerike, Norway (Smelror 1987); upper Llandovery Series, Libya (Hill & Molyneux 1988); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road; common in the lower part of the Lower Elton Formation, decreasing towards the upper part, Goggin Road. Known range: middle Llandovery-lower Ludlow series.

Multiplicisphaeridium arbusculum var. A Pl. 7, fig. 5.

vp. 1970 *Multiplicisphaeridium arbusculiferum* (Downie 1963) Staplin, Jansonius & Pocock 1965; Lister, p. 86-87, pl. 10, fig. 16, 17 (only).

vp. 1970 *Multiplicisphaeridium fisherii* (Cramer 1968) comb. nov.; Lister, p. 89, pl. 11, fig. 3 (only).

Description. Vesicle rhomboidal or polygonal, laevigate. Processes broad based, tapering, laevigate, hollow, open to vesicle interior, simple or branched upto the 4th order from $^1/_2$ to $^2/_3$rds along their length. Excystment mechanism not observed.

Dimensions. V=16-23µm, PL=14-30µm, PØb=3-6µm, PN=6-12 (13 specimens measured).

Remarks. This taxon is the rhomboidal-polygonal counterpart of *M. arbusculum* and appears almost identical, but lacks an ellipsoidal-spherical vesicle. It has been included as a distinct taxon as the stratigraphic ranges of the two taxa are not identical (although they overlap) and the two taxa appear to dominate in different parts of the succession (Appendices 1, 2).

Occurrence. Lower Elton Formation, Ludlow Series, Shropshire (Lister 1970, as *M. fisherii*); upper Wenlock Series-lower Ludlow series, Ludlow and Millichope, Shropshire (Lister 1970, as *M. arbusculiferum*); Much Wenlock Limestone Formation (Pitch Coppice Quarry), Lower Elton Formation (Goggin Road).

Multiplicisphaeridium eltonense Dorning 1981a Pl. 7, fig. 2.

p. 1970 *Multiplicisphaeridium ramusculosum* (Deflandre 1945) comb. nov., emend.; Lister, p. 92-93, pl. 11, figs 8, 11-13, text-fig. 25a (only)..

v* 1981a *Multiplicisphaeridium eltonensis* n. sp.; Dorning, p. 195, pl. 1, figs 5,8.

1990 *Multiplicisphaeridium eltonense* Dorning 1981; Fensome *et al.*, p. 344 (no fig.).

Holotype. Dorning 1981a, pl. 1, fig. 8; from LE34K, X35/4, MPK 2903, Much Wenlock Limestone Formation, Wenlock Series, Ledbury Hill, Herefordshire (SO 716 384).

Diagnosis. (Dorning 1981a, p. 195). "Vesicle subspherical, 20-25µm in diameter, laevigate; 10-18 laevigate processes, 15-20µm long, 2-3µm wide at base, tapering distally, irregularly branching at 20-30° up to fourth order. Excystment by an irregular split."

Description. Vesicle spherical to ellipsoidal, laevigate, with long, slender, hollow, laevigate processes, which taper to simple or branched tips; processes open to the vesicle interior. Branching generally occurs at $^2/_3$rds the way along the processes, though rare examples may show branching from

$^{1}/_{2}$ way; branches ramified, up to 3rd order. On some specimens the tips of the processes, including the branches, are noticeably thinner than the rest of the process. Excystment by unornamented rupture.

Dimensions. V=13-21μm, PL=10-23μm, PØb=1-3μm, PN=8-18 (14 specimens measured).

Remarks. Those forms referred to as *M.* (now *Oppilatala*) *ramusculosum* by Lister (1970), are herein assigned to *M. eltonense*. In the diagnosis of this species, Dorning (1981a, p. 195) referred to the vesicle diameter as being 20-25μm (holotype average V = 20μm), whereas the material recovered here is generally smaller, with vesicle diameters ranging from 13-21μm.

Multiplicisphaeridium variabile can be larger and has a polygonal vesicle with more processes; *M. arbusculum* and *M. arbusculum* var. A are generally larger, with fewer, broader based processes; *Multiplicisphaeridium mingusi* Le Hérissé 1989 has a foveoreticulate vesicle.

Occurrence. Wenlock Shales-Downton Castle Sandstone Formation, Wenlock-Prídolí series, Ludlow and Millichope (Lister 1970); Much Wenlock Limestone Formation-Elton Group, upper Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock-Prídolí series.

Multiplicisphaeridium variabile (Lister 1970) Dorning 1981a Pl. 7, fig. 3.

v* 1970 *Multiplicisphaeridium arbusculiferum* var. *variabile* var. nov.; Lister, p. 87-88, pl. 11, figs 5, 7, 10; text-figs 25d, 26c.

1981a *Multiplicisphaeridium variabile* n. stat.; Dorning, p. 194 (no fig.).

1990 *Multiplicisphaeridium variabile* (Lister 1970) Dorning 1981; Fensome *et al.*, p. 357 (no fig.).

Holotype. Lister 1970, pl. 11, fig. 10; MPK 211; Lower Elton Formation, Ludlow Series, LD3, Pitch Coppice Quarry, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 87). "A generally polygonal variety of *M. arbusculiferum*, usually with numerous processes, more or less equal in length to the vesicle diameter. The processes may be slender, tapering with sharply pointed terminations or forking irregularly at moderate angles up to third order, branches are flexuous, tapering to a point. Excystment by cryptosuture."

Description. Vesicle polygonal, generally hexagonal, moderately thick walled, laevigate, with numerous laevigate, hollow, tapering processes which may be simple, or are more commonly branched (up to 3rd order); branches ramified, processes open to vesicle interior. Excystment mechanism not observed.

Dimensions. V=14-27μm, PL=10-25μm, PØb=1.5-4.5μm, PN=10-22 (26 specimens measured).

Remarks. A polygonal vesicle distinguishes this taxon from *M. eltonense* and *M. arbusculum*, both of which have spherical-ellipsoidal vesicles; *M. arbusculum* var. A has a polygonal vesicle (normally rhomboidal-pentagonal, not hexagonal) but possesses fewer, broader based, processes.

Occurrence. Maplewood Formation, upper Llandovery Series, New York (Fisher 1953 as *Hystrichosphaeridium ramusculosum* (?)); Wenlock Series-Gedinnian Stage, middle Silurian-Lower Devonian, Bassin de Polignac, Sahara (Jardiné & Yapaudjian 1968, provisionally included by Lister 1970); Ludlow Series (especially the Lower Elton Formation), Ludlow and Millichope areas, Shropshire (Lister 1970); Ilion Shale, Wenlock Series, New York (Thusu 1973b); middle Homerian-lowermost Gorstian stages, Britain and Ireland (Aldridge *et al.* 1979); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Wenlock Series, Austria (Priewalder 1987); Llandovery Series, När borehole, Visby, Högklint, Slite, Halla and Mulde formations, Llandovery-Wenlock series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), decreasing rapidly in the Lower Elton Formation, with sparse occurrences in the upper Lower Elton and Middle Elton formations, Goggin Road. Known range: Llandovery Series-Lower Devonian.

Multiplicisphaeridium sp. A   Pl. 6, figs 17-18; Pl. 12, fig. 3.

1970 *Multiplicisphaeridium* cf. *picorricum* (Cramer 1964) comb. nov.; Lister, p. 92, pl. 11, figs 15-16.

Description. Vesicle spherical to ellipsoidal, thin walled, laevigate, with numerous laevigate processes. Some of the processes are broad based and triangular in outline, tapering to simple or branched tips, branching (1st or 2nd order) usually at process tips, though some specimens may show branching from half way. Excystment mechanism not observed.

Dimensions. V=10-18μm, PL=5-12μm, PØb=1.5-4.5μm, PN=10-19 (10 specimens measured).

Remarks. Examples of this species were placed in *M.* cf. *picorricum* by Lister (1970). The holotype of *M. picorricum* (Cramer 1964b, pl. 11, fig. 2), however, shows more numerous processes, which are longer, more complexly branched and lack the triangular shape of those on *Multiplicisphaeridium* sp. A.

Occurrence. Ludlow Series, Ludlow (Lister 1970); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road.

Multiplicisphaeridium sp. B   Pl. 7, fig. 4; Pl. 12, fig. 4.

v. 1970 *Multiplicisphaeridium imitatum* (Deflandre 1945) comb. nov., emend.; Lister, p. 90-91, pl. 11, figs 17-18, text-fig. 26d.

Description. Vesicle ellipsoidal, more commonly polygonal, thin walled, scabrate under transmitted light. With a SEM the processes appear striate and the striations extend down from the processes and radiate out onto the vesicle. Processes long, slender, hollow, open to vesicle interior, tapering, rarely simple, commonly branched $^2/_3$rds along their length. Under transmitted light the processes appear laevigate. The branches are ramified, commonly branching to the 3rd order, though 1st, 2nd and 4th order branching may occur. Excystment mechanism not observed.

Dimensions. V=10-15μm, PL=9-17μm, PØb=1-2.5μm, PN=10-23 (10 specimens measured).

Remarks. Those forms described as *M. imitatum* by Lister (1970) are provisionally included in synonymy. It is clearly apparent that they do not belong in *M. imitatum*, as the holotype (Deflandre 1945, pl. 3, fig. 1) has more numerous, less complexly branched processes. In the emended diagnosis of *M. imitatum*, Lister (1970), did not mention the presence of vesicle ornament.

Occurrence. Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Pfídolí series, Ludlow and Millichope (absent from the Leintwardine-Whitcliffe groups in the Millichope area), Lister (1970, as *M. imitatum*); rare over the Much Wenlock Limestone-Middle Elton formations, Pitch Coppice Quarry and Goggin Road

Multiplicisphaeridium sp. C Pl. 7, fig. 10; Pl. 12, fig. 5.

Description. Vesicle spherical to ellipsoidal, laevigate, with numerous, short, hollow, laevigate, slightly tapering processes. Processes open to the vesicle, rarely simple, commonly with short branches at their tips; branching simply digitate or irregular to the 2nd order. Excystment mechanism not observed.

Dimensions. V=16-26μm, PL=7-13μm, PØb=1.5-3μm, PN=24-33 (9 specimens measured).

Remarks. In some respects the branching resembles that of *G. succinum*; the processes are, however, hollow, not solid. *Multiplicisphaeridium triangulatum* (Downie 1963) Dorning 1981a, of which I have seen the holotype, is nearly identical but differs in having shorter processes (upto 5μm vs' 7-13μm).

Occurrence. Rare in the Lower and Middle Elton formations, Goggin Road.

Genus **Neoveryhachium** Cramer 1970a

Type Species. By original designation, *Veryhachium carminae* Cramer 1964b, p. 307, 309, pl. 14, fig. 16, pl. 16, figs 1-3, text-fig. 28:1; from the San Pedro Formation, Ludlow Series-lower Gedinnian Stage, La Vid de Gordón, NW Spain.

Diagnosis. (Cramer 1970a, p. 110). "Vesicle symmetry regular, morphology determined by number of processes. Central body polygonal. The processes are the simple kind; ornamentation by sculpture, minor. The vesicles open through pylomes. Vesicle wall double; the ectoderm is tightly enveloped by a third wall layer, the periderm."

(Diagnosis of *Neoveryhachium carminae* Cramer 1970a, p. 112). "The vesicle is of rectangular outline and is slightly inflated, giving the vesicle the appearance of a poor quality pillow. The vesicle walls are psilate, but are covered by a characteristic system of linear thickenings (not: folds) on the external side of the ectoderm. The general morphology of these ridges is a fairly constant character, and is useful to differentiate the species from taxa of a similar general outline wich [*sic*] belong to the

Veryhachium/Micrhystridium Unit. Occasionally, specimens with three or five processes are found; these processes are always situated in the same plane. The outline of forms bearing five processes is still basically rectangular. In well preserved specimens, a very thin membrane, or periderm, may be seen around the central portion of the vesicle, but apparently is absent around the processes."

Remarks. Confusion has arisen over the nature of the vesicle wall of *Neoveryhachium*, as both the original diagnosis of Cramer (1970a) and emended diagnosis of Sarjeant & Stancliffe (1994, p. 42) state that the vesicle is double walled. The type species, *N. carminae* (see diagnosis above), however, does not have two walls, but thickenings on the vesicle surface that give the impression of two walls. For this reason the emended diagnosis of Sarjeant & Stancliffe (1994) is not used herein. The diagnosis of Cramer (1970a) requires emendation, but this is outside the scope of the present paper.

Taxa have been assigned to this genus if they have simple, hollow processes, open to the vesicle interior, that lie in a single plane, and have vesicles with thickenings on the surface and a polygonal outline (see diagnosis *N. carminae* above).

Neoveryhachium mayhillense Dorning 1981a Pl. 7, fig. 6.

v* 1981a *Neoveryhachium mayhillensis* n. sp.; Dorning, p. 196, pl. 2, fig. 13.
1990 *Neoveryhachium mayhillense* Dorning 1981; Fensome *et al.*, p. 364 (no fig.).
1994 *Neoveryhachium mayhillense* Dorning 1981; Sarjeant & Stancliffe, p. 42 (no fig.).

Holotype. Dorning 1981a, pl. 1, fig. 13; WG30K, W25/2, MPK 2910; from the Lower Elton Formation, Ludlow Series, Wood Green, May Hill, Gloucestershire (SO 6930 1655).

Diagnosis. (Dorning 1981a, p. 196). "Vesicle subrectangular in outline, 30-35µm wide, dorso-ventrally flattened, laevigate but with striae parallel to the vesicle sides; four processes at the corners of the vesicle, 35-45µm long, 4-5µm wide at base, tapering distally to a simple sharp termination. Excystment mechanism not observed."

Description. Vesicle square or rectangular, single walled, laevigate, with folds parallel to the sides. Processes long, slender, laevigate, hollow and open to the vesicle interior. Excystment mechanism not observed.

Dimensions. V=20-34µm, PL=18-39µm, PØb=1.5-7µm, PN=4 (10 specimens measured).

Remarks. This species does not possess two walls, but like the type species *N. carminae*, has linear thickenings on the vesicle surface. It is these thickenings which distinguish *N. mayhillense* from examples of *D. rhomboidium* with four processes; *D. rhomboidium* is also generally smaller and can have granulate processes.

Occurrence. Elton Group, Ludlow Series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), rare occurrences in the upper part of the Lower Elton Formation and uppermost Middle Elton Formation, Goggin Road. Known range: upper Homerian-lower Gorstian stages.

Genus **Onondagella** Cramer 1966c emend. Playford 1977

Type species. By original designation, *Veryhachium asymmetricum* Deunff 1954a, fig. 15 (a *nomen nudum* until Deunff 1961); from the Devonian of Canada.

Diagnosis. (Playford 1977, p. 30). "Vesicle hollow, with three processes, one developed at each apex of the invariably triangular vesicle. Vesicle wall one-layered, psilate or finely sculptured. Processes also psilate or finely sculptured; heteromorphic, to the extent that two are similar in form and size (i.e., are prominent, tapering, spinelike, subequal projections with closed tips), whilst the third is relatively short and stout and often has the appearance of being broken. Distal extremity of latter process has a circular opening or potential opening considered to be a cyclopyle (circular excystment opening: Eisenack, 1969) which in intact examples is seen to be closed by a thickened plug, subspherical or hemispherical in shape and here termed an epibystra. The interiors of all three processes open into and communicate freely with vesicle cavity."

Remarks. The method of excystment was considered by Playford (1977) to be via the tip of the larger process; this was considered impractical by Le Hérissé (1989), who considered that excystment took place via a rupture situated between the two similar processes.

Onondagella deunffii Cramer 1966c emend. Le Hérissé 1989 Pl. 7, fig. 12.

1966c *Onondagella deunffi* n. sp.; Cramer, p. 87-88, pl. 2, figs 12-13.

1989 *Onondagella deunffi* Cramer emend.; Le Hérissé, p. 169, pl. 20, figs 5-6.

1990 *Onondagella deunffii* Cramer 1966b; Fensome *et al.*, p. 372 (no fig.).

Holotype. Cramer 1966c, pl. 2, fig. 13; from the San Pedro Formation, Ludlow Series-lower Gedinnian Stage, León, NW Spain.

Diagnosis. (Translated from Le Hérissé 1989, p. 169). "Vesicle triangular with three processes at the corners, the wall is simple, unilayered, smooth or weakly ornamented. Two of the processes are similar, cylindrical, with rounded and closed extremities; they communicate with the central cavity. The third process has a different morphology; it is generally longer, with the form of a cylindrical tube with parallel sides. This process has, on its upper part, a more transparent section of variable length, closed at the base by a sort of cork and open at the top. The form is generally asymmetrical with a vesicle whose sides are straight to slightly concave. The opening observed at the extremity of one of the processes is not considered as functional for excystment; the real structure of excystment is represented by a simple split, situated between the two homomorphic processes."

Description. Vesicle triangular, hollow, laevigate, with three processes at each corner. Two of the processes are nearly identical, with simple, rounded tips; one process is broader, tapers less and can have a solid plug at, or near, its tip. The processes have a gradational contact with the vesicle and, on most specimens, their bases can not be defined. Processes hollow, laevigate, open to vesicle interior; excystment mechanism not observed.

Dimensions. T = 58-78μm (10 specimens measured).

Remarks. As the vesicle-process contact is poorly defined, the size of those forms recovered in this study was measured between the tip of the broader process, which bears the thickened tip, and the opposite side of the vesicle.

Occurrence. Ludlow Series-lower Gedinnian Stage, Silurian-Devonian, NW Spain (Cramer 1966c, 1969b); Ludlow Series, France (Deunff *et al.* 1971); subsurface Florida, Llandovery-Prídolí series (Cramer & Diez 1972); Prídolí Series, Podolia (Kiryanov 1978); Ludlow Series-Siegenian Stage, Algerian Sahara (Jardiné *et al.* 1972); Tanezzuft and Acacus formations, Wenlock-Ludlow series, Libya (Richardson & Ioannides 1973); Ludlow Series-Gedinnian Stage, Algeria (Jardiné *et al.* 1974); Silurian-Devonian, France (Rauscher 1973, Rauscher & Robardet 1975); Wenlock-Ludlow (? Prídolí) series, France (Deunff & Chateauneuf 1976); Leintwardine-Whitcliffe groups, Ludlow Series, Welsh Borderland (Dorning 1981a); Hemse (unit a, «marl NW», «marl SE», «marl top»), Eke (lower and upper) and Hamra (unit a) formations, Gorstian and Ludfordian stages, Ludlow Series, Gotland (Le Hérissé 1989); Llandovery-Ludlow series, Jordan (Keegan *et al.* 1990); rare over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), becoming more common in the Lower Elton and Middle Elton formations. Known range: Llandovery Series-Gedinnian Stage.

Genus **Oppilatala** Loeblich Jr. & Wicander 1976

Type Species. By original designation, *Oppilatala vulgaris* Loeblich Jr. & Wicander 1976, p. 20, pl. 6, figs 11-13; Lower Devonian, Oklahoma, USA.

Diagnosis. (Loeblich Jr. & Wicander 1976, p. 19). "Vesicle circular in outline, with variable number of processes clearly delineated from the vesicle and variously multifurcate; wall variously ornamented, double layered, the processes formed by the outer layer, processes commonly constricted proximally and plugged for a short distance with material resembling the vesicle wall, processes do not communicate with the vesicle; excystment by a simple rupture of the vesicle wall."

Remarks. Species assigned to *Multiplicisphaeridium* in having a sharp vesicle-process contact and have processes which are not plugged proximally; *Ozotobrachion* have fewer processes, which lack clear plugs at the bases; *Baltisphaeridium* have generally simple processes.

Oppilatala ramusculosa (Deflandre 1942 ex Deflandre 1945) Dorning 1981a

Pl. 7, fig. 9.

1942 *Hystrichosphaeridium ramusculosum* n. sp; Deflandre, figs 2-6 (*nomen nudum*).

1945 *Hystrichosphaeridium ramusculosum* Deflandre; Deflandre, p. 63, pl. 1, figs 8-16, text-figs 38-39.

1959 *Baltisphaeridium ramusculosum* (Deflandre); Downie, p. 59-60, pl. 11, fig. 13.

1970 *Evittia ramusculosa*; Lister, p. 67 (no fig.) (invalid combination).

v 1970 *Multiplicisphaeridium*? cf. *eoplanktonicum* (Eisenack 1955) comb. nov.; Lister 1970, pl. 12, fig. 17, text-fig. 25f.

non. 1970 *Multiplicisphaeridium ramusculosum* (Deflandre, 1945) comb. nov., emend.; Lister, p. 92-93, pl. 11, figs 8, 11-14, text-fig. 25a.

1974 *Peteinosphaeridium ramusculosum*; Piskun, pl. 12, fig. 9 (invalid combination).

1981a *Oppiltala ramusculosa* n. comb.; Dorning, p. 196 (no fig.).

1990 *Oppilatala ramusculosa* (Deflandre 1945a) Dorning 1981; Fensome *et al.*, p. 373 (no fig.).

Holotype. Deflandre 1945, pl. 1, figs 8-10; AY19; from the Silurian, Montagne Noire, France.

Diagnosis. (Deflandre 1945, p. 63, translation from Lister 1970, p. 93). "Globular vesicle, in some cases ellipsoidal or subspherical, ornamented with processes which are usually greater in length than $^1/_2$ the shell diameter, and perhaps equal to this diameter. The processes are of two types. Some are simple and pointed. The others, very characteristic, are ramified in an irregular manner and in addition often carry spines on the main trunk of the process."

Description. Vesicle spherical to ellipsoidal, with a single, moderately thick wall which appears faintly ornamented under transmitted light; vesicle thicker walled than processes. Thin, tubular, hollow, laevigate processes have a sharp contact with the vesicle. The bases of the processes are thicker walled and plugged and their interiors do not communicate with the vesicle cavity. Processes may rarely be simple, more commonly they are branched in a ramified fashion to the 3rd or 4th order; branching normally occurs $^2/_3$rds along the processes, rarely $^1/_3$ or $^1/_2$ the way along. Excystment by unornamented rupture, which almost divides the vesicle in two.

Dimensions. V=21-31μm, PL=15-27μm, PØb=1.5-2μm, PN=8-12 (10 specimens measured).

Remarks. The emended diagnosis of Lister (1970, p. 93) is not used as it is based on incorrectly identified specimens; examples illustrated by Lister (1970) have been placed in *M. eltonense* herein. The spines referred to in the diagnosis of Deflandre (1945) have not been observed in any specimens recovered. Although Lister (1970, p. 92) validly transferred this species to *Multiplicisphaeridium*, he also proposed transferring the variety *Baltisphaeridium ramusculosum* var. *spinosum* Deunff, a *nomen nudum*, to *Evittia* (Lister 1970, p. 67). In erecting *O. ramusculosa* var. *ramusculosa*, the autonym of *O. ramusculosa*, Cramer & Diez (1972) failed include the holotype of *O. ramusculosa*, figured by Deflandre (1945, pl. 1, figs 8-10), in synonymy. Instead, they defined one of their own specimens from the Alger Formation, Ohio, as holotype (specimen 55088f, pl. 34, fig. 41).

Occurrence. Silurian, Montagne Noire (Deflandre 1942, 1945); Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959); Elton Group, Ludlow Series, Ludlow (Lister 1970, as *M.*? cf. *eoplanktonicum*); Buildwas Formation-Leintwardine Group, Wenlock-Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); rare in the Much Wenlock Limestone Formation, with two grouped appearances from the middle

Lower Elton-basal Middle Elton formations and central Middle Elton Formation. Known range: upper Llandovery-lower Ludlow series.

Oppilatala septispinosa (Lister 1970) Le Hérissé 1989 Pl. 7, fig. 8.

v* 1970 *Multiplicisphaeridium*? *septispinosum* sp. nov.; Lister, p. 94-95, pl. 12, figs 9-16, text-figs 19b, c, 25e.

1989 *Oppilatala* cf. *septispinosum* (Lister) n. comb.; Le Hérissé, p. 179, pl. 24, fig. 10, text-fig. 14.1.

Holotype. Lister 1970, pl. 12, fig. 9; MPK230; from the Lower Bringewood Formation, Ludlow Series, sample LD8, Wigmore Road, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 94). "Vesicle hollow, smooth, spherical, relatively thin walled; processes, few in number, are long slender tubes which distally may become strap-like and which divide into delicate fingers sometimes regularly, sometimes irregularly; proximally the processes communicate freely with the vesicle cavity but are invariably septate about $^1/_4$ of the way along their length."

Description. Vesicle spherical, more commonly ellipsoidal, laevigate, slightly thicker walled than the processes. There is a sharp contact between the processes and vesicle; processes laevigate, hollow, long and slender, tubular to slightly tapering, straight or commonly flexuous, rarely simple, commonly branched at $^2/_3$rds, or rarely $^1/_2$ way along their length. Processes plugged at, or near, their bases and closed to the vesicle interior. Excystment by unornamented rupture, which almost divides the vesicle in half.

Dimensions. V=16-21µm, PL=29-43µm, PØb=1.5-2.5µm, PN=5-8 (10 specimens measured).

Remarks. This species was considered a junior synonym of *Multiplicisphaeridium* (now *Oppilatala*) *eoplanktonicum* (Eisenack 1955) by Eisenack *et al.* (1973, p. 617). The holotype of *O. eoplanktonicum* (Eisenack 1955) Dorning 1981a appears morphologically similar to *O. septispinosa*, but from the illustration it is impossible to determine whether the processes are proximally plugged. Until the holotype of *O. eoplanktonicum* is examined, and the nature of the processes ascertained, it is wiser to place those forms recovered here into *O. septispinosa*, a taxon whose morphology is more fully documented. *Oppilatala insolita* (Cramer & Diez 1972) Dorning 1981a is almost identical to *O. septispinosa*, differing only in having processes which are branched to a much higher degree. *O. ramusculosa ramusculosa* has more numerous, shorter processes, which are branched to a higher degree

Occurrence. Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Přídolí series, Ludlow and Millichope, Shropshire (Lister 1970); Hemse Formation, Ludlow Series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: upper Wenlock-Přídolí series.

Genus **Ozotobrachion** Loeblich Jr. & Drugg 1968

Type species. By original designation, *Ozotobrachion dactylos* Loeblich Jr. & Drugg 1968, p. 130-132, pl. 1, figs 1-6; [senior synonym: *Baltisphaeridium* (now *Ozotobrachion*) *palidodigitatum* Cramer 1966a; according to Cramer 1970a, p. 169 and Playford 1977, p. 31; synonymy rejected herein]; Haragan Formation, upper Gedinnian Stage, Oklahoma.

Diagnosis. (Loeblich Jr. & Drugg 1968, p. 130). "Vesicles triangular in plan view, more rarely ovate or subquadrangular. An elongate process is present at each angle; commonly there are three, rarely only two or as many as four processes. The thin-walled processes are dichotomously branched or digitate and may be open or closed distally. Proximally they are closed by a thickened plug at the juncture of the vesicle. Probable pylome represented by a split or rent between two processes. Vesicle wall thicker than that of processes, the possibility of a two-layered wall impossible to determine optically."

Remarks. The proposed synonymy of *O. palidodigitatum* and *O. dactylos* is rejected herein as the two species have different branching styles. The branches of *O. dactylos* are short and complex, whereas the branches of *O. palidodigitatum* are long and rarely subdivide.

Ozotobrachion cf. **dicros** Loeblich Jr. & Drugg 1968 — Pl. 7, fig. 7.

p. 1968 *Ozotobrachion dicros* n. sp.; Loeblich Jr. & Drugg, p. 132, 134, pl. 2, figs 1-2, 4-7 (only).

1970a *Baltisphaeridium dicros* (Loeblich & Drugg 1968) Cramer (New combination); Cramer, p. 170, pl. 13, fig. 189, text-fig. 52k (misspelt genus as *Ozotobranchion*).

1973 *Multiplicisphaeridium dicros* (Loeblich & Drugg 1968); Eisenack *et al.*, p. 605-606 (misspelt genus as *Ozotobranchion*).

1975 *Ozotobrachion* cf. *dicros* Loeblich y Drugg; Pöthé de Baldis, p. 500, pl. 1, fig. 1, pl. 2, fig. 1.

1977 *Ozotobrachion furcillatus* (Deunff 1955a); Playford, p. 31, pl. 13, figs 1-9, pl. 14, figs 13-16.

Holotype. Loeblich Jr. & Drugg, pl. 2, fig. 1; no. 67-193(6)54-100; paratypes pl. 2, figs 2-7; nos. 67-193(5)46-99; 67-193(3)48-110; 67-193, 980; 67-193(4)33-101.5; 67-193(3)27-96; 67-193, 988; from the lower part of the Haragan Formation, upper Gedinnian Stage, Oklahoma.

Diagnosis. (Loeblich Jr. & Drugg 1968, p. 132). "Similar to the type species, but with processes more slender, tapering gradually, and closed terminally. Near the distal end they branch dichotomously, with two or four successive dichotomies, each branch being of still less diameter. As in the type species, most specimens have three processes, and one specimen had only two. Process walls are thin, their surface smooth or bearing scattered grana. Plugs at the process bases are about 1 to 2 μ thick. Vesicle wall about 0.5 to 1 μ thick, with smooth to finely granulate surface.

Vesicle from 20 to 27 μ in diameter, commonly about 25 μ. The processes range from 27 to 56 μ in length, average 36 μ, and are 3 to 4 μ in width, average 3 μ."

Description. Vesicle commonly tetrahedral, rarely square, appears laevigate or finely granulate under transmitted light. The processes are thinner walled than the vesicle, hollow, laevigate or finely echinate, columnar or slightly tapering, occasionally simple, or with long, digitate branches of up to 2nd, rarely 3rd order. Striations are sometimes visible on the bases of the processes, which extend a short distance onto the vesicle. The processes are closed to the vesicle interior. In square forms, excystment via an unornamented rupture, which almost divides the vesicle in two. No excystment structures observed in tetrahedral forms.

Dimensions. V=15-20μm, PL=23-33μm, PØb=2-3.5μm, PN=4-5 (6 specimens measured).

Remarks. This taxon was considered to be a junior synonym of *Ozotobrachion furcillatus* (Deunff 1955) Playford 1977 by Playford (1977, p. 31), a synonymy rejected herein. The holotype of *O. furcillatus* has slender, elongate processes, which bifurcate, whereas the holotype of *O. dicros* has shorter, broader processes, with complex branching.

The form with elongate processes illustrated by Loeblich Jr. & Drugg (1968, pl. 2, fig. 3) appears to lack the two walled structure characteristic of this taxon, and is considered, probably, to be a species of *Dateriocradus*. Those forms illustrated as *O. dicros* by Cramer (1970a) and Eisenack *et al.* (1973) probably represent the type species of this genus, *Ozotobrachion dactylos* Loeblich Jr. & Tappan 1968, which has shorter, more complex branches.

Specimens have been assigned to *O.* cf. *dicros* as they are generally smaller than the type material and commonly have four processes and tetrahedral or rectangular vesicles; vesicles of the type material are generally triangular, bearing three processes. Examples recovered here appear similar to forms from the Lower Devonian and assigned to *O. furcillatus* by Playford (1977). These forms show a variety of vesicle and process ornament, with some showing striations at the process-vesicle contact.

Occurrence. Haragan Formation, upper Gedinnian Stage, Oklahoma (Loeblich Jr. & Drugg 1968); Los Espejos Formation, Wenlock Series, Argentina (Pöthé de Baldis 1975, as cf. *dicros*); Haragan and Bois d'Arc formations, upper Gedinnian Stage, Oklahoma (Loeblich Jr. & Wicander 1976); Lower-Middle Devonian, Moose River Basin, Ontario, Canada (Playford 1977, as *O. furcillatus*); Silurian, Argentina (Rubinstein 1993, as *O.*? cf. *dicros*); sparse occurrences in the Much Wenlock Limestone to Middle Elton formations, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock Series-Middle Devonian.

Genus **Percultisphaera** Lister 1970

Type Species. By original designation, *Percultisphaera stiphrospinata* Lister 1970, p. 96-97, pl. 13, figs 1-7, 9, text-fig. 19d-f, h, 27d; MPK 238, LD34; Lower Leintwardine Formation, Ludlow Series, Whitcliffe, Ludlow, Shropshire.

Diagnosis. (Lister 1970, p. 96). "Vesicle hollow, subspherical to ovoidal, moderately thin-walled. Ornamentation of two orders: a minor ornamentation comprising small (0.5-1μ) close-set, evenly-spaced, uniform, subconical to tubular elements, with capitate or distally expanded terminations, and a major ornamentation of slender solid spines, irregularly spaced and which may be simple or branching. Excystment aperture apical or near-equatorial in position, and of subhexagonal outline."

Remarks. The type species of this genus appears morphologically similar to *H. pseudodictyum* and *H. latispinosum*, but differs in having a second ornament of thin, solid, wiry, processes. Originally the genus contained only one species, though Lister (1970) did discuss the possibility that *Lophosphaeridium pilosum* Downie 1963 may belong in this genus; this species was transferred to *Percultisphaera* by Dorning 1981a.

Percultisphaera stiphrospinata Lister 1970 Pl. 7, figs 13-14; Pl. 12, figs 8, 11.

v* 1970 *Percultisphaera stiphrospinata* sp. nov.; Lister, p. 96-97, pl. 13, figs 1-7, 9, text-figs 19d-f, h, 27d.

1990 *Percultisphaera stiphrospinata* Lister 1970; Fensome *et al.*, p. 388 (no fig.).

Holotype. Lister 1970, pl. 13, fig. 1; MPK 238, LD34; Lower Leintwardine Formation, Ludlow Series, Whitcliffe, Ludlow, Shropshire, UK.

Diagnosis. (Lister 1970, p. 96, as for genus).

Description. Vesicle ellipsoidal, rarely spherical, covered in a dense, regular ornament of short cones or capitate processes. From between this minor ornament, long, slender, solid, wiry processes emerge, which may taper to simple tips, or be complexly branched. Excystment mechanism not observed.

Dimensions. V=25-35μm, minor ornament=0.25-0.5μm, major ornament=6-14μm (10 specimens measured).

Remarks. The minor ornament of *P. stiphrospinata* resembles that of *H. pseudodictyum* and *H. latispinosum*, which lack thin, solid, wiry processes. The diagnosis refers to the excystment structure as having a sub-hexagonal outline and what were believed to be isolated opercula were illustrated (Lister 1970, pl. 13, figs 6-7); no isolated opercula have been recovered herein. Specimens were also illustrated with large ruptures (Lister 1970, pl. 13, figs 2, 4, 9) and these structures have been seen in the present study.

Occurrence. Lower Elton-Downton Castle Sandstone formations, Ludlow-Přídolí series, Millichope and Ludlow area, Shropshire (Lister 1970); Middle Elton -Downton Castle Sandstone formations, Ludlow-Přídolí series, Ludlow area (Lister & Downie 1974); San Pedro Formation, Ludlow Series-lower Gedinnian Stage, NW Spain (Cramer *et al.* 1976); uppermost Elton-Whitcliffe groups, Ludlow Series, Britain and Ireland (Aldridge *et al.* 1979); Elton-Whitcliffe groups, Ludlow Series, Welsh Borderland (Dorning 1981a); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); Mulde-Hamra formations, Wenlock-Ludlow series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); upper Middle Elton Formation, Goggin Road. Known range: Wenlock Series-lower Gedinnian Stage.

Genus **Psenotopus** Tappan & Loeblich Jr. 1971 emend.

Type Species. By original designation, *Psenotopus chondrocheus* Tappan & Loeblich Jr. 1971, p. 408, pl. 11, figs 1-6; Waldron Formation, Wenlock Series, Silurian, Tunnel Mill, SW$^{1}/_{4}$ sec, 11, T6N, R8E, Jennings County, Indiana.

Diagnosis. (Tappan & Loeblich Jr. 1971, p. 406). "Vesicle spherical, surface gemmate, ornamented with low tubercles or processes arranged in patches or bands separated by bare and laevigate areas; processes apparently solid, low, circular in plan view, varying in size, rounded and smooth to slightly knobby, with a slight tendency to appear aculeate at the tips; wall thin, smooth but commonly with microridges and small, rare, scattered granules; excystment by a simple rupture of the vesicle."

Emended diagnosis. Excystment by relatively large, circular pylome.

Remarks. The diagnosis has been emended to reflect recognition of the true excystment mechanism. A simple rupture in the vesicle wall was indicated as the most likely excystment mechanism by Loeblich Jr. & Tappan (1971, pl. 11, fig. 5); in examples recovered here, however, pylomes have been found on several specimens and the splitting of the vesicle wall appears to be preservational. The localisation of the ornament into bands, which separate bare areas, distinguishes this genus from *Lophosphaeridium* and *Helosphaeridium*, species of which excyst via ruptures.

Psenotopus chondrocheus Tappan & Loeblich Jr. 1971 emend. Pl. 7, figs 15-16.

1971 *Psenotopus chondrocheus* n. sp.; Tappan & Loeblich Jr., p. 408, pl. 11, figs 1-6.

1990 *Psenotopus chondrocheus* Tappan & Loeblich Jr. 1971; Fensome *et al.*, p. 421 (no fig.).

Holotype. Tappan & Loeblich Jr. 1971, pl. 1, fig. 3; holotype 69-63(SEM2885), isotypes 69-63(SEM2465-2466; SEM 2706, 2709) and 69-63(10) 49.2-106.1; Waldron Formation, Wenlock Series, Silurian, Tunnel Mill, SW$^{1}/_{4}$ sec, 11, T6N, R8E, Jennings County, Indiana.

Diagnosis. (Tappan & Loeblich Jr. 1971, p. 408). "Vesicle spherical, in compression commonly somewhat angular; surface gemmate, ornamented with low, apparently solid tubercles or processes that occur in patches or bands separated by bare areas; tubercles low, circular in plan view, ranging in size from 0.7 to 1.5 μ, irregularly spaced from 0.6 to 5.3 μ apart, in side view commonly tending to become weakly aculeate, with small projections at the summit; in compression or under high vacuum in an evaporator the areas of bare surface tend to collapse, whereas the bands or patches carrying the tubercles are stronger and stand up owing to the added thickness of the wall; wall thin, about 0.5 μ in thickness, smooth or with minute spherical gemmules and a fine series of irregular ridges; excystment by a simple rupture and splitting of the vesicle wall."

Emended diagnosis. Excystment by relatively large, circular pylome.

Description. Vesicle laevigate, spherical to ellipsoidal, with a relatively thick, single wall. The vesicle surface is divided into a series of fields by bands of solid ornament. The ornament can appear bulbous, rounded, or parallel sided with capitate tips; on any single specimen the tubercles are of generally uniform size. Excystment by a relatively large, circular, pylome, often surrounded by processes.

Dimensions. V=58-65µm, F=13-35µm, PL=0.5-2µm, W=0.5-2µm, pylome=13-15µm (7 specimens measured).

Remarks. The diagnosis has been restricted and emended with regard to the method of excystment (see *Psenotopus*-Remarks above). Specimens recovered in this present study are generally smaller than those forms described by Loeblich Jr. & Tappan (1971, V = 59-65µm vs' 67-80µm).

Occurrence. Waldron Formation, Wenlock Series, Silurian, Indiana (Loeblich Jr. & Tappan 1971); Much Wenlock Limestone Formation-Elton Group, upper Wenlock-lower Ludlow series, Welsh Borderland (Dorning 1981a); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); Llandovery Series, När borehole; Lower and Upper Visby, Högklint (unit a) and Slite (unit f) formations, Llandovery-middle Wenlock series, Gotland (Le Hérissé 1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); rare over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), present in most Lower Elton Formation samples, rarer in the Middle Elton Formation, Goggin Road. Known range: Llandovery-lower Ludlow series.

Genus **Pulvinosphaeridium** Eisenack 1954

1978 *Rhiptosocherma* n. gen.; Loeblich Jr. & Tappan, p. 1284. (The synonymy of this genus to *Estiastra* proposed by Sarjeant & Stancliffe 1994, p. 50 is rejected herein)

.1994 *Chalaziosphaeridium* n. gen.; Sarjeant & Stancliffe, p. 48.

Type species. By original designation, *Pulvinosphaeridium pulvinellum* Eisenack 1954, p. 210, pl. 1, fig. 10; Upper Visby Marl, upper Llandovery Series, Lickershamn, Gotland, Sweden.

Diagnosis. (Eisenack 1954, p. 210, translation by Sarjeant & Stancliffe 1994, p. 52). "Hystrichospheres whose appendages are attached broadly to the central body in such a way that a boundary does not exist between appendages and vesicle, together producing a star-shaped, branching shell with several arms."

Remarks. The diagnosis of *Pulvinosphaeridium* was emended by Sarjeant & Stancliffe (1994, p. 52), to include only those forms with blunt, rounded processes, in a single plane. To accommodate specimens with processes in more than a single plane they erected *Chalaziosphaeridium.* This emendation is not followed here and the genus *Chalaziosphaeridium* is considered a junior synonym of *Pulvinosphaeridium*, as there appears to be no reason to restrict *Pulvinosphaeridium* to species with processes in a single plane. Although the holotype of the type species, *P. pulvinellum*, has four processes in a single plane, the diagnosis refers to the vesicle shape as being tetrahedron-like to star-like (see new translation Sarjeant & Stancliffe 1994, p. 53). This clearly implies that some specimens of *P. pulvinellum* have processes in more than a single plane. Unlike *Veryhachium* and *Dorsennidium*, where the plane of process development has some use for creating more easily understood morphotaxa, the application to genera such as *Pulvinosphaeridium* accomplishes nothing.

Pulvinosphaeridium dorningii sp. nov. Pl. 8, figs 2-3.

p. 1970 *Baltisphaeridium cantabricum* Cramer 1964, emend.; Lister, p. 58-59, pl. 3, figs 3, 8, 10 (only).

Name. Species name *dorningii*, after K. J. Dorning who has extensively worked on British Silurian acritarchs and prasinophyte algae.

Holotype. Pl. 8, fig. 3; GOG2/69-A (2)-N22; Lower Elton Formation, Goggin Road, Mortimer Forest, Ludlow.

Description. Vesicle poorly defined, formed by the fusion of the process bases, though some processes have a distinct vesicle contact. Wall thin, transparent or darkened; some specimens, usually the darker ones, show a linear structure within the wall sub-parallel to the longest axis of the processes. Processes broad based, hollow, open to vesicle interior, tapering to blunt, rounded or slightly rounded tips. Excystment mechanism not observed.

Dimensions. V=140-240µm, PØb=19-47µm, PN=6-9 (15 specimens measured).

Remarks. This species is similar overall to *P. oligoprojectum*, which differs in having fewer (3-5), generally broader based (37-75µm) processes, which have an indistinct vesicle contact; some processes of *P. dorningii* sp. nov. have a distinct contact with the vesicle. *Pulvinosphaeridium improcerum* (Loeblich Jr. 1970) Fensome *et al.* 1990 is very similar to *P. dorningii* sp. nov. in that it also possesses striae parallel to the longest axis of the processes. It differs in having more processes (8-11), which can have wrinkled or crenulate ends.

Occurrence. Lower Elton Formation, Ludlow series, Ludlow and Millichope, Shropshire (Lister 1970, as part of *B. cantabricum*); middle Lower Elton Formation, Goggin Road. Known range: lower Gorstian Stage.

Pulvinosphaeridium oligoprojectum Downie 1959 emend. Pl. 7, fig. 17; Pl. 8, fig. 1.

v* 1959 *Pulvinosphaeridium oligoprojectum* sp. nov.; Downie, p. 64, pl. 10, fig. 12; pl. 12, fig. 12.

.1978 *Pulvinosphaeridium striatulum* sp. nov.; Kiryanov, p. 81, pl. 14, fig. 7.

1994 *Chalaziosphaeridium oligoprojectum* (Downie 1959); Sarjeant & Stancliffe, p. 50 (no fig.).

Holotype. Downie 1959, pl. 10, fig. 12, paratype, pl. 12, fig. 12; holotype Mik(P)12002, paratype, Mik(P)16001; Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1959, p. 64). "Hollow test, walls thin, yellow-brown, surface matt, five broad hollow rounded processes unite to form the ill-defined body, overall size 150 to 250μ."

Emended Diagnosis. A large acritarch whose poorly defined vesicle is formed by the fusion of the process bases. Some specimens appear thin and almost transparent, whilst the wall of others can appear darkened. Processes broad based, tapering to blunt, rounded tips; occasionally, along the processes, a linear structure approximately parallel to the longest axis is visible. These linear structures appear to be within the wall, not an external ornament; they are generally only visible on the darker specimens. Excystment mechanism not observed.

Dimensions. T=128-220μm, PØb=37-75μm, PN=3-5 (12 specimens measured).

Remarks. The holotype and paratype of this taxon are thin walled and the linear wall structures are discernible on the paratype. The emended diagnosis includes forms with a larger range of processes (PN = 3-5) than specimens described from the Wenlock Series by Downie (1959).

The taxa *P. oligoprojectum* and *P. pulvinellum* were considered synonymous by Downie (1963, p. 638), though *P. oligoprojectum* was retained and transferred to *Chalaziosphaeridium* by Sarjeant & Stancliffe (1994, p. 50). Although very similar to *P. pulvinellum*, there are marked differences that dictate its separation. The processes of *P. oligoprojectum* can be more numerous and are always more elongate and lack the cushion-like aspect of *P. pulvinellum.* The process walls of *P. oligoprojectum* also commonly appear striate parallel to their longest axis, whereas the holotype of *P. pulvinellum* appears laevigate under transmitted light; forms illustrated as *P. pulvinellum* by Le Hérissé (1989, pl. 21, figs 5-6) have granulate processes. The author also considers these specimens are probably distinct from *P. pulvinellum*, as they have a greater similarity to *P. oligoprojectum.*

P. oligoprojectum is similar to *Pulvinosphaeridium dorningii* sp. nov., which has more processes (PN = 6-9), which are generally narrower (PØb = 19-47μm). *P. striatulum* was included in synonymy with *P. pulvinellum* by Le Hérissé (1989, p. 185). Because of the striate nature of the processes, this taxon is considered synonymous with *P. oligoprojectum* herein.

Occurrence. These occurrences below are those documented for *P. oligoprojectum* and its synonyms. Many taxa identified as *P. pulvinellum* in the UK are likely to be *P. oligoprojectum*, but as the references lack illustrations, they have not been included. Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959); Silurian, Podolia (Kiryanov 1978, as *P. striatulatum*); Much Wenlock Limestone-Lower Elton formation boundary, Pitch Coppice Quarry and Goggin Road. Known range: Sheinwoodian-Gorstian stages.

Genus **Salopidium** Dorning 1981a

Type Species. By original designation, *Baltisphaeridium brevispinosum* var. *granuliferum* Downie 1959, p. 59, pl. 10, fig. 5; Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Dorning 1981a, p. 198). "Vesicle spherical to subspherical, foveolate; several to numerous laevigate processes taper distally to a simple termination. Excystment by a straight split in the vesicle wall to produce two equal halves."

Remarks. In overall morphology, species of *Salopidium* resembles those of *Ammonidium* and *Gracilisphaeridium* (see *A. waldronense*-below).

Salopidium granuliferum (Downie 1959) Dorning 1981a Pl. 8, fig. 4.

v* 1959 *Baltisphaeridium brevispinosum* var. *granuliferum* nov; Downie, p. 59, pl. 10, fig. 5.
1965 *Micrhystridium granuliferum* (Downie 1959); Deflandre & Deflandre-Rigaud, fiche 2247.
1967 *Baltisphaeridium granuliferum* Downie; Martin, p. 314, pl. 1, fig. 18.
1970 *Baltisphaeridium granuliferum* Downie 1959; Lister, p. 56, pl. 2, figs 2-5.
1981a *Salopidium granuliferum* n. comb.; Dorning, p. 198 (no fig.).
1990 *Salopidium granuliferum* (Downie 1959) Dorning 1981; Fensome *et al.*, p. 445 (no fig.).

Holotype. Downie 1959, pl. 10, fig. 5; Mik(P)22001; from the Coalbrookdale Formation, Wenlock Series, Wenlock Edge, Shropshire.

Diagnosis. (Downie 1963, p. 59). "A small variety of *B. brevispinosum* with relatively numerous processes, the test surface ornamented with small granules 1μ apart."

Description. Vesicle ellipsoidal, rarely spherical, with a thin, foveolate, wall. Processes numerous, thin, hollow, open to vesicle interior, tapering to simple, unbranched tips. Excystment by unornamented rupture, which almost divides the vesicle in two.

Dimensions. V=18-30μm, PL=7-13μm, PØb=0.5-2.5μm (10 specimens measured).

Remarks. This species is almost identical to two other taxa, *A. waldronense* and *Gracilisphaeridium encantador* Cramer 1970a. The processes of *A. waldronense* differ in having a rosette arrangement of short branches at their tips; processes of *G. encantador* also have a rosette of branches, but the branches are joined together in a series of loops. Le Hérissé (1989) described an intraspecific variation between two extremes of *A. microcladum* (assigned to *A. waldronense* herein), which he also reported to be apparent in *S. granuliferum* and *G. encantador* (Le Hérissé 1989; see *A. microcladum*-Remarks above).

The holotype of *S. granuliferum* is almost identical to that of *Salopidium wenlockense* (Downie 1959) Dorning 1981a, which was considered a junior synonym of *Baltisphaeridium* (now *Polygonium*) *nanum* (Deflandre 1945) Downie 1959 by Lister (1970). The processes bases of the holotype of *S. wenlockense* are slightly broader than those of *S. granuliferum*, though this probably represents an intraspecific variation. If the two taxa were treated as synonymous, *S. wenlockense* would be the senior name.

Occurrence. Coalbrookdale Formation, Shropshire (Downie 1959); upper Llandovery-lower Wenlock series, Belgium (Martin 1967, 1969); Ludlow Series, Ludlow and Millichope, Shropshire (Lister 1970); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Llandovery Series-Lower Elton Formation, Ludlow Series, Britain and Ireland (Aldridge *et al.* 1979); Hughley Shales-Elton Group, Llandovery-Ludlow series, Welsh Borderland (Dorning 1981a); Wenlock Series, Ayrshire (Dorning 1982); lower Silurian, Ringerike, Norway (Dorning & Aldridge 1982, as *S.* cf. *granuliferum*); Much Wenlock Limestone Formation, Wenlock Series, Dudley, UK (Dorning 1983); middle-upper Llandovery Series, Llandovery type area (Hill & Dorning 1984); (Armstrong & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Llandovery-Wenlock series, Austria (Priewalder 1987); lower Silurian, Ringerike, Norway (Smelror 1987); upper Llandovery Series, Libya (Hill & Molyneux 1988); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); upper Llandovery Series, När borehole-upper Mulde Formation, upper Wenlock Series, Gotland (Le Hérissé 1989); Silurian, Argentina (Rubinstein 1993); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Llandovery-lower Ludlow Series.

Salopidium sp. A Pl. 8, fig. 6.

1989 *Salopidium granuliferum* malformés; Le Hérissé, pl. 30, figs 11-12, 17.

Description. Vesicle thin walled, ellipsoidal, foveolate, with numerous processes. The processes can be columnar with rounded tips or columnar with bulbous tips, often the bulbous tips have a single, short spine at their apices. This spine gives the process an appearance similar to the sting of a scorpion. Excystment by unornamented rupture, which almost divides the vesicle in two.

Dimensions. V=19-26μm, PL=4-8μm, PØb=1-2μm (4 specimens measured).

Remarks. Few specimens of this taxon were recovered; similar specimens were referred to as malformed *S. granuliferum* by Le Hérissé (1989). It is only the columnar or bulbous nature of the processes that separates this taxon from the otherwise identical *S. granuliferum.*

Occurrence. rare from the Much Wenlock Limestone-Middle Elton formations, Goggin Road.

Genus **Schismatosphaeridium** Staplin, Jansonius & Pocock 1965

Type species. By original designation, *Schismatosphaeridium perforatum* Staplin *et al.* 1965, p. 179, pl. 18, figs 4-6, 11, 12; Imp. 5099- #8, slide 5-110.8 x 37.3; from the Upper Visby Formation (marl), upper Llandovery Series, Västkinde, Gotland.

Diagnosis. (Staplin *et al.* 1965, p. 178). "Vesicle lenticular, ellipsoidal or spherical; one side has a rent or slit, the opposite side a round pylome; wall firm, smooth or with minute sculpture; no processes, no wall canals."

Remarks. The split in the vesicle wall, on the opposite side to the pseudopylome, distinguishes this genus from *Leiosphaeridia.*

Schismatosphaeridium rugulosum Dorning 1981a emend. Pl. 8, figs 7-8.

v* 1981a *Schismatosphaeridium rugulosum* n. sp.; Dorning, p. 199, pl. 3, fig. 4

1989 *Schismatosphaeridium guttulaferum* n. sp.; Le Hérissé, p. 191, pl. 25, figs ?5, 6.

1990 *Schismatosphaeridium rugulosum* Dorning 1981; Fensome *et al.*, p. 447 (no fig.).

Holotype. Dorning 1981a, pl. 3, fig. 4; LH82K, R41/0, MPK2931; from the Coalbrookdale Formation, Wenlock Series, Longhope Hill, May Hill, Gloucestershire (SO 695 185).

Original Diagnosis. (Dorning 1981a, p. 199). "Vesicle subspherical, 35-40µm across, rugulate to foveolate; at one pole a pore 8-10µm wide, at the other pole a split 25-30µm long."

Emended Diagnosis. Vesicle spherical, foveolate, shagrinate, granulate or with short, solid projections (simple, capitate and bulbous). One side of the vesicle has a relatively large pseudopylome, with a thickened rim; the opposing side of the vesicle has a unornamented rupture (not open on all specimens) which may extend across the whole vesicle. The ornament appears to be concentrated around the equator and is reduced or absent in the areas surrounding the pseudopylome and rupture.

Dimensions. V=28-44µm, pseudopylome=5-12µm, ornament height=up to 1.5µm, W=0.5-1.5µm (8 specimens measured).

Remarks. The ornament of this taxon is quite variable, ranging between forms with foveolate and chagrinate vesicles, with few or no projections, to examples which have only solid projections. *S. guttulaferum* corresponds to the latter category and is considered here to be a junior synonym of *S. rugulosum.* The diagnosis has been emended to encompass the wider variation found in this taxon.

Occurrence. Hughley Shales-middle Coalbrookdale Formation, Llandovery-middle Wenlock Series, Welsh Borderland (Dorning 1981a); lower Silurian, Ringerike, Norway (Smelror 1987); middle Wenlock Series, Cheviot Hills, NE England (Barron 1989); Llandovery-Wenlock series boundary and upper Wenlock Series (Mulde Formation), Gotland (Le Hérissé 1989); Lower Elton Formation, Goggin Road. Known range: Llandovery-lower Ludlow Series.

Schismatosphaeridium sp. A Pl. 8, figs 19-20.

1981a *Schismatosphaeridium perforatum* Staplin *et al.* 1965; Dorning, pl. 3, fig. 3.

Description. Vesicle ellipsoidal, rarely subspherical, laevigate or granulate. On one side of the vesicle there is a small pseudopylome, around which is a thickened rim; positioned on the opposite side of the vesicle is a linear fold or rupture.

Dimensions. V=23-29µm, W=0.25-1µm, pseudopylome=1-3µm, thickened rim=0.5-2µm (15 specimens measured).

Remarks. This taxon was illustrated as *S. perforatum* by Dorning (1981a, pl. 3, fig. 3); the holotype of *S. perforatum* Staplin *et al.* 1965, however, appears to possess a much larger pseudopylome (*c.* 9µmm diameter).

Occurrence. Lower Elton Formation, Pitch Coppice Quarry; Much Wenlock Limestone-Middle Elton formation, Goggin Road (particularly the Middle Elton Formation).

Genus **Stellechinatum** Turner 1984

Type Species. By original designation, *Veryhachium celestum* Martin 1969, p. 89, pl. 3, fig. 147, pl. 4, fig. 206, pl. 6, fig. 252; from the Llandovery Series-Tarannonian, Silurian, Belgium.

Diagnosis. (Turner 1984, p. 137). "Vesicle hollow with polygonal or sub-polygonal outline. Wall thin (<1µm), single layered. Eight or more simple, hollow, proximally open, tapering processes having wide bases, curving proximal contacts and acuminate distal terminations. Process stems ornamented with small grana or spines that may become hair like distally. This ornament may extend onto the vesicle surface."

Remarks. This genus is distinguished from *Polygonium* Vavrdová 1966 and *Goniosphaeridium* Eisenack 1969 by the presence of ornament on the processes, which extends onto the vesicle (Turner 1984).

Stellechinatum ? sp. A — Pl. 8, fig. 5; Pl. 12, figs 9-10.

Description. Vesicle thin, hollow, laevigate, rhomboidal, polygonal or circular in outline. Processes hollow, open to vesicle interior, simple, granulate or finely echinate along length. Excystment mechanism not observed.

Dimensions. V=18-25µm, PL=18-26µm, PØb=1.5-6µm, PN=6-13 (13 specimens measured).

Remarks. This taxon has been provisionally assigned to *Stellechinatum*, as it does not conform to the present diagnosis. The diagnosis restricts the vesicle shape of *Stellechinatum* to polygonal or sub-polygonal, whereas examples recovered here can possess spherical/ellipsoidal, rhomboidal or polygonal vesicles. The grana and fine echinae tend also to be restricted to the processes, whereas in *Stellechinatum* they pass onto the vesicle.

Specimens assigned to *Stellechinatum* ? sp. A are similar to *D. rhomboidium*, *D. pentagonale* and *M. inflatum*, but differ in having generally broader based processes which have an ornament of grana or fine echinae, not fine granulations. The four taxa are easily confused as the ornament of cf. *Stellechinatum* sp. A is not easily visible under transmitted light, even on well preserved specimens.

Occurrence. Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. This taxon occurs in very high numbers around the Lower-Middle Elton formation boundary and in the centre of the Middle Elton Formation at Goggin Road.

Genus **Tunisphaeridium** Deunff & Evitt 1968

Type species. By original designation, *Tunisphaeridium concentricum* Deunff & Evitt 1968, p. 3, pl. 1, figs 1-12; USNM 139392 (R4.2 + 5.4); from the Maplewood Formation, upper Llandovery Series, Silurian, Genesee River, Rochester, New York. [Taxonomic senior synonym: *Baltisphaeridium* (now *Tunisphaeridium*) *tentaculaferum* Martin 1967, p. 312, pl. 1 fig. 23 according to Cramer (1970a, p. 192) and Eisenack *et al.* (1973, p. 1057-1059)].

Diagnosis. (Deunff & Evitt 1968, p. 2). "Acritarchs with an overall spherical to ellipsoidal or pyriform outline composed of a central sphaeroidal [*sic*] vesicle bearing numerous rodlike, apparently solid, processes whose extremities are interconnected by a diaphanous membrane alone, by a membrane reinforced with a network of faint to conspicuous filaments that radiate from the process tips, or by such filaments with only traces of a membrane. No pylome observed."

Remarks. An outer membrane, supported by the processes and surrounding the vesicle, distinguishes this genus from any other.

Tunisphaeridium tentaculaferum (Martin 1967) Cramer 1970a Pl. 8, fig. 10.

1967 *Baltisphaeridium tentaculaferum* nov. sp.; Martin, p. 312, pl. 1, fig. 23, text-fig. 3.
1968 *Tunisphaeridium concentricum* n. sp.; Deunff & Evitt, p. 3, pl. 1, figs 1-12.
1966a *Tunisphaeridium venosum* Deunff 1965; Cramer, p. 235 (no fig.) (*nomen nudum*).
1968a *Tunisphaeridium venosum* Deunff 1966(?); Cramer, p. 66, pl. 1, fig. 5 (*nomen nudum*).
1970a *Tunisphaeridium tentaculiferum* (Martin 1967) Cramer (New Combination); Cramer, p. 192-193, pl. 6, figs 105-106, 108-109.
1990 *Tunisphaeridium tentaculaferum* (Martin 1967) Cramer 1970; Fensome *et al.*, p. 498 (no fig.).

Holotype. Martin 1967, pl. 1, fig. 23; preparation 1508; from the Silurian, outcrop 12, Parc de Neuville-sous-Huy, Belgium.

Diagnosis. (Cramer 1970a, p. 192). "Central body spherical, hollow; clearly differentiated from the processes. Numerous (30 to 40, rarely up to 50) slender, cylindrical processes are present; about ten are visible in optical section. The processes appear to be solid. Distally, the processes are interconnected by a more or less regular set of complex pinnae forming an open-mazed net which is concentric with the central body. The net varies from widely mazed in which the braided pinnae are relatively unbranched, to a net in which the pinnae are highly branched secondarily and the mazes of the net are narrow."

Description. Most specimens fragmented or poorly preserved. Vesicle ellipsoidal, thin walled, almost transparent. Processes solid, wiry, with slightly expanded bases; process tips are complexly branched to form a net-like structure, which, in well preserved specimens, encompasses the inner vesicle. In poorly preserved specimens the majority of this net-like structure is missing, with only fragments being attached to individual processes. An excystment structure was not directly observed, but what appeared to be several unattached, circular, opercula, with processes, were observed, suggesting that excystment takes place via a relatively large, circular pylome.

Dimensions. V=22-32µm, PL=10-18µm (8 specimens measured).

Remarks. The species *Tunisphaeridium venosum* Deunff, a *nomen nudum*, was described in a preprint informally distributed by the CIMP (group 9, acritarchs) in May 1965. The specific epithet of this taxon has also been misspelt as *tentaculiferum* (e.g. Cramer 1970a, Cramer & Diez 1972).

Occurrence. Maplewood Formation, upper Llandovery Series, New York (Evitt 1961, Cramer 1968a, Deunff & Evitt 1968); upper Llandovery Series, Belgium (Martin 1966a, 1967); San Pedro Formation, upper Ludlow Series, NW Spain (Cramer 1966a); Maplewood Formation, upper Llandovery Series, New York (Cramer 1968a); Red Mountain Formation, Llandovery Series, Alabama, Georgia; Crab Orchard Formation, upper Llandovery Series, Kentucky; Osgood and Alger shales, upper Llandovery, Kentucky, Indiana and Ohio; subsurface material (?late upper Silurian), Libya; Neahga Shale, upper Llandovery Series, New York and Ontario (Cramer 1970a); subsurface Florida (Llandovery-Pridolí series); Maplewood and Neahga formations, upper Llandovery Series; Osgood Formation, upper Llandovery Series, Kentucky; basal Red Mountain Formation, lower-upper Llandovery Series; Rose Hill Formation, upper Llandovery Series, Virginia; Waldron Formation, upper Wenlock Series, Indiana and Kentucky (Cramer & Diez 1972); Devonian, Ontario (Legault 1973); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Llandovery-lower Wenlock series, Llandovery type area and Welsh Borderland (Hill 1974); Ludlow Series, Algeria (Jardiné *et al.* 1974); Lower-Middle Devonian, Moose River Basin, Ontario, Canada (Playford 1977); Upper Visby-Högklint formations, lower Wenlock Series, Gotland (Cramer *et al.* 1979); Turkey (Erkman & Bozdogan 1979); Silica Formation, Givetian Stage, Ohio (Wicander & Wood 1981); Los Espejos Formation, lower Ludlow Series, Argentina (Pöthé de Baldis 1981); upper Llandovery-lower Wenlock series, Welsh Borderland (Dorning 1981a); Middle Devonian, Ohio (Wicander & Wright 1983); middle Llandovery Series, Llandovery type area (Hill & Dorning 1984); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Haragan Formation, Lower Devonian, Oklahoma (Wicander 1986); lower Silurian, Ringerike, Norway (Smelror 1987); Llandovery Series, Libya (Hill & Molyneux 1988); Llandovery-Wenlock series, Gotland (Le Hérissé 1989); rare over the Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road) and lower Elton Formation (Goggin Road), becoming more common in the upper Middle Elton Formation (Goggin Road). Known range: Llandovery Series-Middle Devonian.

Genus **Veryhachium** Deunff 1954b emend. Sarjeant & Stancliffe 1994

Type species. By subsequent designation, *Hystrichosphaeridium trisulcum* Deunff 1951, p. 322, fig. 3; phosphatic nodule base, Kermeur sandstone, Caradoc Series, Crozon Peninsula, Brittany.

Diagnosis. (Sarjeant & Stancliffe 1994, p. 33). "Vesicle cushion-shaped, triangular to quadrangular in outline, with sides convex to concave, eilyma thin, single-layered or apparently so. Spines arise from the angles and proximally merge so smoothly with the vesicle wall that no exact limit can be set on their bases. They are arranged in a single plane, though a single accessory spine of markedly smaller size may be developed on one surface of the vesicle. Spines hollow, cuneiform to acuminate in shape and uniform in size or nearly so; distally they are closed, simple and pointed. The spine cavity communicates freely with the interior of the vesicle. Surface of vesicle and spines laevigate to granulate, but without verrucae, striae or secondary spinelets. Escape structure, where developed, typically an epityche but, in quadrangular forms, may be a linear slit."

Remarks. A comprehensive list of authors who have emended the diagnosis of this genus, and a historical background, is given by Sarjeant & Stancliffe (1994, p. 6-10, 33) and by Stancliffe & Sarjeant (1995, p. 223-225, 229). The latest emendation to the diagnosis stipulates that species assigned to *Veryhachium* must have processes in a single plane. This distinguishes it from *Dorsennidium*, which generally have processes in more than a single plane, though there are exceptions (see *Dorsennidium*-Remarks above).

The constituent species of *Veryhachium* were recently assessed and reassessed (Sarjeant & Stancliffe 1994, Stancliffe & Sarjeant 1995). Two subgenera were distinguished, *Veryhachium* subgenus *Veryhachium* and *Veryhachium* subgenus *Tetraveryhachium*; recognised by the presence of three or four processes respectively. The 65 species assigned to *Veryhachium* in Sarjeant & Stancliffe (1994) were reduced to 34 in Stancliffe & Sarjeant (1995) by grouping species with similar morphologies together. These groups were based on several morphological features (shape, excystment method, process-vesicle contact, wall structure, process number, process shape and structure, ornament, ultrastructure, dimensions, clustering and variety). Species were divided into eight categories, four in each subgenera, with two extra categories, one in each subgenus, for taxa that could not be placed in the other groups. To each of these categories typical species were assigned, to which other, morphologically similar, species were synonymised. Although probably correct in their assertion that *Veryhachium* contained too many species for such a simple morphology, Stancliffe & Sarjeant (1995) appear to have forced species together with, seemingly, little regard for the subtle features on which the species were erected and, thus, the proposed categories are not used herein.

Veryhachium trisphaeridium Downie 1963 emend. Pl. 8, fig. 14.

	1959	*Veryhachium trispinosum* (Eisenack); Downie, pl. 12, fig. 7.
	1963	*Veryhachium trispinosum* (Eisenack); Downie, p. 636 (no fig.).
v*	1963	*Veryhachium trisphaeridium* sp. nov.; Downie, p. 637, pl. 92, fig. 7.
	1990	*Veryhachium trisphaeridium* Downie 1963; Fensome *et al.*, p. 525 (no fig.).
	1994	*Veryhachium trisphaeridium* Downie 1963; Sarjeant & Stancliffe, p. 35 (no fig.).
	1995	*Veryhachium trisphaeridium* Downie 1963; Stancliffe & Sarjeant, p. 234 (no fig).

Original diagnosis. (Downie 1963, p. 637). "A species of *Veryhachium* with three simple spines and an equilateral thin walled subtriangular test. The spines are equal in length or longer than the sides of the test. The test is constricted midway between the spine bases forming a Y-shaped furrow clearly visible when the spines are more or less in the same plane."

Emended diagnosis. Vesicle laevigate, triangular, with straight or slightly convex sides. Processes slender, straight or slightly flexuous, hollow, open to vesicle interior; laevigate or finely granulate. Excystment via an epityche.

Dimensions. V=12-24µm, PL=16-39µm, PØb=1-3µ (13 specimens measured).

Remarks. The characteristically inflated vesicle of *V. trisphaeridium*, illustrated by Downie (1963, pl. 92, fig. 7), has been found in specimens recovered during the present study and appears to be the result of preservation. It was decided to use the name *trisphaeridium* for those simple, three spined veryhachiids recovered here, as the type material comes from the Wenlock Series of Shropshire. *V. trisphaeridium* may prove to be synonymous with other, similar, three spined taxa (e.g. *Veryhachium trispinosum* (Eisenack 1938) Stockmans & Willière 1962a or *Veryhachium downiei* Stockmans & Willière 1962a); it is treated as separate until re-examination of all the holotypes.

Under the classification of Stancliffe & Sarjeant (1995), forms assigned to this species would be placed in category 2 (forms with small vesicles and long processes) and would probably be assigned to *Veryhachium (Veryhachium) triqueter* Sarjeant 1973, which typifies this category.

Occurrence. Wenlock Series, Shropshire (Downie 1959, 1963); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Wenlock-Ludlow series.

Genus **Visbysphaera** Lister 1970 emend. Kiryanov 1978 emend. Le Hérissé 1989

Type Species. By original designation, *Baltisphaeridium dilatispinosum* Downie 1963, p. 642, pl. 92, fig. 4; sample BS/3, Buildwas Formation, Wenlock Series, Wenlock Edge, Shropshire [senior synonym = *Visbysphaera pirifera* (Eisenack 1954) Kiryanov 1978].

Diagnosis. (Translated from Le Hérissé 1989, p. 199). "Vesicle spherical to subspherical, wall double layered, thickness variable, smooth or lightly ornamented, numerous heteromorphic processes, hollow, formed by the thin external wall, length of processes less than half vesicle diameter; the processes, which do not communicate with the vesicle interior, are generally expanded distally: on all their length (pyriform ornament) with the median part (spinose ornament) or distally (club like ornament with rounded extremities); the processes are simple, simply bifurcate, wreathed in short spines or filamentous spines disposed in the same plane, sometimes anastomosing, the processes are randomly distributed, without preferential orientation, or are aligned along the crests or folds of the wall, delineating smooth polygonal areas (restricted distribution). Several species show an endopylome opening, with a simple split, as the equivalent to the pylome, on the external wall."

Remarks. This genus was considered a junior synonym of *Multiplicisphaeridium* by Eisenack *et al.* (1973, p. 1075), but was retained by Kiryanov (1978), and differs in having two walls and short, spinose or club-like processes.

Visbysphaera microspinosa (Eisenack 1954) Lister 1970 Group Pl. 8, figs 16-17; Pl. 12, figs 12-14.

1954 *Hystrichosphaeridium microspinosum* n. sp.; Eisenack, p. 209-210, pl. 1, fig. 8.
1959 *Baltisphaeridium microspinosum* (Eisenack); Downie, p. 60, pl. 10, fig. 10.
1963 *Lophosphaeridium microspinosum* (Eisenack); Downie, p. 632, pl. 92, fig. 11.
nonv. 1970 *Visbysphaera microspinosa* (Eisenack 1954) comb. nov.; Lister, p. 99-100, pl. 13, figs 11, 12, text-fig. 19g, m.
1971 *Buedingisphaeridium microspinosum* (Eisenack 1954a); Gardiner & Vanguestaine, p. 183-184, (invalid combination).
1973 *Baltisphaeridium microspinosum* (Eisenack 1954); Eisenack *et al.*, p. 145-146.
1978 *Baltisphaeridium listeri* sp. nov.; Kiryanov, p. 26-27, pl. 9, fig. 11, pl. 10, fig. 1.
1987 *Visbysphaera* cf. *microspinosa* (Eisenack 1954) Lister 1970; Priewalder, p. 62, pl. 16, figs 2-4, pl. 21, fig. 4.
1989 *Visbysphaera microspinosa* (Eisenack) group; Le Hérissé, p. 210-211, pl. 29, figs 9-14.
1990 *Visbysphaera microspinosa* (Eisenack 1954a) Lister 1970; Fensome *et al.*, p. 531 (no fig.).

Holotype. Eisenack 1954, pl. 1, fig. 8; EC(SMF) preparation E1, Gotland, No. 5; from the Upper Visby Formation, upper Llandovery Series, Lickershamn, Gotland.

Diagnosis. (Eisenack 1954, p. 209-In German).

Description. Vesicle spherical to ellipsoidal, with a moderate to thick wall, bearing a range of ornament (granulations, spines or baculae); ornament apparently solid in most cases, though some does appear hollow. The cavities of hollow processes are not open to the vesicle interior. With a SEM, the vesicle surface between the ornament can be smooth or show a series of small, irregularly arranged grooves (also recorded by Le Hérissé 1989); under transmitted light the vesicle appears laevigate. Excystment via unornamented rupture.

Dimensions. V=37-67µm, OH=upto 3.5µm, W=1-2.5µm (17 specimens measured).

Remarks. Specimens assigned to the *V. microspinosa* Group display a variety of ornament, from fine granulations, baculae, to short or long spines. This variation is almost identical to that illustrated in material from Gotland by Le Hérissé (1989).

Occurrence. Uppermost Ludlow Series, Estonia (Eisenack 1954); Upper Visby Marl, Llandovery, Gotland (Eisenack 1954, 1955, 1965a & b, 1969); Buildwas and Coalbrookdale formations, Wenlock Series, Wenlock Edge, Shropshire (Downie 1959, 1963); Ludlow Series, Ludlow and Millichope (Lister 1970); Much Wenlock Limestone-Downton Castle Sandstone formations, upper Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974); upper Llandovery -Wenlock series, Podolia (Kiryanov 1978); Buildwas Formation, lower Wenlock Series, Welsh Basin (Aldridge *et al.* 1981); lower Silurian, Norway (Dorning

& Aldridge 1982); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); Llandovery Series, Libya (Hill *et al.* 1985); upper Ludlow-lower Prídolí series, Austria (Priewalder 1987); basal Llandovery (Aeronian Stage); lower Silurian, Ringerike, Norway (Smelror 1987); Visby Formation, Llandovery-Wenlock series; Högklint (units a & b), Slite (unit d, marl, marl of NW) and basal Mulde formations, Sheinwoodian and Homerian stages, Wenlock Series (Le Hérissé 1989). Specimens recovered from the Ordovician by Górka (1969) and Kjellström (1971) were considered to be distinct from *V. microspinosa* by Le Hérissé (1989); Coalbrookdale Formation, Wenlock Series, Shropshire (Turner *et al.* 1995, as *V. microspinosa* group); Much Wenlock Limestone-Middle Elton formation, Pitch Coppice Quarry and Goggin Road. Known range: Llandovery-Prídolí series.

Visbysphaera pirifera (Eisenack 1954) Kiryanov 1978 Pl. 8, fig. 15.

	1954	*Hystrichosphaeridium pirifera* n. sp.; Eisenack, p. 206-207, pl. 1, figs 1a, b, text-fig. 1.
v*	1963	*Baltisphaeridium dilatispinosa* sp. nov.; Downie, p. 642, pl. 92, fig. 4.
	1963	*Baltisphaeridium piriferum* (Eis. 1954) comb. nov.; Downie & Sarjeant, p. 90 (no fig.) (invalid combination, basionym not fully referenced).
	1965	*Baltisphaeridium piriferum* (Eisenack 1954); Downie & Sarjeant, p. 94 (no fig.).
	1968	*Baltisphaeridium hermosum* n. sp.; Cramer & Diez, p. 567, pl. 3, figs 4-7 (*nomen nudum*).
	1970	*Visbysphaera dilatispinosa* (Downie 1963) comb. nov. emend.; Lister, p. 98-99, pl. 13, fig. 16, text-figs 19j, 27f.
	1973	*Multiplicisphaeridium dilatispinosa* (Downie 1963); Eisenack *et al.*, p. 611.
	1973	*Multiplicisphaeridium piriferum piriferum* (Eisenack 1954); Eisenack *et al.*, p. 737-739
	1978	*Visbysphaera pirifera* var. *pirifera* (Eisenack 1954); Kiryanov, p. 89-90, pl. 12, figs 2, 3, 5.
	1990	*Visbysphaera dilatispinosa* (Downie 1963) emend. Lister 1970; Fensome *et al.*, p. 530 (no fig.).
	1990	*Visbysphaera pirifera* (Eisenack 1954a) Kiryanov 1978; Fensome *et al.*, p. 531 (no fig.).

Holotype. Eisenack 1954, pl. 1, figs 1a, b; preparation E 1; from the Upper Visby Formation, upper Llandovery Series, Lickershamn, Gotland.

Diagnosis. (Kiryanov 1978, p. 89-In Russian).

Description. Vesicle spherical, ellipsoidal or subspherical, thicker walled than processes, often folded; laevigate under transmitted light, laevigate or slightly roughened with a SEM. Processes generally broad based, circular in cross-section, with most possessing expanded, echinate tips; the processes are hollow and closed to the vesicle interior. The processes may be randomly positioned over the vesicle surface, or may be concentrated along linear folds in the vesicle wall. Excystment mechanism not observed.

Dimensions. V=36-53μm, PL=5-18μm, PØb=1.5-11μm, W = <1μm (10 specimens measured).

Remarks. Although Lister (1970) proposed the transfer of this species to *Visbysphaera*, he did not clearly use the name *V. pirifera* and the combination was therefore not validly published. *V. dilatispinosa* was considered a junior synonym *V. pirifera* by Eisenack (1965a, p. 263); Eisenack *et al.* (1973, p. 611) stated that *V. dilatispinosa* was "probably a practical junior synonym of *M. piriferum*", this raised some uncertainties over the synonymy, leading Fensome *et al.* (1990, p. 530, 531) to treat them as distinct. The argument for the retention of the two taxa as distinct has been based on the fact that the echinae present on the process tips of *V. dilatispinosa* are not visible on the holotype of *V. pirifera*, which may be due to pyrite deformation. The presence-absence of echinae is regarded here as an intraspecific characteristic and *V. pirifera* and *V. dilatispinosa* are considered synonymous, as they are in Le Hérissé (1989, p. 212), who provides a comprehensive synonymy list.

Those specimens described and illustrated as *Baltisphaeridium* cf. *dilatispinosum* from the middle Ordovician by Burmann (1970, p. 310, pl. 12, fig. 4) are considered here to be distinct from *V. pirifera.*

Occurrence. Upper Llandovery-lower Wenlock Series, Gotland (Eisenack 1954, 1965a); Buildwas Formation, Wenlock Series, Shropshire (Downie 1963); Silurian, Belgium (Martin 1967, 1969); San Pedro and Furada formations, Ludlow Series, NW Spain (Cramer 1964b, 1966a & b, 1969b; Cramer & Diez 1968); Gotlandian (Silurian), Alabama (Cramer 1968b); Tuscarora and Rose Hill formations, upper Llandovery Series, Pennsylvania (Cramer 1969a); Much Wenlock Limestone-Lower Elton formations and Whitcliffe Group, Wenlock-Ludlow series, Ludlow (Lister 1970); Alger Formation, upper Llandovery Series; Estill Shale, upper Llandovery Series; subsurface Florida (Llandovery-Prídolí series); Jupiter Formation, upper Llandovery; Osgood Formation, upper Llandovery, Kentucky; Quoddy Formation, upper Llandovery Series; Red Mountain Formation, lower-upper Llandovery Series; Rochester Formation, Wenlock Series; Rose Hill Formation, upper Llandovery, Pennsylvania and Virginia; Waldron Formation, upper Wenlock Series, Kentucky (Cramer & Diez 1972); Rochester Formation, Wenlock Series, Ontario (Thusu 1973a); Ilion Shale, Wenlock Series, New York (Thusu 1973b); Much Wenlock Limestone-Downton Castle Sandstone formations, Wenlock-Prídolí series, Ludlow (Lister & Downie 1974); upper Llandovery-lower Ludlow series, Britain and Ireland (Aldridge *et al.* 1979); Buildwas Formation, lower Wenlock Series, Welsh Basin (Aldridge *et al.* 1981); Wenlock Series, Dudley, England (Eisenack 1965a, Dorning 1983); Silurian, Moscow and Baltic (Umnova 1975); Silurian, Podolia (Kiryanov 1978); Rochester Formation, Indiana, Ohio and Kentucky; Red Mountain Formation, Georgia, Alabama and Tennessee; Rose Hill Formation, Pennsylvania; Crab Orchard Formation, Tennessee; Llandovery-Ludlow series borehole, Florida, Libya and Tunisia (Cramer 1970a, Cramer & Diez 1972); Tanezzuft and Acacus formations, Wenlock-Ludlow series, Libya (Richardson & Ioannides 1973); Llandovery-lower Wenlock series, Welsh Borderland (Hill 1974); Ludlow Series, Algeria (Jardiné *et al.* 1974); upper Ludlow Series, Sahara (Jardiné & Yapaudjian 1968); Upper Visby-Högklint formations, lower Wenlock Series, Gotland (Cramer *et al.* 1979); Llandovery-basal Ludlow series, Welsh Borderland (Dorning 1981a); Wenlock Series, Ayrshire (Dorning 1982);

lower Silurian, Ringerike, Norway (Dorning & Aldridge 1982); upper Llandovery-lower Wenlock series, Wenlock type area (Mabillard & Aldridge 1985); lower Silurian, Ringerike, Norway (Smelror 1987); Lower, Upper Visby and Högklint formations, Llandovery-Wenlock Series, Gotland (Le Hérissé 1989); Much Wenlock Limestone-Lower Elton formation boundary (Pitch Coppice Quarry and Goggin Road), decreasing in abundance through the Lower Elton Formation, with only sparse occurrences in the Middle Elton Formation (Goggin Road). Known range: Llandovery-Pŕídolí series.

Visbysphaera sp. A Pl. 8, fig. 18.

v? 1970 *Visbysphaera oligofurcata* comb. nov.; Lister, p. 100, pl. 13, figs 14-15, text-fig. 19k.

Description. Vesicle spherical to ellipsoidal, thin to moderately thick walled, laevigate to rugulate under transmitted light. Numerous, thin, slender processes, with expanded bases, arise from the vesicle surface. Most appear solid, though some are hollow; the cavities of the hollow processes are not open to the vesicle interior. The processes may be simple spines, though are more commonly columnar, with bulbous, rarely branched tips. Excystment by large, unornamented, rupture, which almost divides the vesicle in two.

Dimensions. V=31-60μm, PL=1.5-5.5μm, PØb=0.2-0.5μm, W=0.5-1μm (5 specimens measured).

Remarks. This taxon is very rare and only a few specimens were found in the present study. It differs from *V. microspinosa* in possessing fewer, thinner processes, which are generally longer; these may have expanded, bulbous tips, which can be rarely branched. Most specimens recovered possess a large, unornamented, rupture in the vesicle wall. Forms from the Upper Whitcliffe Formation, assigned to *V. oligofurcata* by Lister (1970), appear morphologically similar to those forms recovered herein.

Occurrence. Rare in the Much Wenlock and Lower Elton formations, Goggin Road.

CHAPTER 3

BIOSTRATIGRAPHY

INTRODUCTION

At present it is the graptolites that have been studied to the highest degree and have proven to be the most effective group for Silurian biostratigraphy. A number of other biozonation schemes based on different groups have recently been proposed (conodonts-Aldridge & Schönlaub 1989, acritarchs-Martin 1989, chitinozoans-Verniers *et al.* 1995). The distribution of graptolites is, however, generally restricted to basin or shelf edge deposits. The potential of using acritarchs and prasinophyte algae in biostratigraphy is being realised to a greater extent, though little intensive work has been completed. As the majority of acritarchs and prasinophyte algae were probably planktonic, perhaps phytoplanktonic (Martin 1993, Colbath & Grenfell 1995), with some having evolutionary links to the dinoflagellates (Moldowan *et al.* 1996), and as they have a maximum diversity and abundance within open marine shelf environments (e.g. Staplin 1961, Dorning 1981a), they should become increasingly important in future biostratigraphic work.

PREVIOUS BIOSTRATIGRAPHIC SCHEMES

The major biostratigraphic schemes for the Ludlow Series are based on benthic macrofossils (type area only), graptolites, acritarchs, chitinozoans and conodonts. Schemes for the Gorstian Stage in the Ludlow area are described below and illustrated in Text-fig. 3.1:

BENTHIC MACROFOSSILS. The benthic macrofossils of the Ludlow Series (Lawson 1960, Holland *et al.* 1963, Calef & Hancock 1974, Lawson 1975, Watkins 1979) are recognised to be environmentally controlled. The benthic fauna of the Ludlow Series at Ludlow is divided into one assemblage for each of the Elton, Bringewood, Leintwardine and Whitcliffe groups (Lawson 1975). It is recognised that a more refined subdivision of up to nine assemblages is possible, one for each of the formations (Holland *et al.* 1963). There are similarities between these assemblages and the diachronous, environmentally controlled, brachiopod dominated assemblages described by Ziegler *et al.* (1968) for the Llandovery Series. The assemblages of the Ludlow Series appear less diachronous as they do not extend beyond biozones established by more reliable index fossils (Lawson & White 1989, p. 77).

In the upper, nodular, part of the Much Wenlock Limestone Formation crinoid columnals are common, along with the brachiopods *Atrypa reticularis* (Linnaeus) and *Leptaena rhomboidalis* (Wilckens). Corals are represented by *Favosites* spp. and *Heliolites interstinctus* (Linné), with the trilobites *Calymene* sp., *Dalminites myops* (König) and *Poleumitia discors* (J. Sowerby) also being recorded.

Many components of the Homerian shelly benthos persist into the Lower Elton Formation (*Favosites* spp., *H. interstinctus*, *A. reticularis*, *L. rhomboidalis*) and *Reserella* cf. *elegantula* (Dalman) becomes more important. Important taxa include dalminellids, *Aegiria grayi* (Davidson), *Dicoelosia*

Chronostratigraphy		Lithostratigraphy			Rickards 1989	Lawson & White (1989)	Dorning (1981a)	Martin (1989))	Verniers *et al.* (1994)	Richardson & Edwards (1989)	Aldridge & Schonlaub (1989)
Series	Stage	Formation	Thickness	Lithology	Graptolites	Benthic Macrofossils	Acritarchs		Chitinozoans	Sporomorphs	Conodonts
Ludlow	Ludfordian	Lower Leintwardine Formation	30m	Thinly flaggy calcareous siltstones	***leintwardinensis***	***Sphaerirhynchia wilsoni*** Association	L3	zone 6	***A. elongata***	B	***P. siluricus***
	Gorstian	Upper Bringewood Formation	12 -45m	Irregularly flaggy or nodular silty limestones	***tumescens/ incipiens***	***Kirkidium knightii*** Association	L2			***libycus - poecilomorphus*** Biozone	***A. ploeckensis***
		Lower Bringewood Formation	50 -60m	Flaggy calcareous siltstones with limestone nodules		***Mesopholidostrophia lepisma*** Association					
		Upper Elton Formation	45 -75m	Well bedded, flaggy calcareous siltstones with flaggy limestone bands		Benthic fauna rare	L1				
		Middle Elton Formation	45 -105m	Conchoidally fracturing, shaly and thinly flaggy, muddy siltstones	***scanicus***			zone 5			
		Lower Elton Formation	30 -45m	Irregularly bedded, shaly and flaggy, calcareous silty mudstone	***nilssoni***	***Glassia obovata*** Association				A	
Wenlock	Homerian	Much Wenlock Limestone Formation	60 -135m	Flaggy, silty limestones alternating with calcareous silty shales, 15-18m of nodular limestones at top	***ludensis***		W3			cf ***protophanus*** - cf ***S.verrucatus*** Biozone	***O. bohemica bohemica***

Text-fig. 3.1. Chronostratigraphy, lithostratigraphy and biostratigraphy of the Gorstian Stage, Ludlow Series in the Ludlow area (after Holland *et al.*, 1963; Lawson & White, 1989). The palaeobotanical event horizons (Richardson & Edwards 1989) are: (A) earliest lycopod *Baragwanathia* and the diversification of sculpture in miospores with trilete murinate, crassitate and patinate spores. (B) first apiculate miospores.

biloba (Linnaeus), *Glassia* sp. and *Gypidula* cf. *galeata* (Dalman). In general the size and abundance of individuals decreases over the Wenlock-Ludlow series boundary.

At the Lower -Middle Elton formation boundary there is a change from a brachiopod to graptolite/orthocone dominated fauna. Brachiopods are still found, including *A. grayi* and *Hemsiella maccoyana* (Jones), but are small in size. The trilobite *D. myops* is found, sometimes in bands of quite large numbers.

In the Upper Elton Formation graptolites and orthocones continue to dominate, though not to the same extent as in the Middle Elton Formation. Brachiopods found include *A. grayi*, *Mesopholidostrophia lepisma* (J. de C. Sowerby), *Strophonella euglypha* (Dalman), *H. maccoyana*, *Shagamella minor* (Salter) and *Lingula lata* J. de C. Sowerby.

At the base of the Lower Bringewood Formation, graptolite/orthocone faunas are replaced by diverse and abundant brachiopod faunas. Strophomenid brachiopods become more common and important taxa include *M. lepisma*, *Leptostrophia filosa* (J. de C. Sowerby), *Protochonetes ludloviensis* Muir-Wood, *S. euglypha*, *Gypidula lata* Alexander, *A. reticularis*, *Leptaena depressa* (J. de C. Sowerby), *S. minor*, *Amphistrophia funiculata* (M'Coy), *Sphaerirhynchia wilsoni* (J. Sowerby), *Isorthis orbicularis* (J. de C. Sowerby), *Poleumita globosa* (Schlotheim), *Howellella elegans* (Muir-Wood), *H. maccoyana* and *D. myops*.

The brachiopod *Kirkidium knightii* (J. de C. Sowerby) occurs at its highest abundance within the Upper Bringewood Formation, occasionally in coquinas, and the tabulate corals *Favosites gothlandicus* Lamark and *H. interstinctus* are found in bands. Many taxa important in the Lower Bringewood Formation continue to be so in the Upper Bringewood Formation. Above this level *Favosites* spp., *D. myops*, *A. funiculata*, *G. lata*, *S. euglypha*, *M. lepisma*, *P. globosa* are absent or rare.

Important taxa in the Lower Leintwardine Formation are *S. wilsoni*, *A. reticularis*, *L. depressa*, *I. orbicularis*, *S. minor*, *Dayia navicula* (J. de C. Sowerby), *Microsphaeridiorhynchus nucula* (J. de C. Sowerby), *Salopina lunata* (J. de C. Sowerby), *P. ludloviensis*, *H. elegans* and *Orbiculoidea rugata* (J. de C. Sowerby). In this formation brachiopods are dominant, often occurring in coquinas.

GRAPTOLITES. The British graptolites of the Wenlock and Ludlow series have been extensively studied (e.g. Lapworth 1880, Wood 1900, Elles & Wood 1901-1918, Holland *et al.* 1969, Rickards 1976, 1989, 1995). The graptolites are the most important group in Silurian correlation, with the Silurian being divided into 42 zones, giving an average of 0.7 Ma per zone (Rickards 1995, p. 135).

The *Pristiograptus ?ludensis* (Murchison) Biozone is the youngest biozone of the Wenlock Series (Text-fig. 3.1), through which a decline in graptolite diversity, but not abundance, occurs to the point of near extinction (Rickards 1989, p. 272).

In the Gorstian Stage there is an increase in diversity with the introduction of many new genera (Rickards, 1989). The base of the Ludlow Series is believed to be practically coincident with the base of the *Neodiversograptus nilssoni* Biozone (White, 1981). This conclusion is based on the recovery of poorly preserved *?Saetograptus varians* (Wood) and *?Neodiversograptus nilssoni* (Barrande) from 0.03 m and 0.23 m above the base of the Lower Elton Formation at Pitch Coppice Quarry (White, 1981).

Further evidence comes from the discovery of a well preserved *Monograptus uncinatus* (Tullberg) *orbatus* Wood, indicative of the *nilssoni* Biozone, from approximately 3 m above the base of the Lower Elton Formation at Millichope near Much Wenlock, Shropshire (White, 1974). Other genera associated with the *nilssoni* Biozone are *Colonograptus colonus* (Barrande), *Colonograptus varians varians* (Wood) and *Spinograptus spinosus* (Wood), all of which occur in the lowest Middle Elton Formation (Lawson & White 1989, p. 79).

Higher in the Middle Elton Formation *Saetograptus chimaera chimaera* (Barrande), *Saetograptus chimaera semispinosus* (Elles & Wood) and *Pristiograptus dubius* (Suess) occur, all of which are assignable to the *Lobograptus scanicus* Biozone (Lawson & White, 1989).

The *tumescens/incipiens* Biozone is identified in the Upper Elton Formation by *Pristiograptus tumescens* (Wood), and Holland *et al.* (1963) recorded *Monograptus leintwardinensis incipiens* (Wood) in the Upper Bringewood Formation. A decline in graptolite abundance occurs in the Lower and Upper Bringewood formations (Lawson & White, 1989).

Within the Lower and Upper Leintwardine formations graptolite abundance increases. *Saetograptus leintwardinensis* (Hopkinson) occurs throughout, especially in the Upper Leintwardine Formation (Lawson & White, 1989).

CONODONTS. The first conodont biostratigraphic scheme for the Silurian System was developed by Walliser (1962, 1964, 1971), and the British Silurian conodonts have been described by Aldridge (1975, 1985). The biozones of Walliser are based on material recovered, mainly, from the Cellon Section, Carnic Alps, Austria. Aldridge & Schönlaub (1989, fig. 173) based their provisional reference biozonation (Text-fig. 3.1) on the scheme of Walliser (1964).

Ozarkodina bohemica bohemica (Walliser) is recorded in the Wenlock Series of the type area and only higher in Bohemia (*nilssoni* graptolite Biozone, see Aldridge & Schönlaub 1989, p. 277) and a borehole from Wenlock Edge, Shropshire (Aldridge, pers. comm.). In the Ludlow type area conodonts are rare across the Wenlock-Ludlow series boundary, with generally only long ranging taxa being present (*Ozarkodina confluens* (Branson & Mehl), *Ozarkodina excavata* (Branson & Mehl), *Panderodus* spp.).

The *Ancoradella ploeckensis* Biozone has yet to be identified in the British Isles, or conclusively in Gotland, though it is found in the USA and Australia (Aldridge & Schönlaub 1989, p. 277). *Kockelella variabilis* Walliser has been used by Barrick & Klapper (1976) to define a local biozone in the Clarita Formation, Oklahoma. This taxon is important in identifying the earliest Ludlow Series *A. ploeckensis* Biozone, and is followed by the *Polygnathoides siluricus* Biozone in Oklahoma. *K. variabilis* occurs in the UK near the Wenlock-Ludlow series boundary and the youngest occurrence is in the earliest Ludfordian Stage (Aldridge, 1975).

The *P. siluricus* Biozone, previously unreported from the British Isles, has its base placed in the Upper Leintwardine Formation on graptolite evidence(Jeppsson 1983). Recent unpublished work has located specimens of *P. siluricus* in the Upper Bringewood Formation, Beechenbank Quarry, Shropshire, at a level 5.7 m below the unconformable contact with the Lower Leintwardine Formation (pers. comm., P. C. J. Donoghue).

OSTRACODS. The British Wenlock and Ludlow series ostracods have been documented by Siveter (1978, 1980, 1984, 1989) and Lundin *et al.* (1991). Characteristic taxa of the Much Wenlock Limestone Formation include *Strepula concentrica* Jones & Holl, *Sleia pauperata* (Jones), *Beyrichia clausa* Jones & Holl, *Amphitoxotis repanda* Siveter, *Tinotoxotis velivola* Siveter, *Sarmatotoxotis phracta* Siveter, *Tinotoxotis praegnans* Siveter, *Garniella* spp., *Xystista auricularis*, *Octonaria octoformis* Jones, *Jonesites excavata* (Jones & Holl), *Thlipsura corpulenta* Jones & Holl, *Primitivothlipsurella v-scripta* (Jones & Holl), *Primitiopsis valida* (Jones & Holl), *Microcheilinella* cf. *convexa* Pranskevichius, *Columatia variolata* (Jones & Holl), *Kuresaaria* sp., *Daliella carbuloides* (Jones & Holl), *'Cytherellina'* sp. nov. Lundin *et al.*, *Microcheilinella ovalis* (Jones), *'Longiscula' smithii* (Jones), *'Bairdiocypris' crassula* (Jones), *Scaldaniella simplex* (Krause) and *'Cytherellina' elegans* (Jones) (Siveter 1989, p. 256; Lundin *et al.* 1991, fig. 4, p. 183). The Homerian Stage is divided on the presence-absence of *Rectella* sp. nov. Lundin *et al.*, which occurs in the latest part (Lundin *et al.* 1991)

Most taxa present in the latest Homerian Stage persist into the earliest Ludlow Series and 'ignore' the Wenlock-Ludlow series boundary; no new distinctive taxa occur in the early Gorstian Stage (Siveter 1989, p. 256). *T. corpulenta* and *Aechmina cuspidata* Jones & Holl are recorded through the Gorstian Stage, but generally faunas are not well known due to recovery problems (Siveter 1989, p. 256).

SPOROMORPHS. Sporomorphs recovered from the British Wenlock and Ludlow series are well documented (Richardson & Lister 1969, Richardson & Ioannides 1973, Richardson & McGregor 1986, Burgess & Richardson 1991). The sporomorph biozones (Text-fig. 3.1) were described in detail by Richardson & McGregor (1986)

The ?*Emphanisporites* cf. *protophanus* -cf. *Synorisporites verrucatus* Assemblage Biozone has its base defined at Horton Wood Quarry, Shropshire. Characteristic species are ? *E.* cf. *protophanus* Richardson & Ioannides, cf. *S. verrucatus* Richardson & Lister, *Ambitisporites dilutus* (Hoffmeister), *Archaeozonotriletes chulus* (Cramer), ?*Archaeozonotriletes divellomedium* Chibrikova and *Retusotriletes abundo* Rodriguez.

At the base of the *Synorisporites libycus*-? *Lophozonotriletes poecilomorphus* Assemblage Biozone (defined in BP borehole B2-34, Libya), there is the development of trilete, murinate, crassitate and patinate miospores (event A, Text-fig. 3.1). This biozone is identified in the Ludlow type area by this event horizon as the zone taxa are unrecorded. Characteristic taxa are *S. libycus* Richardson & Iaonnides, ?*L. poecilomorphus* Richardson & Ioannides, ?*E. protophanus*, ?*E.* cf. *protophanus*, *Emphanisporites neglectus* Vigran, cf. *Synorisporites downtonensis* Richardson & Lister, *S.* cf. *verrucatus* and *Triletes variabilis* Cramer. At the Gorstian-Ludfordian stage boundary there is a development of apiculate miospores (event B, Text-fig. 3.1).

CHITINOZOANS. Chitinozoans of the Welsh Borderland have been sparsely documented (Dorning 1981b, Sutherland 1994). The global chitinozoa biozonation for the Silurian proposed by Verniers *et al.* (1995) is outlined in Text-fig. (3.1). A local scheme for the Welsh Basin has been described by Sutherland & Dorning (1994).

The *Angochitina elongata* Biozone is recognised in by the first occurrence of *A. elongata* Eisenack 24m below the top of the Middle Elton Formation in the Welsh Borderland (Sutherland 1994, Verniers *et al.* 1995). *Cingulochitina convexa* (Laufeld) appears near the base of the biozone and the top is marked by an increase in *Eisenackitina lagenomorpha* (Eisenack) (Verniers *et al.* 1995). Other taxa present include *Ancyrochitina desmea*, *Angochitina echinata* Eisenack, *Belonechitina lauensis* (Laufeld) and *Belonechitina latifrons* (Eisenack).

ACRITARCHS AND PRASINOPHYTE ALGAE. There have been several studies produced on the Wenlock-Ludlow series acritarchs and prasinophyte algae of the Welsh Basin (Downie 1959, 1963; Lister 1970; Hill 1974; Dorning 1981a, 1983; Dorning & Bell 1987; Turner *et al.* 1995). Five Ludlow Series biozones (Text-fig. 3.1) are recognised in the Welsh Basin, and to some degree in other areas of the British Isles (Dorning 1981a).

Zone W3 is identified by *Eisenackidium wenlockense* Dorning, *Estiastra granulata* Downie and *Multiplicisphaeridium wrensnestense* Dorning, with *Leptobrachion arbusculiferum* (Downie) being common. In the upper part of the zone *Dictyotidium stenodictyum* Eisenack, *Melikeriopalla amydra* Tappan & Loeblich Jr. and *Polyedrixium wenlockium* (Dorning) occur.

Zone L1 is identified by *Leptobrachion longhopense* Dorning and *Veryhachium pertonense* Dorning. In the lowest part of the zone *Dateriocradus tribrachiata* (Lister) and *Neoveryhachium mayhillense* Dorning occur, with *Tylotopalla* (= *Beudingiisphaeridium*) *pyramidale* Lister and *Cymatiosphaera gorstia* Dorning identifying the uppermost part.

Zone L2 is identified by *Ammonidium ludloviense* (Lister), *Florisphaeridium castellum* Lister, *Gorgonisphaeridium bringewoodense* Dorning, with common *Cymatiosphaera ledburica* Dorning and *Dilatisphaera laevigata* Lister.

Zone L3 has its base at the Gorstian-Ludfordian stage boundary and is identified by *Cymbosphaeridium pilar* (Cramer), *Leoniella carminae* Cramer, *Multiplicisphaeridium paraguaferum* (Cramer), *Veryhachium leintwardinense* Dorning, *Leiofusa estrecha* Cramer, with *Onondagella* sp. becoming more common.

Martin (1989) divided the Silurian into six, informal, global biozones, two of which occur in the latest Wenlock and Ludlow Series (Text-fig. 3.1). Zone 5 (Homerian-Gorstian stages) was recognised by the appearance of *Psenotopus chondrocheus* Tappan & Loeblich Jr., *C. pilar* and *Cymbosphaeridium* ? *cariniosum* (Cramer), the last taxon being absent from the UK. Zone 6 (Gorstian-Ludfordian stages, ? Prídolí Series) is identified by *L. carminae* and *Onondagella* sp., with *Percultisphaera stiphrospinata* Lister in Shropshire. Martin (1989, p. 209) identified the base of zone 6 in the lowest Gorstian Stage (*nilssoni* or *scanicus* biozones); the first recorded occurrence of *L. carminae* in Shropshire is in the Lower Bringewood Formation (Lister & Downie 1974).

CHAPTER 3

RECOGNITION OF PREVIOUS BIOSTRATIGRAPHIC SCHEMES

The stratigraphic ranges of taxa recovered herein are summarised in Text-fig. 3.2. It is possible to identify the informal zones of Martin (1989), with the biozones of Dorning (1981a) being recognised to some extent.

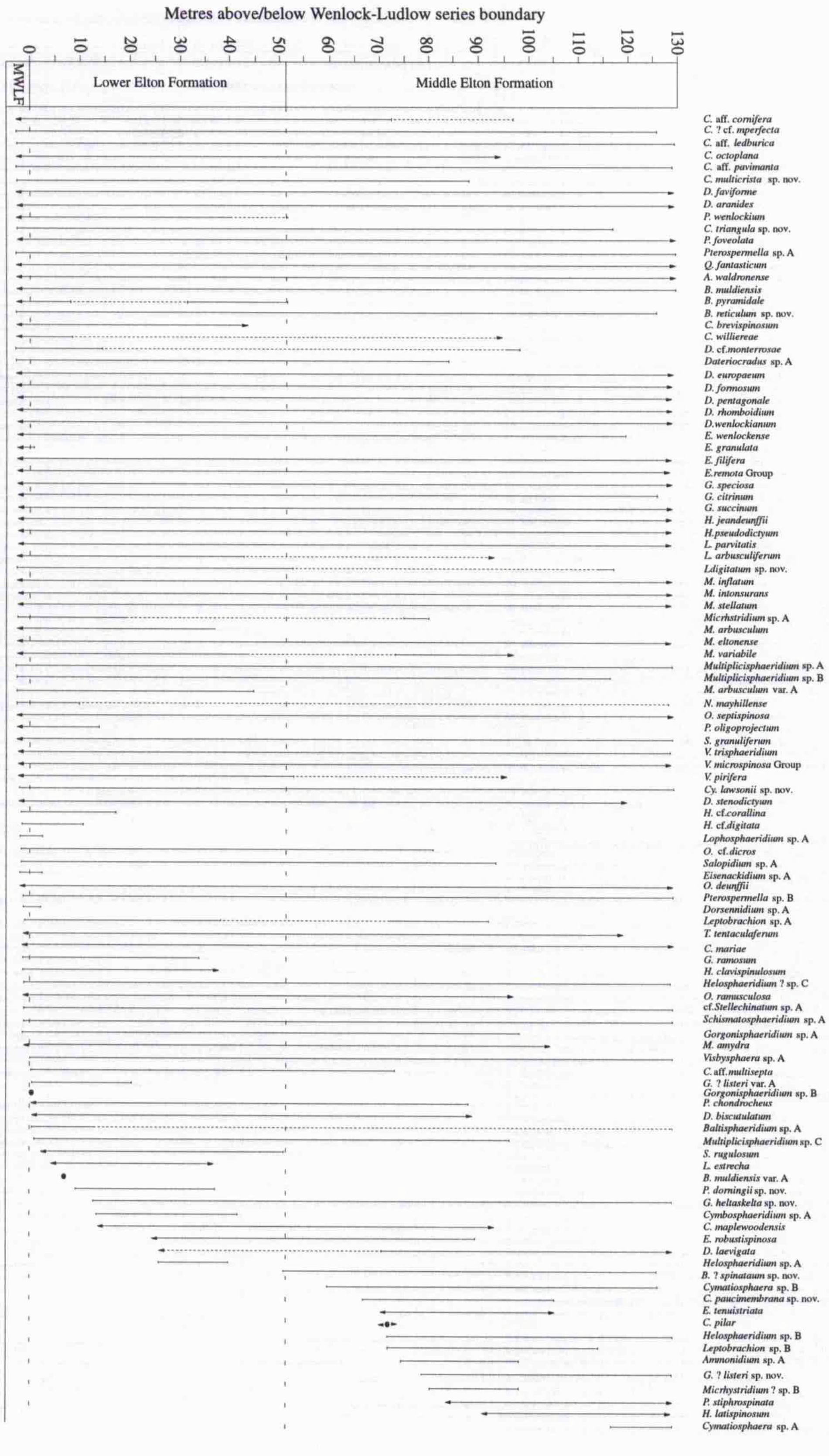
In the succession at Ludlow, the base of zone 6 (Martin 1989) is identified by the first occurrence of *P. stiphrospinata* 83.5m above the series boundary. This taxon has been recorded in the Wenlock Series (Mulde Formation, Homerian Stage) of Gotland (Le Hérissé 1989), but has a lowest recorded occurrence in the UK of Lower Elton Formation (Millichope area, Welsh Borderland, Lister 1970). The extension of the range of *P. stiphrospinata* into the Wenlock Series may cast doubt on its use in future schemes.

The presence of *Onondagella* sp. and *Leoniella carminae* Cramer, was cited as indicative of zone 6 by Martin (1989, p. 209). Examples of *Onondagella* sp. have been recovered herein from the topmost Wenlock Series. No specimens of *L. carminae* have been recovered and it is first recorded in the Lower Bringewood Formation of the Welsh Borderland (Lister & Downie 1974). *P. chondrocheus*, the first appearance of which denotes the base of zone 5 (Homerian-Gorstian stages), just extends into zone 6 (range top = 87.765m at Goggin Road); this is in accordance with the scheme of Martin (1989). The use of *P. chondrocheus* in defining the base of the underlying zone 5 must also be questioned, as this taxon has been recorded in the Telychian Stage, upper Llandovery Series, of Gotland (Le Hérissé 1989). The last occurrence of *V. dilatispinosa* (senior synonym = *V. pirifera*) was reported by Martin (1989) to be in the base of zone 6; the last recorded occurrence herein is in the Middle Elton Formation at Goggin Road (95.73m), which concurs with the scheme of Martin (1989). The last recorded occurrence in the Ludlow area, however, is in the Prídolí Series (Lister & Downie 1974); this appears to correlates with the doubtful occurence of Martin (1989, fig. 150).

The biozones proposed by Dorning (1981a) can be recognised to some extent, although the ranges of some taxa used to identify the biozones have been extended. The range top of *E. wenlockensis* has been extended from the basal Lower Elton Formation to within the Middle Elton Formation and *M. wrensnestensis* has not been recovered in this study. *E. granulata* has a range top herein of 0.54m above the series boundary, which concurs with the basal Lower Elton Formation range top listed by Dorning (1981a, table 1). Biozone W3 of Dorning (1981a) is also identified by the presence of common *L. arbusculiferum*, with *D. stenodictyum*, *M. amydrum* and *P. wenlockium* in the upper part. *L. arbusculiferum* has its highest relative frequencies over the series boundary, as does *D. stenodictyum* (see Appendix 2). The highest relative frequencies of *P. wenlockium* and *M. amydra* occur, however, higher in the Lower Elton Formation (Appendix 2).

Zone L1 has been recognised in the type area by the occurrence of *N. mayhillensis* and *B. pyramidale*. The ranges of these taxa have, however, been extended into the topmost Wenlock Series, creating an overlap between the top of biozone W3 and base of biozone L1.

Zone L2 may possibly be recognised in the topmost Middle Elton Formation. Specimens of *A. ludloviense* have not been recovered herein and no examples of *F. castellum*, which has a recorded range



Text-fig. 3.3. Stratigraphic ranges of the acritarchs and prasinophyte algae recovered from Pitch Coppice Quarry and Goggin Road. MWLF - Much Wenlock Limestone Formation. Arrows indicate that the recorded stratigraphic range extends beyond the section studied.

of Upper Elton-Upper Bringewood formations (Lister 1970), have been recovered. Dorning (1981a) incorrectly included specimens illustrated as *Gorgonisphaeridium* sp. nov. Lister 1970 (pl. 8, figs 5-7; = *Gorgonisphaeridium* ? *listeri* sp. nov. herein) in synonymy with his new zone taxon *Gorgonisphaeridium bringewoodensis*. No specimens that resemble the holotype of *G. bringewoodense* (Dorning 1981a, p. 2, fig. 5) have been recovered, though specimens now assigned to *G.* ? *listeri* sp. nov. have been recovered in the Middle Elton Formation (from 78.435m above the series boundary). *C. ledburica* has not been recovered herein, but *D. laevigata* becomes more common in the uppermost Middle Elton Formation (above 113.715m).

IMPORTANT TAXA

It is impossible to produce biozones for the Wenlock-Ludlow series boundary or earliest Ludlow Series on the limited data available. As this study has been conducted in the type area, however, those taxa which are considered to be potentially important in any future biostratigraphic schemes are highlighted. It should be noted that the applicability of these taxa for biostratigraphy outside the type area is unknown.

The Wenlock-Ludlow series boundary is identified by *E. granulata*, which has a range top 0.54m above the series boundary. *E. granulata* has a lowest recorded occurrence in the topmost Coalbrookdale Formation (Dorning 1981a), though the degree to which this taxon is environmentally controlled is unknown. *Estiastra*, along with *Pulvinosphaeridium* and *Hoegklintia* were suggested to be cysts of benthic thallose macroalgae (Dorning 1981a, p. 192), though Colbath & Grenfell (1995) stated that these taxa had little resemblance to the modern disseminules of macroalgae. *E. granulata* has been recovered throughout the Welsh Borderland (Downie 1963, Eisenack 1965a, 1977, Lister 1970, Dorning 1981a and herein; Coalbrookdale-Lower Elton formation, top Wenlock-basal Ludlow series) and possibly from Gotland (Eisenack 1965a; Slite Formation, Sheinwoodian-Homerian stages)

Dorsennidium sp. A is recovered in very low numbers at the level of the boundary (range top = -0.015m (Goggin Road); 2.165m (Pitch Coppice)). In the type area the series boundary may also be located by several taxa, the ranges of which extend higher, but which are particularly common around the boundary level (*P. oligoprojectum*, *Cymatiosphaera triangula* sp. nov., *Cymatiosphaera multicrista* sp. nov., *D. stenodictyum*, *C. brevispinosum*, *C. williereae*, *E. wenlockense*, *G. succinum*, *H.* cf. *corallina*, *H.* cf. *digitata*, *L. arbusculiferum*, *Leptobrachion digitatum* sp. nov., *Lophosphaeridium* sp. A and *N. mayhillense*).

Pulvinosphaeridium dorningii sp. nov. has its first appearance at 8.825m above the series boundary and extends to 36.415m. This taxon is very useful for identifying the very lowermost Lower Elton Formation and the base of its range overlaps the top of that of *P. oligoprojectum*. As noted above, however, the distribution of this acritarch may be governed by palaeoenvironmental factors to a large degree. *Cymbosphaeridium* sp. A (13.37m-40.89m) also appears to be important in identifying the earliest Ludlow Series. Common taxa in association include *P. wenlockium* and *P. dorningii* and *Helosphaeridium* sp. A (25.63m-38.67m). Above the range of *Cymbosphaeridium* sp. A no distinctive new elements occur until within the Middle Elton Formation, though *Cymatiosphaera lawsonii* sp. nov. and *B. pyramidale* are particularly common in the upper part of the Lower Elton Formation, with the latter taxon being more common than over the series boundary. *P. wenlockium* may be used to distinguish between the Lower and Middle Elton formations as its last recorded occurrence is 51.25m above the series boundary (very basal Middle Elton Formation), though it is generally most common below 39.71m.

In the Middle Elton Formation, important taxa include *Cymatiosphaera paucimembrana* sp. nov. (65.18m-104.19m), with *E. tenuistriata* (70.715m-104.19m) and *Ammonidium* sp. A (74.075m-97.97m), which is particularly common in the upper half of its range. The range base of *P. stiphrospinata*, 83.465m above the series boundary is higher than the lowest recorded UK occurrence of Lower Elton Formation (Millichope area, Lister 1970), but concurs with the first recorded occurrence in the Ludlow type area of Middle Elton Formation (Lister & Downie 1974). *P. stiphrospinata* has also been recorded from Ireland (Aldridge *et al.* 1979), Argentina (Pöthé de Baldis 1981, Rubinstein 1993) and Gotland (Le Hérissé 1989); as stated previously, the extension of its range into the Wenlock Series of Gotland may cast doubt on its use for recognising the Ludlow Series. Other important taxa for recognising the upper part of the Middle Elton Formation are *H. latispinosum* (above 90.95m) and *Cymatiosphaera* sp. A (above 116.505m). Near the very top of the formation (above 113.715m) *D. laevigata* and *G. ? listeri* sp. nov. become particularly common. This last taxon and *Gorgonisphaeridium ? listeri* var. A may prove to be important in separating the Much Wenlock Limestone, Lower Elton and Middle Elton formations. *G. ? listeri* var. A, characterised by a dense arrangement of processes, has a distribution restricted to the Much Wenlock Limestone and Lower Elton formations; *G. ? listerii* has only been recovered from the Middle Elton Formation.

CONCLUSIONS

The zonal schemes of Dorning (1981a) and Martin (1989) can be recognised in the Ludlow type area to some extent, but this study has extended the ranges of some key taxa. This has, in some instances, negated their usefulness in defining biozones (e.g. *E. wenlockensis*), or has resulted in a repositioning of the biozones (e.g. *N. mayhillense*, *B. pyramidale*). The extension, by Le Hérissé (1989), of the ranges of *P. chondrocheus* and *P. stiphrospinata* into the upper Llandovery Series and upper Wenlock Series of Gotland, respectively, may indicate that these taxa have limited applicability in biostratigraphy. It may also indicate possible problems in the correlation of the samples of Le Hérissé (1989), or with Gotland in general.

The use of acritarchs and prasinophyte algae in biostratigraphy may also be limited as many appear to be controlled by environmental conditions. This leads to sequences of successive appearances and disappearances of the same taxa through time (the Lazarus Effect of Jablonski 1989).

The usefulness of acritarchs in biostratigraphy is also limited by the lack of a definitive classification scheme. As acritarchs are morphotaxa a large range of morphologies can be placed within a single taxon. Successive appearances may also be placed within a single taxon as there is no definitive way in which subtle differences can be expressed, unlike, for example, the way in which changes in paratabulation may be used in dinoflagellates. This is also true when comparing acritarchs from different continents.

Palynofacies analysis of the latest Wenlock-earliest Ludlow series (Silurian) in the Ludlow type area, Welsh Borderland

The Wenlock and Ludlow series are the second and third series of the Silurian and the boundary stratotypes are situated at localities near Much Wenlock and Ludlow in the Welsh Borderland (see Bassett 1989, Lawson & White 1989).

This study has used information from two methods to infer aspects of the latest Wenlock-earliest Ludlow palaeoenvironment of the Welsh Basin. A detailed palynofacies analysis has been undertaken, documenting the absolute and relative abundance, per gram of sediment, of several groups of palynological organic matter (POM). The relative and absolute abundance of individual acritarchs and prasinophyte algal taxa has also been documented. The POM counted is divisible into two broad categories based on source:

i) Land derived sporomorphs and land plants (tracheid-like opaque, semi-opaque and banded tubes, cuticle-like sheets and filamentous macerals). Some of the land plant fragments recovered have similarities with modern hepatics (e.g. liverworts) and are believed to be from bryophytes (e.g. see Gray 1985, Edwards *et al.* 1995).

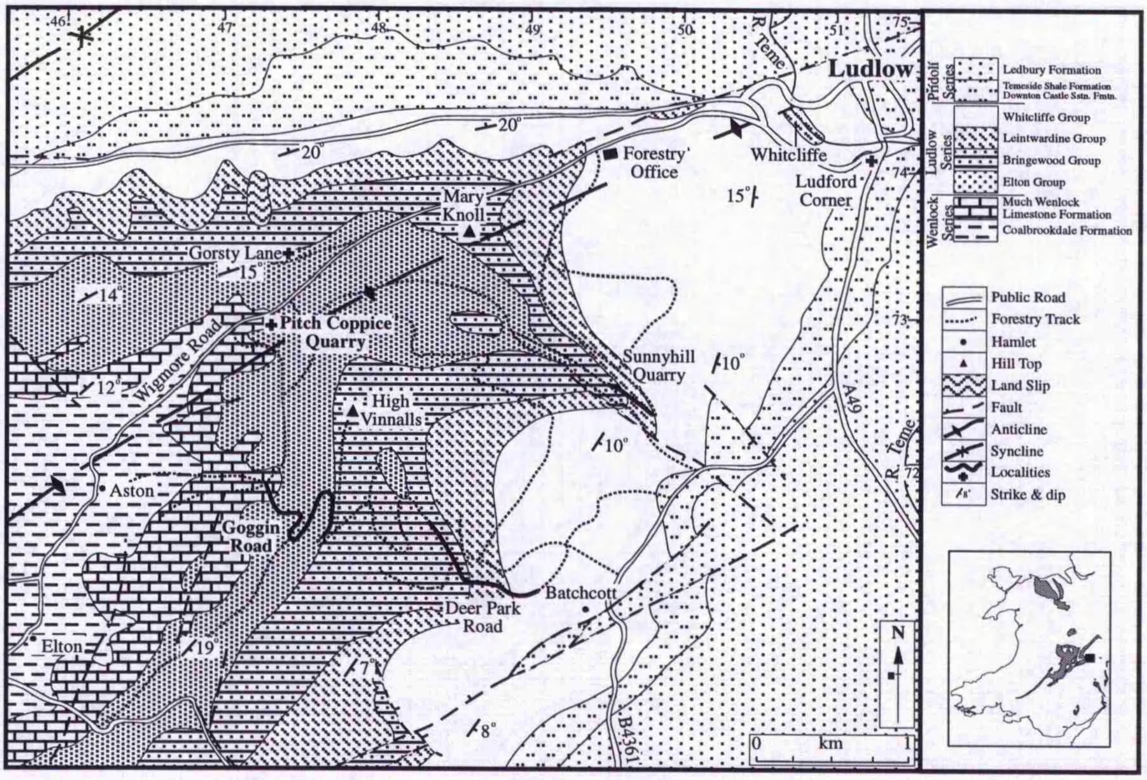
ii) Marine acritarchs (including sphaeromorphs), prasinophyte algae, chitinozoans, scolecodonts, graptolite fragments and amorphous organic matter (AOM). Acritarchs have unknown affinities but the majority are considered to be algal resting cysts, many of which were possibly phytoplanktonic (Martin 1993, Colbath & Grenfell 1995). Chitinozoans have uncertain affinities, with the most favoured hypothesis being that they are the eggs or egg capsules of a soft bodied metazoan (Paris 1981, Grahn 1982, Sutherland 1994, Vernier *et al.* 1995); scolecodonts are the jaw fragments of polychaetes. Graptolite fragments include parts of the nema, virgella, thecae and thecal spines.

Localities

Two localities, Pitch Coppice Quarry and Goggin Road (Text-fig. 4.1), situated on the shelf of the Welsh Basin in latest Homerian and early Gorstian times, were examined (see Chapter 1 for locality details and palaeogeographic maps).

Previous research

Few palynofacies analyses have been completed on the British Silurian sequences and generally only the relative abundance of POM have been documented. A detailed analysis of the relative abundance of palynomorphs across the Ludlow-Prídolí series boundary in the Welsh Basin was completed by Richardson & Rasul (1990). They defined marine influence and inshore indices based on POM and acritarch genera, and used these to identify regressive and 'storm' events. They also proposed the use of palynomorph phases, stratigraphic intervals where assemblages are dominated by one group of acritarchs



Text-fig. 4.1. Geological map of the Ludlow area, Shropshire (after Lawson & White 1989).

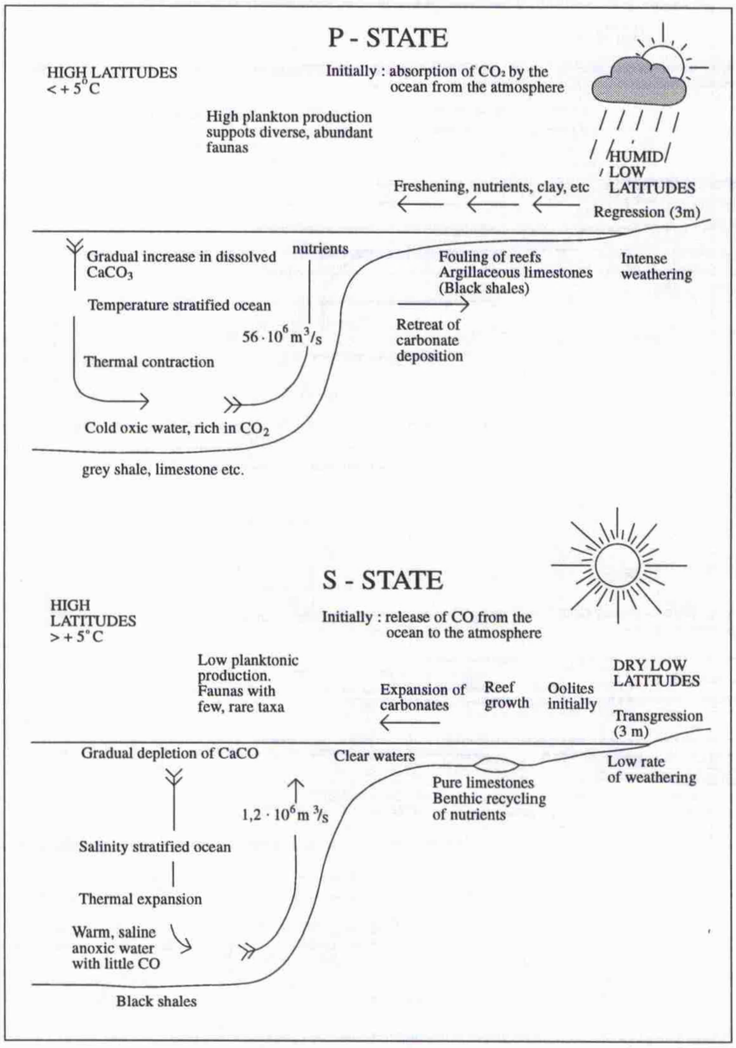
(e.g. visbysphaeriids), in intrabasinal correlation. Dorning (1981c, 1983) and Dorning & Bell (1987) have proposed a number of acritarch and prasinophyte algae assemblages and have, in some instances, related these to distance from shore (e.g. Dorning 1981c, p. 32-33, fig. 3.2). Four palynofacies types, identified by the relative abundance of palynodebris types, were defined in the Wenlock Series of the type area and related to outer shelf, offshore shelf and deep water environments by Burgess & Richardson (1991).

Globally, analyses of Silurian palynofacies are even rarer, but include studies of the relative abundance of palynomorphs in the Tanezzuft and Acacus formations (Wenlock-Ludlow series), Libya (Richardson & Ioannides 1973, Al-Ameri 1983). Al-Ameri (1983) defined five palynofacies types using the relative and absolute abundance of palynomorphs (e.g. acritarchs, chitinozoans, plant tissue *etc.*) and the types of acritarchs (e.g. sphaeromorphs, polygonomorphs *etc.*). These palynofacies types were related to models of distance from shore and were tentatively assigned to lagoonal, intermediate and open marine environments. Colbath (1980) cited the possibility of using abundance fluctuations in upper Ordovician acritarchs to map ancient water masses.

Previous models

Changes in sedimentation (limestone to argillaceous) and dominant fauna (brachiopod to graptolite/orthocone) have been used as evidence to suggest a transgressive pulse beginning in the late Wenlock Epoch, which reached its maximum in the earliest Ludlow Epoch (see McKerrow 1979, p. 140). Other Silurian transgressive and regressive events have been recognised and these have been correlated across the world, which has led to the concept of global eustasy (see Johnson & McKerrow 1991, Johnson *et al.* 1991). The transgression in the early Ludlow Epoch, in particular, was been discussed in great detail by Johnson & McKerrow (1991, p. 160-162), who cited the sea-level change as being somewhere between 50 and 100m. In discussing the biological effects of these proposed sea-level changes, Johnson & McKerrow (1991, p. 162) indicated that changes in benthic assemblages were caused by local facies shifts, and also noted the presence of coincident global extinctions and evolutionary radiations. The driving mechanism behind the transgressive phases was considered to be probably related to periodic melting of South American ice caps (Johnson & McKerrow 1991). The palaeoceanographic consequences of sea-level changes of this magnitude were not discussed in detail. The possibility that the melting of ice caps may have produced major changes in oceanic waters was touched upon, as was the theory that the re-establishment of ice caps would result in a greater quantity of polar sourced deep, cold, bottom water (Johnson & McKerrow 1991, p. 165).

The climatic/oceanic P & S model of Jeppsson (1990) considers the changes in facies, flora and fauna to be the result of a cyclic climate change between a humid low latitude, cooler high latitude P-state and dryer low latitude, warmer high latitude S-state (Text-fig. 4.2). The cyclicity was regarded as possibly self-regulating through changes in the CO_2 storage capacity of the deep ocean. This model has been extensively applied to the lower Silurian (Aldridge *et al.* 1993, Jeppsson *et al.* 1995) and places more emphasis on fluctuating palaeoclimate and the resultant changes in palaeoceanography.



Text-fig. 4.2. Characteristics of the P & S states (after Jeppsson 1990)

Techniques

Sampling.

Thirteen samples were examined from Pitch Coppice Quarry (Much Wenlock Limestone-Lower Elton formations) for both palynofacies analysis and individual taxa, with 103 (individual taxa) and 95 (palynofacies) samples being examined from Goggin Road (Much Wenlock Limestone-Middle Elton formations). Over the majority of the section at Goggin Road samples for palynofacies analysis were examined at approximately two metre intervals, with closer spacing across boundaries; after a promising test run, sample spacing was reduced to roughly one metre intervals in the Middle Elton Formation. For the individual taxa, samples were analysed at approximately metre intervals at Goggin Road, with closer spacing over the boundaries. At Pitch Coppice Quarry samples for both palynofacies analysis and individual taxa were analysed at near metre intervals, with the spacing gradually being reduced to a centimetre level across the Wenlock-Ludlow series boundary.

Laboratory Processing.

See Chapter 1. An exotic spike of *Lycopodium* spores was added to enable the absolute abundance of palynodebris types and taxa to be determined per gram of sediment (see Stockmarr 1971, 1973). Three tablets of *Lycopodium* spores (mean=13911 spores per tablet, standard deviation=689) were added to each sample prior to the second HCl stage and unoxidised residues were strew mounted, with cellosize dispersant, onto rectangular coverslips (22 x 22 mm), dried slowly to avoid particle clumping, and mounted on glass slides with petropoxy.

Counts.

A point counter was used to make 300 counts of POM from two slides per sample (600 counts in total); a separate count of *Lycopodium* spores was also maintained. Palynodebris frequencies are very high in the Middle Elton Formation, resulting in a low *Lycopodium* count, and the number of counts was increased to 600 per slide to improve accuracy. With hindsight, accuracy would have been improved with the addition of more *Lycopodium* tablets. Counts were taken in regularly spaced strips and in samples with sparse POM the coverslip was completely scanned, though in some cases it was impossible to make the requisite counts; these samples are indicated by an asterisk in the appendices.

To calculate the abundance of the individual taxa, 500 counts were made from two coverslips per sample (1000 counts in total) by continually scanning the coverslip in adjacent strips; after completing 200 counts examples of *Evittia remota*, *Micrhystridium stellatum*, *Micrhystridium intonsurans* and *Leiosphaeridia* sp. (except those >132μm in diameter) were not counted further. *Lycopodium* spores were counted separately and, as for the palynofacies analysis, samples in which the requisite number of counts was not reached are indicated by an asterisk in the appendices. The absolute abundance of each palynodebris group or taxon, relative to *Lycopodium*, was calculated using:

$$X = \frac{\text{No. of } \textit{Lycopodium} \text{ spores added to sample}}{\text{Weight of sample processed (g)}}$$

$$Y = \frac{\text{No. of } \textit{Lycopodium} \text{ spores counted}}{X}$$

$$\text{Abundance per gram} = \frac{\text{Count for palynodebris / taxon}}{Y}$$

Problems have been identified with the use of exotic spikes. The method assumes that during processing and mounting the spike and fossil POM behave identically, with the spike:fossil ratio remaining constant (White 1989). The addition of an exotic spike can also produce statistical "noise", which may cause workers to identify non-existent trends, or ignore important changes (Maher 1981, p. 155).

Analysis of results

Marine Index (MI)

To enable the variation between land and marine derived POM to be clearly seen a Marine Index was defined, which is based on the Marine Influence Index of Richardson & Rasul (1990), which was itself based on the ratios used by Traverse (1978) on Recent sediments:

$$\text{Marine Index (MI)} = \frac{\text{Graptolites+Acritarchs+Algae+Chitinozoans+Scolecodonts}}{\text{(above)+Sporomorphs+Land Plants}} \times 100$$

The Marine Influence Index was used as a "general indicator of environment and in particular proximity to the shore" by Richardson & Rasul (1990, p. 676) and such indices have been used to infer changes in sea-level.

An Inshore Index was also defined by Richardson & Rasul (1990, p. 676), a method which is based on similar principles to the inshore-offshore distribution diagrams of Dorning (1981c) and Al-Ameri (1983). This index is not used here as it is based on broad assumptions about the nature of acritarchs and prasinophyte algae and the influences which affected them. The index compares the distribution of particular genera with that of other, morphology based, supergeneric groups (e.g. polygonomorphs, netromorphs). This supergeneric classification is generally no longer in use. In such analyses one must assume that all species of a genus or suprageneric group behave identically and have similar distributions. This assumption is generally untrue as the distribution of a species depends on its own individual environmental tolerances and hydrodynamic properties. Counts of a genus or suprageneric group are, in reality, observations of the distribution of the most dominant taxon or taxa. This is also true of the genera-based palynomorph phases of Richardson & Rasul (1990), though the idea of correlating patterns in the distribution of acritarchs and prasinophyte algae in a depostional basin remains a potentially very powerful tool when applied to individual taxa, or groups of taxa with similar distributions.

Individual acritarch and prasinophyte algal taxa

The distribution of the background taxa was examined to enable the changes in palaeoenvironment to be deduced. Taxa with stratigraphic ranges through the Goggin Road section, and present in more than 80% of samples, were statistically analysed and those with similar distributions were grouped together. The data were initially standardised and then grouped by cluster analysis (Ward's minimum variance method with Euclidean distances (Text-fig. 4.3)-see Swan & Sandilands (1995)). The relative abundance of the taxa in each group were totalled and, to enable the groups to be compared to each other, the results were standardised and plotted (Text-fig. 4.8).

Results (palynofacies analysis)

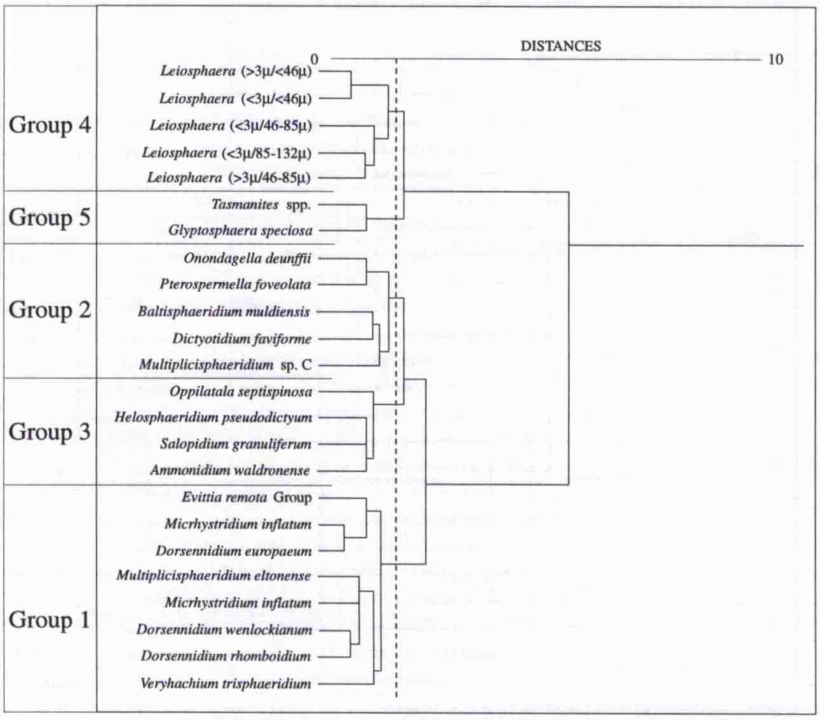
Wenlock - Ludlow series boundary

At both Goggin Road and Pitch Coppice Quarry there is a decline in the MI over the Wenlock-Ludlow series boundary (Text-fig. 4.4). The two minima of the decline are situated, however, at different lithostratigraphic levels at each section. At Pitch Coppice MI values begin to drop steadily from sample PC5-C (-1.31m below the series boundary), before falling rapidly at PC7-C (-0.55m), reaching a minimum value in PC10a-A (-0.135m) before increasing rapidly over the boundary to levels greater than those of the Much Wenlock Limestone Formation (from sample PC14-A, 0.175m).

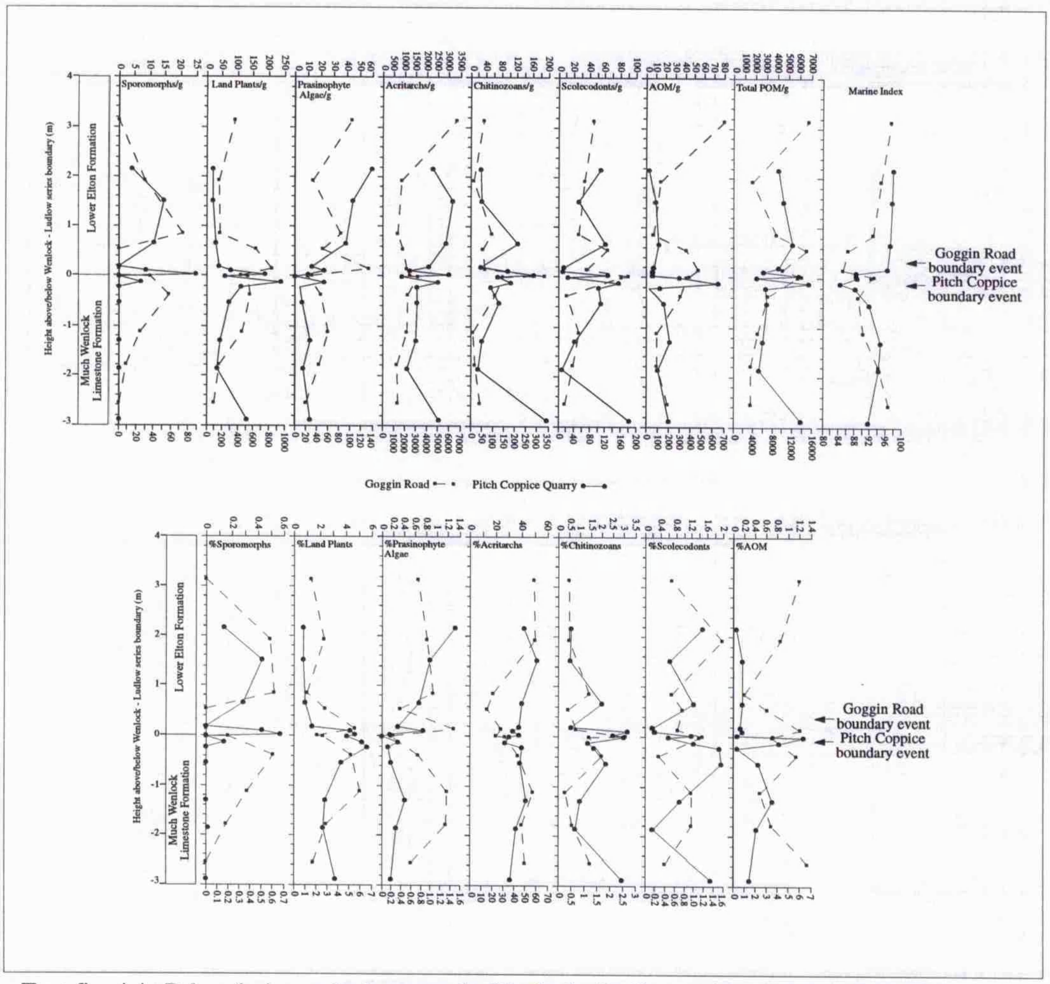
A similar trend is visible at Goggin Road, except the minimum is situated in the Lower Elton Formation (TRENCH1/12-A to 14-A, 0.145m to 0.54m). Above sample TRENCH1/14-A, values increase to their former levels.

The decline in MI over the boundary correlates with a decrease in the relative abundance of acritarchs, which is particularly noticeable at Goggin Road (GOG1/7-A to TRENCH1/23-A, -1.12m to 1.92m), but less so at Pitch Coppice, where the decline takes place over a much shorter interval (PC9-C to 14-A, -0.23m to 0.175m). Also over the boundary there is a marked increase in the absolute and relative abundance of land plants (particularly at Pitch Coppice, with a broader increase at Goggin Road), chitinozoans (both sections), scolecodonts (absolute abundance-Goggin Road only) and AOM (both sections, particularly Pitch Coppice). This event also shows itself as an increase in Total POM at Goggin Road; the Total POM at Pitch Coppice shows no such clear increase.

Within the basal Lower Elton Formation at Pitch Coppice the abundance of the land plants (absolute and relative) declines to levels lower than those in the Much Wenlock Limestone Formation,



Text-fig. 4.3. Dendrogram produced by cluster analysis using the relative abundance data of those acritarch and prasinopyte algal taxa that occur in 80%, or more, of samples from Goggin Road. (Ward minimum variance method, Euclidean distances).



Text-fig. 4.4. Palynofacies analysis across the Wenlock - Ludlow series boundary at Pitch Coppice Quarry and Goggin Road. Solid line - Pitch Coppice Quarry, broken line - Goggin Road.

whereas the abundance (relative and absolute) of prasinophyte algae and acritarchs is higher in the basal Lower Elton Formation than in the topmost Much Wenlock Limestone Formation.

Lower Elton Formation

The most obvious trend in the Lower Elton Formation is the very broad decline in Total POM from near the base of the formation to approximately its mid-section (ca. 20-35m above the boundary); above this level Total POM values increase towards the Middle Elton Formation (Text-fig. 4.5). This trend is also present in the acritarchs (the largest constituent of the POM), prasinophyte algae and land plants. The relative abundance of these groups shows smaller patterns of increasing-decreasing importance and it is clear that there is an inverse relationship between the land plants and acritarchs.

After the moderately high abundance of chitinozoans at the Wenlock-Ludlow series boundary, values decrease in the basal part of the Lower Elton Formation and generally samples contain only broken fragments. This decline is also visible in the scolecodonts, whose values, unlike those of the prasinophyte algae, acritarchs and land plants, do not recover higher in the formation. AOM is found in low abundance through the main part of the Lower Elton Formation, but becomes increasingly important in the upper part, towards the Middle Elton Formation.

The variation in the MI appears to be directly correlated with the fluctuations in the land plants, though, unlike the distribution over the boundary, there are no accompanying fluctuations in other groups (e.g. chitinozoans or scolecodonts).

Lower / Middle Elton formation boundary

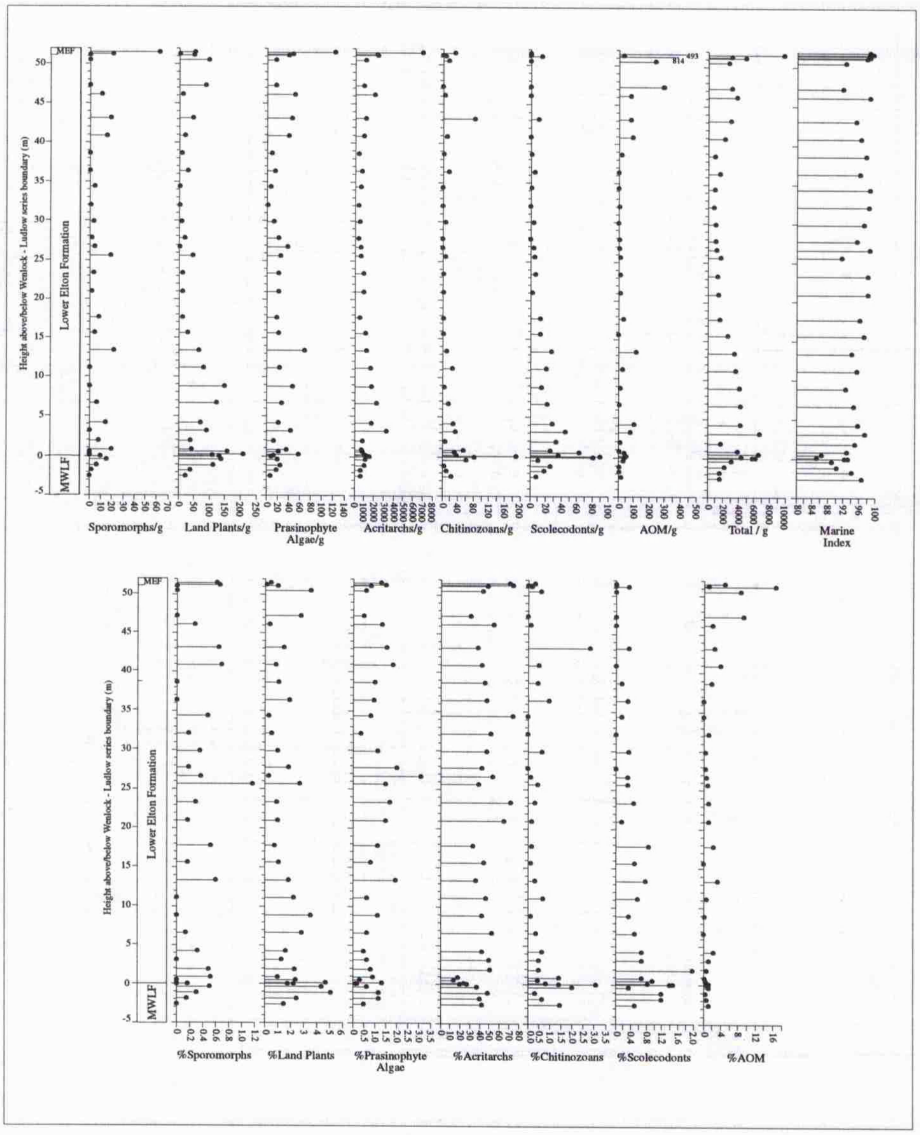
A rapid increase in Total POM (Text-fig. 4.6), contributed to by an increase in the absolute abundance of each group (except land plants), identifies the Lower/Middle Elton formation boundary. It is also within the first few centimetres of the Middle Elton Formation that the first fragments of graptolites occur (sample TRENCH4/ME1-A).

The increase in MI over the boundary (Text-fig. 4.6) results from an increased abundance of acritarchs and prasinophyte algae and a decrease in land plants; although sporomorphs become more common they comprise only a very small percentage of the assemblage.

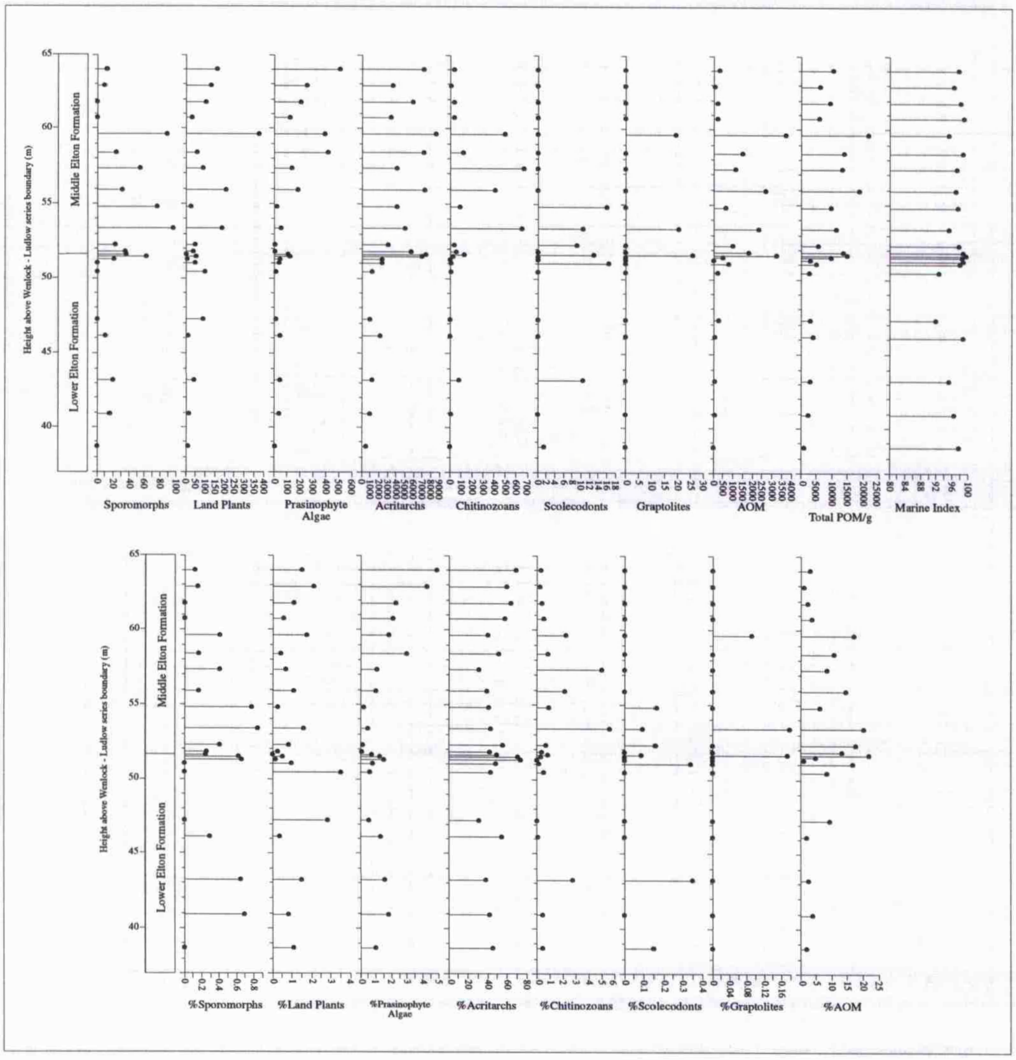
Middle Elton Formation

The most striking feature of the palynofacies analysis in the Middle Elton Formation is the stepped increase in Total POM towards the middle part of the formation (Text-fig. 4.7).

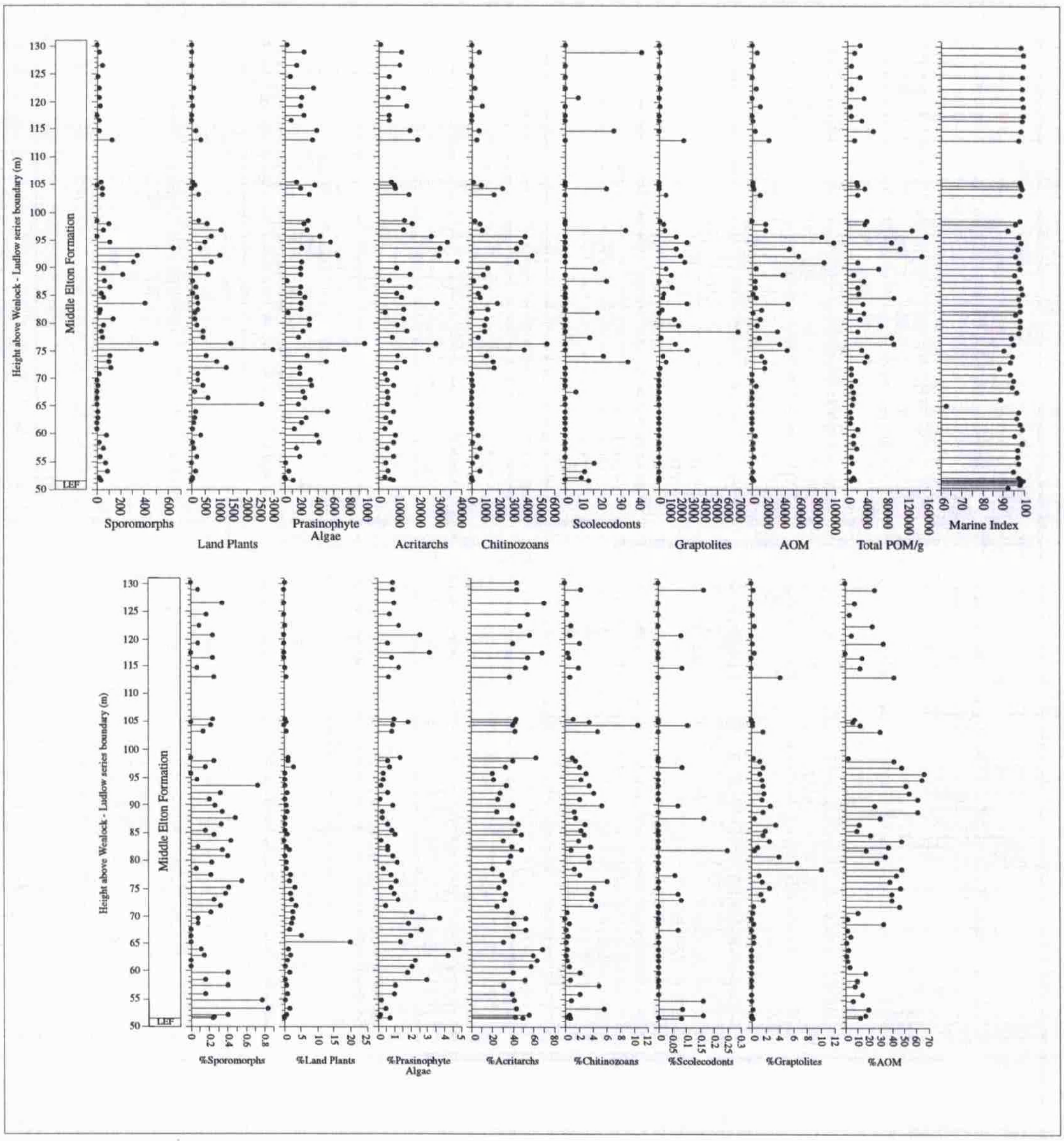
The prasinophyte algae become relatively more important in the interval 56-71m above the series boundary and are dominated by the tasmanitids. Within the basal part of the Middle Elton Formation is a single sample (TRENCH4/200-A, 65.18m) which contains large amounts of land plant



Text-fig. 4.5. Palynofacies analysis of the Lower Elton Formation at Goggin Road. MWLF - Much Wenlock Limestone Formation, MEF - Middle Elton Formation.



Text-fig. 4.6. Palynofacies analsis of the Lower - Middle Elton formation boundary at Goggin Road.



Text-fig. 4.7. Palynofacies analysis of the Middle Elton Formation at Goggin Road.

fragments (2569/g, 20% of the Total POM); the tail end of this increase appears to be visible in sample TRENCH4/204-A.

Between 71m and 77m there is a prominent increase and peak in the Total POM, contributed to by an increase in the abundance of several groups (sporomorphs, land plants, prasinophyte algae, acritarchs and chitinozoans). AOM and graptolite fragments begin to occur in larger numbers and the maximum peak in the absolute and relative abundance of graptolites and land plants is within this interval. As with the interval 71-77m, several groups increase in abundance between 90 and 98m (sporomorphs, land plants, prasinophyte algae, acritarchs, chitinozoans, graptolites and AOM) and this latter interval represents the period of highest abundance in the formation. Higher than 100m the Total POM declines towards values similar to those in the basal part of the formation, though because of the isolated, strike orientated nature of the exposure it would be difficult to rely on any trends observed in this part of the succession.

Discussion (palynofacies analysis)

Wenlock - Ludlow series boundary

The decline in the MI around the Wenlock-Ludlow series boundary at Pitch Coppice and Goggin Road correlates well with the decline of $\partial^{13}C$ illustrated by Corfield *et al.* (1992) in the Ludlow anticline. This depletion in $\partial^{13}C$ was also reported in other sections from both carbonate shelf and offshore, deeper water facies; a second $\partial^{13}C$ decline was also illustrated slightly lower in the Wenlock Series. These changes in the carbon isotope signature were related by Corfield *et al.* (1992) to the major decline in graptolite diversity that began in the latest Wenlock Series *nassa* Biozone, and to the two basin oxygenation events reported by Kemp (1991), which were periods of increased basin ventilation. This was used to suggest that a reduction in ocean-surface productivity resulted in a reduced flux of organic matter to the ocean floor (Corfield *et al.* 1992, p. 373-374). It was further stated that the two $\partial^{13}C$ declines may have represented the same phenomenon, with the decline in graptolite diversity perhaps being stepped (Corfield *et al.* 1992, p. 374).

It is incorrect to assume, however, that a decline in graptolite diversity would necessarily mean a decline in graptolite productivity and indeed Rickards (1989) has stated that although graptolite diversity may be low in the latest Wenlock Series, numbers of specimens may often be high. It is also important to note that although graptolites form an important part of the plankton, it is the algae that represent the largest producers.

The decline in $\partial^{13}C$ in the Ludlow Anticline is contemporary with an increase in the absolute abundance of land plants, prasinophyte algae, large chitinozoans and scolecodonts, AOM and the Total POM. Photosynthetic organisms have tissues that are enriched in ^{12}C relative to atmospheric CO_2, and with time there is also a preferential enrichment of organic matter in $\partial^{12}C$ (Faure 1986). The reduction in $\partial^{13}C$ in the Ludlow Anticline could thus also be explained as a result of transgression- induced sediment reworking (see Galloway 1989). This would have concentrated the larger POM size fraction (particularly the land plants) and also produced an increase in Total POM (this is especially noticeable at Goggin Road).

Lower Elton Formation

The broad decline and subsequent increase in Total POM in the Lower Elton Formation could be explained by either a synchronous change in both marine and terrestrial productivity (changing flux of organic matter to basin floor), or by changes in sedimentation rates (dilution effect). Within the argillaceous middle Lower Elton Formation, values of MI can decline to levels lower than those in the carbonate dominated basal part of the formation (Text-fig. 4.5). If MI is regarded as a measure of distance from shore, this suggests that the change from carbonates to argillaceous deposition was caused by an increase of terrestrially sourced sediment and not by lateral facies migration. The subtle variations in the MI would thereby also probably indicate a series of small transgressive-regressive events through the succession.

Scolecodonts are regarded as being more common in shallow water deposits; they were recorded in increased numbers in the carbonate deposits of Gotland (Bergman 1989). This may be used to suggest that during deposition of the Lower Elton Formation, phased increases-decreases in sedimentation rates and minor transgressive-regressive cycles were superimposed on a general trend of deepening through the formation. If this occurred, one would expect to see a reduction in the abundance of terrestrially derived palynodebris from the base of the formation upwards. Terrestrial palynodebris, however, appears to have similar values in the lower and upper parts of the formation, indicating there was little difference in sea-level. This suggests that there is no general deepening trend, but a change to an environment to which polychaetes were not well adapted.

Middle Elton Formation

The decline in the land plants and increase in acritarchs and prasinophyte algae, along with the appearance of graptolites over the Lower/Middle Elton formation boundary could be explained by a transgressive pulse or by a rapid increase in marine productivity. The rapid increase in Total POM, which results from an increase in the absolute abundance of most groups (except land plants) at the boundary level also suggests a reduction in sedimentation rates. These reduced sedimentation rates concur with the proposed transgressive pulse.

Throughout the remainder of the Middle Elton Formation, three phases of increasing Total POM are visible (Phase 1 = 51-61m, Phase 2 = 72-80m and Phase 3 = 90-98m above Wenlock-Ludlow series boundary). Within these phases the abundance of each group increases and the presence of graptolites (most abundant in Phase 2) has been used as evidence for a peak in the transgressive pulse that began in the Much Wenlock Limestone Formation (e.g. McKerrow 1979). The groups that dominate in each of the palynofacies phases differ. Acritarchs, for example, show a stepped increase from Phase 1 to 3, whereas land plants and graptolites have their highest abundance in Phase 2 (Text-fig. 4.7). This suggests that the increase in abundance is not only a result of decreased sedimentation rates or increased productivity, but is also linked to palaeoenvironmental factors. The generally consistent high values of MI through the Middle Elton Formation could indicate a more offshore setting, and the increase in Total POM could also be explained by a cyclic reduction in sedimentation rates.

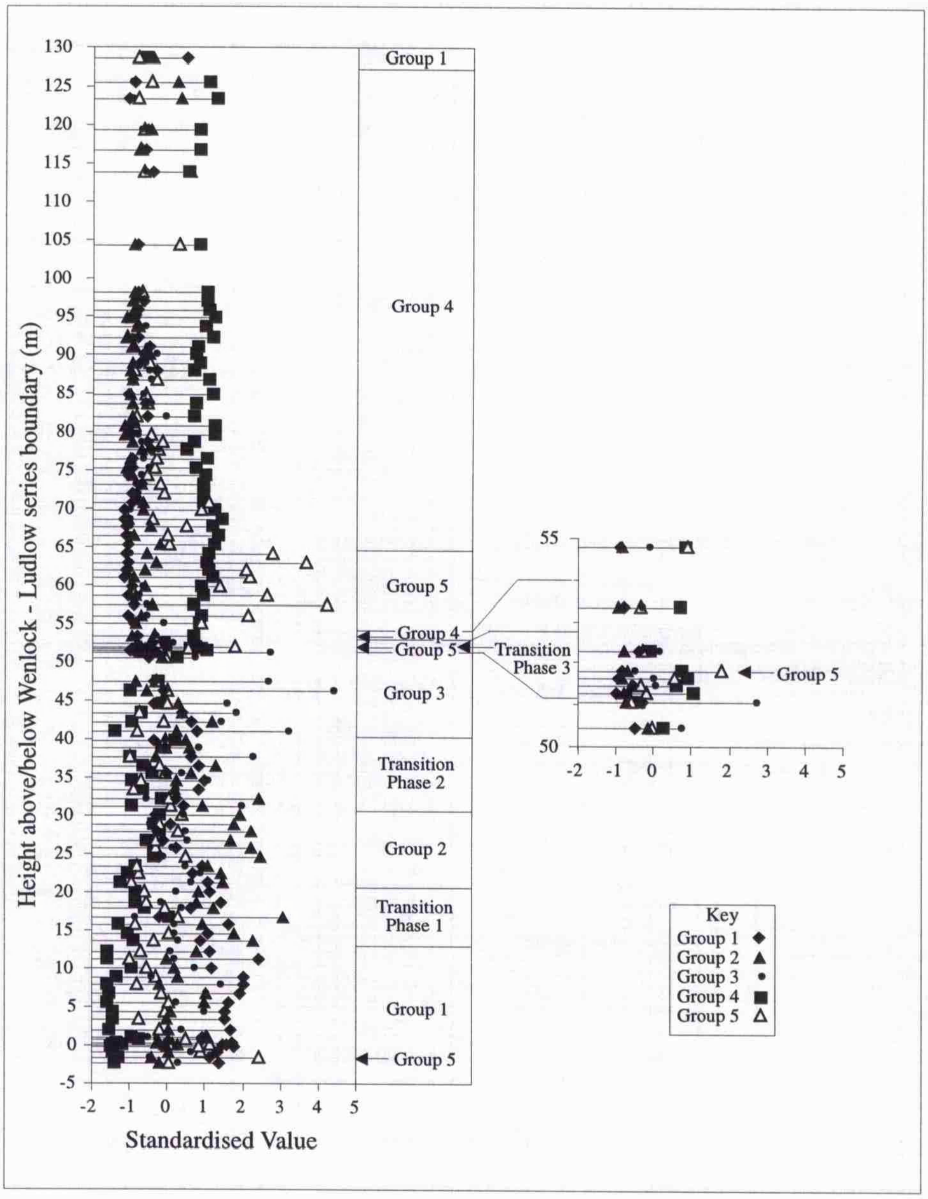
One sample in the Middle Elton Formation (TRENCH4/200-A, 65.18m) contains a large quantity of terrestrially derived plant material, usually large, dark, opaque tubes (there is no noticeable increase in sporomorphs); the acritarch and prasinophyte algae of this sample do not appear to contain species normally associated with supposed shallower water deposits (the sample contains slightly higher numbers of *Onondagella deunffii* Cramer than most other Middle Elton Formation samples). Hand specimens contain graptolites and appear, sedimentologically, no different from other Middle Elton Formation samples. Such a dramatic increase in terrestrially derived material may indicate a storm event, a slump of near shore material into the basin, or an increase in terrestrial run-off. A storm event could be postulated, though the sample above (TRENCH4/204-A), also has an increased amount of terrestrial material and appears to represent the tail end of a dramatic change, not a short lived event. A slump of nearshore material into the basin would result in an influx of acritarchs and prasinophyte algae considered more typical of supposed shallower water deposits, but this is not observed. This suggests that the increase in terrestrial material may be the result of increased terrestrial run-off, though this fails to explain why there is no concurrent rise in the abundance of sporomorphs.

Results (individual acritarch and prasinophyte algal taxa)

When the standardised group data is illustrated through the succession (Text-fig. 4.8) it is clear that a series of events occurred where particular groups became more important. The record of each of these events is separated by a transitional phase, where two, rarely three, groups are present and no one obviously dominates. These events are clearly visible in the Lower Elton Formation, but the Middle Elton Formation is generally dominated by a single group throughout (Group 4), except for the last sample (GOG12/302-A) which is dominated by Group 1.

One important trend is that of Group 5, which dominates just below the levels of the Wenlock-Ludlow series and Lower/Middle Elton formation boundaries and becomes particularly noticeable in the basal Middle Elton Formation.

The start of the Middle Elton Formation is marked by a rapid change from Group 3 to Group 4; this transition occurs over a shorter interval than the preceding transition phases. The background taxa of the Middle Elton Formation appear to indicate a fairly monotonous period with little change. When the trends of other individual, rarer, taxa (with stratigraphic ranges through the succession) are examined, however, a further series of events is visible that correlate with events in the palynofacies record (Text-fig. 4.10, 4.11). An initial event (c. 51-57m) is indicated by a peak in the relative abundance of *Stellechinatum* ? sp. A, with a smaller peak in this taxon being present between c. 73-79m. This minor peak is associated with a prominent peak in the relative abundance of *Schismatosphaeridium* sp. A and



Text-fig. 4.8. Grouped individual acritarch and prasinophyte taxa from Goggin Road.

minor peak in *Tunisphaeridium tentaculaferum*. A further peak in the relative abundance of *Eupoikilofusa tenuistriata* and *T. tentaculaferum* identifies the last event (89-91m).

Discussion (individual acritarch and prasinophyte algal taxa)

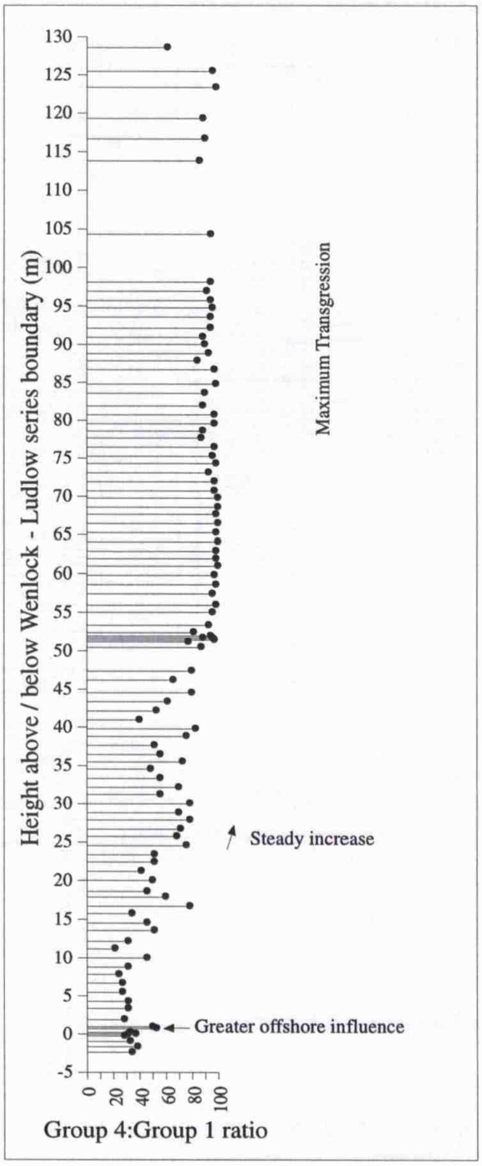
The groups of acritarchs and prasinophyte algae with similar trends could be considered to be controlled in one of two ways. They could be interpreted as reflecting the changing composition of the microflora with distance from shore. A broad transgression from late Wenlock to Middle Elton times could be indicated by the change from Group 1 (shallow water-nearshore) to Group 4 (deeper water-offshore). These two groups have a strong inverse relationship, and a ratio of the two could be considered to be a measure of depth/distance from shore (Text-fig. 4.9). This, in many respects, concurs with the depth/distance from shore model of acritarchs and prasinophyte algae of Dorning (1981c).

The data could alternatively be interpreted as reflecting a change in palaeoceanography through time, with the transition phases representing periods of fluctuation between distinct palaeoceanographic states. Fluctuating water masses are a component of the models that Colbath (1980) proposed to explain the distribution of upper Ordovician organic-walled microplankton.

The distribution pattern of Group 5, which does not follow patterns like those of the other groups, suggests that it is composed of eurytopic taxa (cosmopolitan taxa that become dominant under stressed environments when other, less tolerant taxa, are reduced or excluded (Colbath 1980)). Its main constituent is the prasinophyte alga, *Tasmanites* spp., which is abundant only under special conditions (Tappan 1980, p. 814). The main peak in Group 5 occurs in the basal Middle Elton Formation and thus has similarities with the tasmanites black shale of North Africa (as reported by Tappan 1980, p. 814).

The group data remains fairly monotonous throughout the Middle Elton Formation. Information gained from individual taxa, however, clearly shows changes in the flora related to events observed in the palynofacies analysis (see above). Between approximately 51 and 57m there is a prominent peak in the relative values of *Stellechinatum* ? sp. A, which becomes a very important constituent of assemblages. This taxon is morphologically similar to *Stellechinatum celestum* (Martin 1969) Turner 1984, which was considered to be eurytopic by Colbath (1980). This increase in *Stellechinatum* ? sp. A corresponds to the initial increase in Total POM above the Lower/Middle Elton formation boundary (see above). A second event (73-79m) is identified by the presence of *Stellechinatum* ? sp. A and *T. tentaculaferum* (minor peaks) and *Schismatosphaeridium* sp. A. This corresponds to the peaks in the land plants, prasinophyte algae and graptolites in the palynofacies analysis (Text-fig. 4.7). The final event (89-90m) is marked by increased occurrences of *E. tenuistriata* and *T. tentaculaferum*. In the palynofacies a peak in the Total POM was observed around this level.

The change from assemblages dominated by Group 4 to Group 1 at the top of the Middle Elton Formation indicates that sample GOG12/302-A lies within the transition phase that separates the Middle and Upper Elton formations. Examination of the stratigraphic duration of previous transition phases suggests that this sample may lie within 2-10m below the Middle/Upper Elton formation boundary; this



Text-fig. 4.9. Ratio of Group 4 to Group 1. This measurement could be considered a measure of offshore influence.

concurs with the proposal that these beds were transitional to typical Upper Elton Formation lithologies (White & Lawson 1978, p. 3).

The fact that apparently eurytopic taxa have rapid alternations in their relative abundance suggests that the periods of increased Total POM observed in the palynofacies are associated with distinct changes in the palaeoenvironment. The initial event (c. 51-61m) is similar to that higher up (c. 72-80m), as both are indicated by peaks in the relative abundance of *Stellechinatum* ? sp. A (Text-fig. 4.10). The first and third event were caused by conditions distinct from one another as there are no corresponding peaks between *Stellechinatum* ? sp. A and *E. tenuistriata* or *T. tentaculaferum*. The second and third events are, however, similar, as there is a correlation between the major peak in *Schismatosphaeridium* sp. A and the minor peak of *T. tentaculaferum*. This suggests, very strongly, that there was a periodic change in the palaeoenvironment during Middle Elton times.

Conclusions

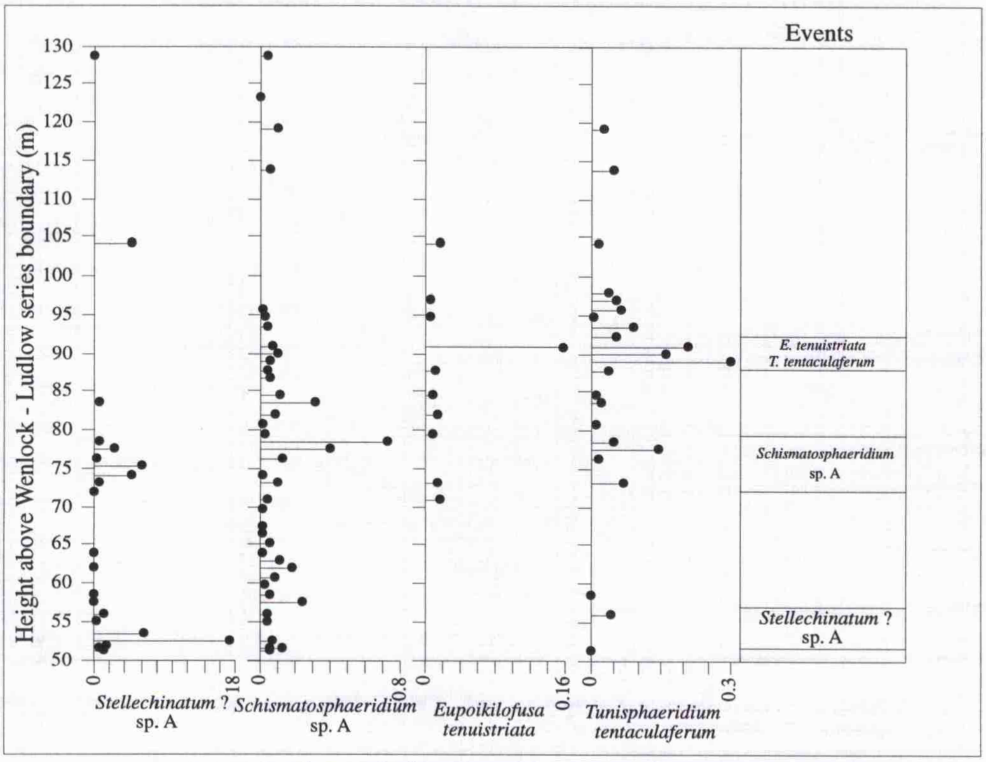
The palaeoenvironmental conclusions of this analysis are summarised in Text-figs 4.9 and 4.11 and are briefly discussed below.

Wenlock - Ludlow series boundary

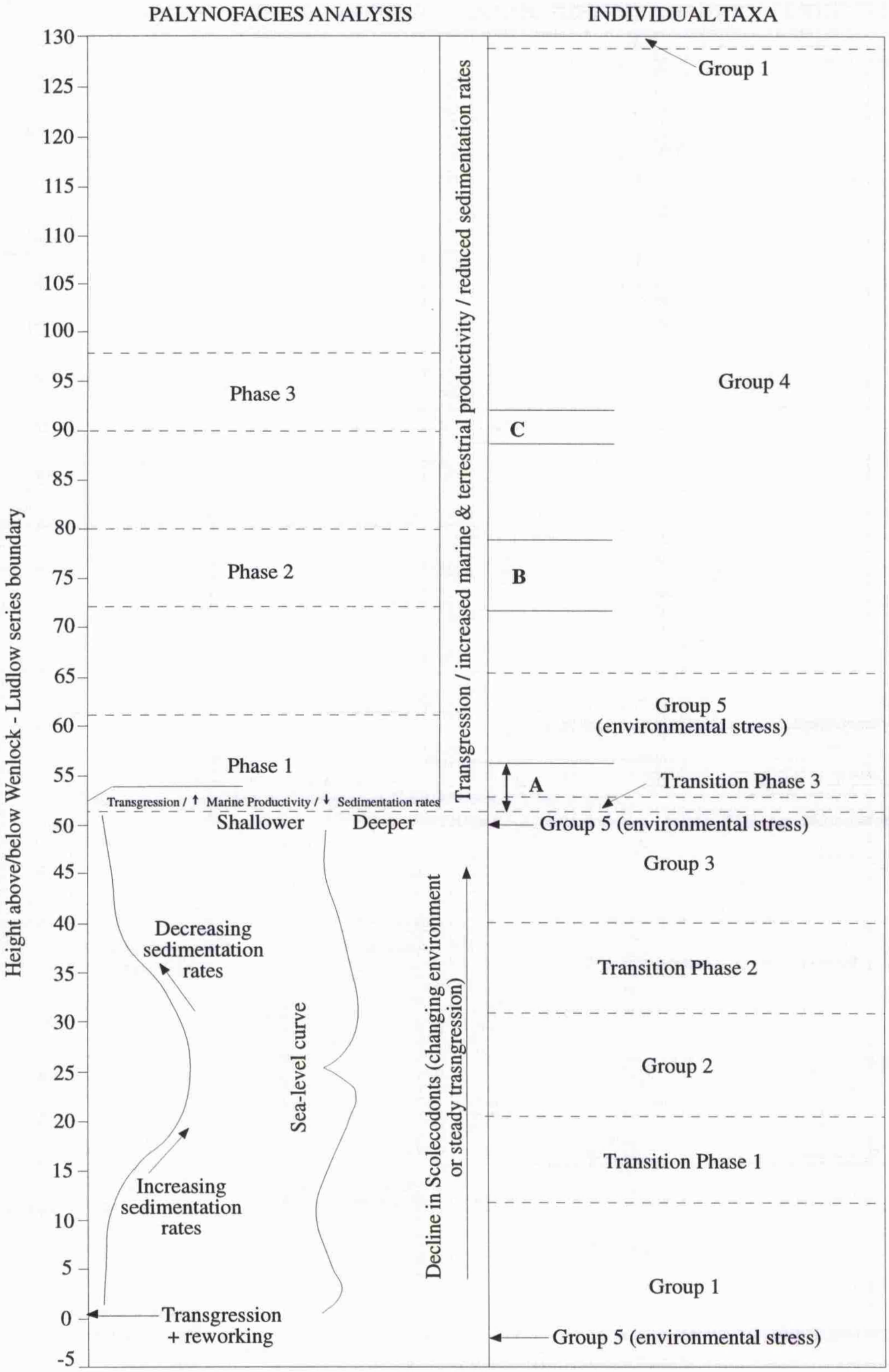
Immediately below the series boundary Group 5 dominates (Text-figs 4.8, 4.11), suggesting a period of environmental stress. The first event visible in the palynofacies is just below the boundary at Pitch Coppice (-0.135m) and just above the boundary at Goggin Road (0.145m to 0.54m). At this point there is an increase in several palynofacies groups (land plants, chitinozoans, scolecodonts and AOM), the Marine Index and the Total POM (Text-fig. 4.4). This appears to have resulted from a transgression induced phase of reworking (see Galloway 1989). This conclusion is further strengthened by the Group 4-Group 1 ratio (a possible measure of distance from shore) which shows a peak (possible more offshore influence) in Goggin Road at the level of the reworking (Text-fig. 4.9). At Pitch Coppice this event correlates with the decline in $\partial^{13}C$ observed in the Ludlow anticline by Corfield *et al.* (1992). It is probable that this decline is a result of the transgression-induced reworking, which has concentrated a larger amount of organic matter rich in ^{12}C, especially the large size fraction. The fact that the two events are displaced between Pitch Coppice and Goggin Road may suggest that there is a degree of diachronity between the two sections.

Lower Elton Formation

Through the Lower Elton Formation there is a broad decline in Total POM followed by an increase to former levels (Text-fig. 4.5). Possible explanations are fluctuating sedimentation rates (dilution effect) or changing marine and terrestrial productivity (changing flux of organic matter to basin floor). In the Lower Elton Formation the Marine Index fluctuates (Text-fig. 4.5), perhaps indicating a



Text-fig. 4.10. Relative abundance of selected taxa through the Middle Elton Formation, showing periodic events.



Text-fig. 4.11. Comparison of the results of the palynofacies analysis with those for the individual taxa. **A** = *Stellechinatum* ? sp. A Event; **B** = *Schismatosphaeridium* sp. A Event; **C** = *Eupoikilofusa tenuistriata - Tunisphaeridium tentaculaferum* Event.

period of alternating high and low sea-levels; Marine Index values are approximately equal in the lower and upper parts of the formation, suggesting no general deepening trend. There is, however, other evidence to suggest that there was a general deepening through the Lower Elton Formation. Scolecodonts are common in the lower part of the formation, but decline to low numbers, or are absent higher up. This may, however, indicate a change to an environment to which polychaetes were not well adapted. The Group 4-Group 1 ratio also steadily increases from the lower to upper parts of the formation, perhaps also indicating a gradual deepening. The individual taxa show a change from Group 1 to Group 3 which strengthens the evidence for a change in palaeoenvironment between the lower and upper parts of the formation, though this need not have been driven by changes in sea-level. The changes in individual taxa also appear to correlate with the fluctuating Total POM (Text-fig. 4.11). Group 1-Transition Phase 1-Group 2 and Transition Phase 2-Group 3 correlate with the decrease and increase in Total POM respectively. Just before the Lower/Middle Elton formation boundary, the dominance of Group 5 indicates another period of environmental stress (Text-figs 4.8, 4.11).

Middle Elton Formation

At the boundary level there is a rapid increase in Total POM which may indicate reduced rates of sedimentation (Text-fig. 4.6). There is, however, also a decline in land plants and increase in Marine Index which suggests either a transgressive pulse or increase in marine productivity.

Above the boundary level the land plants are recorded in higher numbers, though the Marine Index and Group 4-Group 1 ratio are consistently high (Text-figs 4.6, 4.7, 4.9). These high values may indicate increased marine productivity or a transgression with increased offshore influence. The absolute values of all palynofacies groups, and Total POM, increase in the Middle Elton Formation (Text-fig. 4.7), which may indicate lower sedimentation rates or increased marine and terrestrial productivity. Transition Phase 3 occurs over a shorter range than lower transition phases (Text-figs 4.8, 4.11), which is also consistent with reduced sedimentation rates. A period of highly stressed environment at the beginning of the formation is indicated by the dominance of Group 5 (Text-figs 4.8, 4.11). Immediately above this level of environmental stress occurs the massive increase in land plant fragments observed in the palynofacies analysis (TRENCH4/200-A, 65.18m, Text-fig. 4.11). This is attributed to a period of more intense run-off, resulting in greater terrestrial input (though there is no concurrent rise in the sporomorphs).

The palynofacies analysis has recorded distinct phases where the abundance of individual palynodebris types and Total POM increases (51-61m, 72-80m and 90-98m above the series boundary, Text-fig. 4.11). These phases cannot be attributed simply to reduced sedimentation rates or increased productivity, as there are differences in the composition of each phase. For example, the acritarchs increase in a stepped fashion from Phase 1 to 3, whereas graptolites and land plants have their highest abundance in Phase 2. This suggests that there are palaeoenvironmental differences between each phase. This is also strengthened by the correlation of these palynofacies phases to events in the individual taxa (*Stellechinatum* ? sp. A event (51-57m); *Schismatosphaeridium* sp. A event (73-79m); *E. tenuistriata-T.*

tentaculaferum event (89-90m)). The different abundance of these taxa between each event also indicate a stepped change in the palaeoenvironment.

The final feature of the Middle Elton Formation is the change from assemblages dominated by Group 4 to Group 1 in sample GOG12/302-A. This suggests that this sample lies within the transition phase separating the Middle and Upper Elton formations. Drawing inferences from the stratigraphic length of lower transition phases it is possible to suggest that GOG12/302-A lies approximately 2-10m below the Middle/Upper Elton formation boundary. The presence of thin calcareous siltstones at this level was used to suggest a possible transition to typical Upper Elton Formation lithologies by White & Lawson (1978, p. 3).

Discussion

It is clear that the possible palaeoenvironmental changes used to explain the events observed in the palynofacies analysis and the individual taxa could support aspects of either the eustatic or P & S models. What is clear, however, is that the results of this analysis show that the events in the earliest Ludlow Series are much more complex than the scenarios proposed by either model.

There is evidence to suggest a steady transgression spanning the Lower Elton Formation, which reaches a peak in the Middle Elton Formation. There is also evidence to suggest that the Lower Elton Formation had either a period of fluctuating sea-level or a trend of general deepening before a main transgressive pulse at the start of the Middle Elton Formation. This appears to confirm the eustatic model. This model, however, does not deal in detail with the palaeoclimatic or palaeoceanographic effects that would be linked to eustatic changes. Indeed, sea level changes in the magnitude of 50-100m have been proposed for the Wenlock-Ludlow series transgression (Johnson & McKerrow 1991, p. 162), though the potentially catastrophic impact of such changes on the pattern of circulation in the palaeo-ocean and its effect on the fauna and flora was barely touched upon.

There is also evidence to support the P & S model. An increase in sedimentation rates is seen in the basal Lower Elton Formation, though this increase is short lived. The increase in Marine Index in the Middle Elton Formation may result from a greater marine productivity. The change in the dominance of groups based on individual taxa may also reflect changes in the surface water type. This theory is further strengthened by looking at the distribution of the eurytopic taxa, especially Group 5, which show periods of high environmental stress that can be located around the formation boundaries. The P & S model attempts to explain the changes observed in facies, flora and fauna by fluctuations in the global palaeoclimate and palaeoceanography. As such it attempts a more holistic approach and manages to explain the broad changes in Silurian facies, fauna and flora well (see Aldridge *et al.* 1993, Jeppsson *et al.* 1995). The model as it stands, however, does not yet contain enough detail for the events recorded herein to be clearly related.

CONCLUSIONS

TAXONOMY.

- Ten new species of acritarch and prasinophyte alga are described and illustrated: *Cymatiosphaera lawsonii*, *Cymatiosphaera multicrista*, *Cymatiosphaera paucimembrana*, *Cymatiosphaera triangula*, *Baltisphaeridium ? spinatum*, *Buedingiisphaeridium reticulum*, *Glyptosphaera heltaskelta*, *Gorgonisphaeridium ? listeri*, *Leptobrachion digitatum* and *Pulvinosphaeridium dorningii*.
- Thirty-one acritarch and prasinophyte algal taxa are described under open nomenclature.
- The diagnosis of *Psenotopus* is emended to take into account the true nature of excystment, as is the diagnosis of its only species, *P. chondrocheus*. The diagnoses of a further eight species are emended: *Cymatiosphaera octoplana*, *Dorsennidium europaeum*, *Dorsennidium rhomboidium*, *Eupoikilofusa filifera*, *Evittia robustispinosa*, *Pulvinosphaeridium oligoprojectum*, *Schismatosphaeridium rugulosum* and *Veryhachium trisphaeridium*.
- Six new combinations are proposed: *Comasphaeridium brevispinosum*, *Dorsennidium pentagonale*, *Dorsennidium wenlockianum*, *Evittia aculeata*, *Evittia almarada* and *Gorgonisphaeridium citrinum*.

BIOSTRATIGRAPHY. The acritarch/prasinophyte algal biozones of Dorning (1981a), for the Welsh Basin, and the informal global zones of Martin (1989) can be recognised in the type area to some extent. The use of *P. stiphrospinata* to identify the base of the zone 6 (Gorstian-Ludfordian stages) of Martin (1989) must now be questioned as this taxon has been recovered from the Mulde Formation, Wenlock Series, of Gotland (Le Hérissé 1989). In the Welsh Borderland, *P. stiphrospinata* has a first recorded occurrence in the Lower Elton Formation of the Millichope area (Lister 1970). In the Ludlow type area it has previously been recovered from the Middle Elton Formation (Lister & Downie 1974); its range base is identified in the Middle Elton Formation herein, 83.5m above the Wenlock-Ludlow series boundary. *L. carminae*, another taxon cited as indicative of zone 6 by Martin (1989), has not been recovered in this study and has a first recorded occurrence in the Lower Bringewood Formation of the Ludlow area (Lister & Downie 1974). Under the scheme of Martin (1989) the ranges of *P. chondrocheus* and *V. dilatispinosa* (= *V. pirifera* herein) extend just into the base of zone 6. In this study, *P. chondrocheus* and *V. pirifera* have their range bases in the Middle Elton Formation, 87.765m and 95.73m above the series boundary respectively; this concurs with the scheme of Martin (1989). Lister & Downie (1974) recorded *V. dilatispinosa* (=*V. pirifera* herein) into the basal Prídolí Series, which appears to correlate with the doubtful occurrence listed by Martin (1989, fig. 150).

The range of *E. wenlockensis* (Biozone W3 of Dorning 1981a), most frequent across the series boundary, is extended into the Middle Elton Formation. *E. granulata* (Biozone W3) has a range top, herein, 0.54m above the series boundary (Lower Elton Formation), which concurs with the scheme of Dorning (1981a). The use of this taxon in biostratigraphy must be questioned, however, as it may be strongly facies controlled (see Dorning 1981a, p. 192). Biozone W3 is also identified by common *L. arbusculiferum*, with *D. stenodictyum*, *M. amydra* and *P. wenlockium* occurring in the upper part of the zone (Dorning 1981a). The relative frequencies of these taxa, as recorded herein (Appendix 2), concur, in part, with the scheme of Dorning (1981a). The highest relative frequencies of *L. arbusculiferum* and *D. stenodictyum* occur around the series boundary; *P. wenlockium* and *M. amydra*, however, have their highest relative frequencies higher in the Lower Elton Formation (Appendix 1), within what Dorning (1981a) identified as Biozone L1. Biozone L1 is identified herein by *B. pyramidale* and *N. mayhillense*; their ranges are extended into the Much Wenlock Limestone Formation, creating an overlap between Biozones W3 and L1. Biozone L2 may possibly be recognised in the uppermost Middle Elton Formation sampled herein. Material identical to *G.* ? *listeri* sp. nov. was incorrectly included in synonymy with one of the zone taxa, *G. bringewoodense*, by Dorning (1981a). No specimens resembling the holotype of *G. bringewoodense* have been found.

PALYNOFACIES ANALYSIS. At Pitch Coppice Quarry a Wenlock-Ludlow boundary event, marked by the increase in abundance of several palynofacies groups and fluctuations in the individual taxa, correlates with the carbon isotope event of Corfield *et al.* (1992). This carbon isotope event was related to a decline in graptolite diversity (*nassa* Biozone) and to the oxygenation events in the basin (Kemp 1991). The true cause of this $\partial^{13}C$ decline appears to have been transgression-induced sediment reworking which concentrated organic matter rich in ^{12}C, especially the large size fraction. The increase in values of the Group 4:Group 1 ratio at this level may also indicate a greater offshore influence. This event in the palynofacies and individual taxa is also present at Goggin Road, though it is recorded at a slightly higher level, suggesting the event is diachronous between the two localities.

The palynofacies analysis and frequencies of individual acritarch and prasinophyte algal taxa suggest a series of events through the Lower and Middle Elton formations that can be broadly correlated, though the exact driving mechanisms are debatable. Evidence can be used to suggest fluctuations in sea level, marine and terrestrial productivity, sedimentation rates or palaeoenvironment/palaeoceanography. They can also indicate, in some instances, periods of increased environmental stress or terrestrial run-off. The evidence supports aspects of both the eustatic model (e.g. McKerrow 1979) and climatic/oceanic (P&S) model of Jeppsson (1990). It is apparent, however, that the events suggested by the palynofacies analysis and individual taxa are more complex than can be adequately explained by either model.

FUTURE RESEARCH. Before the biostratigraphic scheme of Dorning (1981a) can be emended, contiguous sections, that occupied positions on the shelf or shelf edge during latest Wenlock-earliest Ludlow times, need to be examined.

The combination analysis of palynofacies and individual taxa shows great potential for detailing aspects of palaeoenvironment. Similar analyses need to be completed through a larger time span to ascertain whether the events recorded herein are restricted to the Ludlow Series, or whether they are repeated cyclically through the stratigraphic column. With more analyses, not only in different ages, but also in contiguous sections here and abroad, it will be possible to more rigorously test the eustatic and climatic/oceanic (P & S) models.

In general, the prospects for using acritarchs and prasinophyte algae in biostratigraphy would be greatly improved if a definitive scheme of classification was developed for them. At present, the differences in value, with regards to use in classification, assigned to each morphological features varies author to author.

REFERENCES

ACHAB, A. 1976. Les Acritarches de la Formation d'Awantjish (Llandoverien supériur) du sondage Val Brillant, Vallée de la Matapédia, Québec. *Canadian Journal of Earth Sciences*, **13**, (9), 1310-1318, pls 1-3.

AL-AMERI, T. K. 1983. Acid resistant microfossils used in the determination of Palaeozoic palaeoenvironments in Libya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **44**, 103-116.

ALDRIDGE, R. J. 1975. The stratigraphic distribution of conodonts in the British Silurian. *Journal of the Geological Society, London*, **131**, 607-618, 3 pls.

--------- 1985. Conodonts of the Silurian System from the British Isles. In: HIGGINS, A. C. & AUSTIN, R. L. (eds.). *A stratigraphical index of conodonts*. 68-92, pls 3.1-3.4. Ellis Harwood, Chichester.

--------- DORNING, K. J., HILL, P. J., RICHARDSON, J. B. & SIVETER, D. J. 1979. Microfossil distribution in the Silurian of Britain and Ireland. In: The Caledonides of the British Isles - reviewed. *Special Publication of the Geological Society of London*. **8**, 433-438.

--------- --------- & SIVETER, D. J. 1981. Distribution of Microfossil Groups across the Wenlock Shelf of the Welsh Basin. In: NEALE, J. W. & BRASIER, M. D. (eds.). *Microfossils from Recent and fossil shelf seas*, 18-29, pls 2.1-2.3.

--------- & SCHÖNLAUB, H. P. 1989. Conodonts. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). *A Global Standard for the Silurian System*, 274-279. National Museum of Wales, Geological Series No. 9, Cardiff.

--------- JEPPSSON, L. & DORNING, K. J. 1993. Early Silurian oceanic episodes and events. *Journal of the Geological Society, London*, **150**, 501-513.

AMIRIE, G. H. B. 1984. Phytoplankton aus dem Frasne des bergischen Landres, rheinisches Schiefergebirge. *Geologisches Institut der Universität zu Köln Sonderveröffentlichungen, no. 49,* 1-99, pls 1-16.

BARRON, H. F. 1989. Mid-Wenlock acritarchs from a Silurian inlier in the Cheviot Hills, NE England. *Scottish Journal of Geology*, **25**, (1), 81-98, 4 pls.

BASSETT, M. G. 1989. The Wenlock Series in the Wenlock area. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). *A Global Standard for the Silurian System*, 51-73. National Museum of Wales, Geological Series No. 9, Cardiff.

--------- HOLLAND, C. H., INGHAM, J. K., LAWSON, J. D., RICKARDS, R. B. & TEMPLE, J. T. (compil). 1979. *Field meeting, Great Britain. March 30-April 11, 1979.* 48pp. IUGS, Subcommission on Silurian stratigraphy, Ordovician-Silurian Boundary Working Group.

--------- LAWSON, J. D. & WHITE, D. E. 1982. The Downton Series as the fourth Series of the Silurian System. *Lethaia*, **15**, 1-24.

--------- BLUCK, B. J., CAVE, R., HOLLAND, C. H. & LAWSON, J. D. 1992. Silurian. In: COPE, J. C. W., INGHAM, J. K. & RAWSON, P. F. (eds.). Atlas of Palaeogeography and Lithofacies. *The Geological Society Memoir No. 13*, 37-56.

BERRY, W, B, N. & BOUCOT, A, J. 1970. Correlation of North American Silurian Rocks. *Geological Society of America, Special Paper*, **102**, 1-289.

--------- --------- 1973. Glacio-eustatic control of Late Ordovician - Early Silurian platform sedimentation and faunal changes. *Geological Society of America, Bulletin*, **84**, 272-284.

BOUCOT, J. C. 1975. Evolution and Extinction Rate Controls, 427pp.

BRITO, I. M. 1965. Novos microfosseis Devonianos do Maranhao. Universidade da Bahia, *Escola de Geologia*, **2**, 1-4, 1 pl.

--------- 1966. Contribuiçaõ ao conhecimento dos micrôfósseis Silurianos e Devonienos da Bacia do Maranhao. Acritarcha. Polygonomorphitae e Pteromorphitae. *Publs. Soc. Bras. Geol. Nucleo Rio de Janeiro*, **1**, 78-79.

--------- 1967. Silurian and Devonian Acritarcha from Maranhao Basin, Brazil. *Micropaleontology*, **13**, (4), 473-482, pls 1-2.

--------- & SANTOS, A. de S. 1965b. Contribuiçao ao conhecimento dos micrôfósseis Silurianos e Devonianos da Bacia do Maranhao. *Departamento Nacional du Produçao Mineral, Divisao de Geologia e Mineralogia, Notas Preliminares e Estudos (Rio de Jeneiro, Brasil), no. 129*, 1-21, pls 1-2

BUJAK, J. P. & WILLIAMS, G. L. 1981. The evolution of dinoflagellates. *Canadian Journal of Botany*, **59**, 2077-87.

BURGESS, N. D. & EDWARDS, D. 1991. Classification of uppermost Ordovician to Lower Devonian tubular and filamentous macerals from the Anglo-Welsh Basin. *Botanical Journal of the Linaean Society*, **106**, (1), 41-66.

--------- & RICHARDSON, J. B. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology*, **34**, (3), 601-628, 2 pls.

BURMANN, G. VON. 1970. Weitere organische Mikrofossilien aus dem unteren Ordivizium. *Paläontologische Abhandlungen, Abt. B*, **3**, (3-4), 289-332, pls 2-19.

CALEF, C. E. & HANCOCK, N. J. 1974. Wenlock and Ludlow marine communities of Wales and the Welsh Borderland. *Palaeontology*, **17**, 779-810.

CHALONER, W. G. & ORBELL, G. 1971. A palaeobiological definition of sporopollenin. In: BROOKS, J., GRANT, P. R., MUIR, M. D., VAN GIJZEL, P. & SHAW, G. (eds.). *Sporopollenin.*, 273-294. Academic Press, London.

CHRISTENSEN, T. 1962. Alger. In: BÖCHER, T. W., LANGE, M. & SØRENSEN, T. *Botanik (Systematisk Botanik)*, 172pp.

COLBATH, G. K. 1979. Organic-walled microphytoplankton from the Eden Shale (Upper Ordovician), Indiana, USA. *Palaeontographica Abt. B*, **171**, (1-3), 1-38, pls 1-14.

--------- 1980. Abundance fluctuations in Upper Ordovician organic-walled microplankton from Indiana. *Micropaleontology*, **26**, (1), 97-102.

--------- 1983. Fossil prasinophycean phycomata (Chlorophyta) from the Silurian Bainbridge Formation, Missouri, U.S.A. *Phycologia*, **22**, (3), 249-265, figs 2-45.

--------- 1987. *Orygmahapsis*, a new genus of prasinophyte phycoma from the Siluro - Devonian. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **42**, (2), 65-68. pl. 1.

--------- & GRENFELL, H. R. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including "acritarchs'). *Review of Palaeobotany and Palynology*, **86**, 287-314, pls 1-9.

COMBAZ, A., LANGE, F. W. & PANSART, J. 1967. Les "Leiofusidae" Eisenack, 1938. *Review of Palaeobotany and Palynology*, **1**, 291-307, pls 1-2.

COOKSON, I. C. & EISENACK, A. 1958. Microplankton from Australian and New Guinea Upper Mesozoic sediments. *Proceedings of the Royal Society of Victoria*, **70**, (1), 19-79, pls 1-12.

CORFIELD, R. M., SIVETER, DEREK, J., CARTLIDGE, J. E. & McKERROW, W. S. 1992. Carbon isotope excursion near the Wenlock - Ludlow (Silurian) boundary in the Anglo-Welsh area. *Geology*, **20**, 371-374.

CRAMER, F. H. 1963. Nota provisional sobre la presencia de microplankton y esporomorfas en las rocas sedimentarias del Devónico Inferior en las Montañas Cantábricas. *Estudios geologicos*, **19**, 215-218, pls 1-2.

--------- 1964a. Some acritarchs from the San Pedro Formation (Gedinnien) of the Cantabric Mountains in Spain. *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **73**, (1), 33-38, pls 1-2.

--------- 1964b. Microplankton from three Palaeozoic formations in the Province of León, NW Spain. *Leidse Geologische Medelelingen*, **30**, 253-361, pls 1-24.

--------- 1966a. Palynology of Silurian and Devonian rocks in Northwest Spain. *Instituto Geologico y Minero de España, Boletin*, **77**, 225-286, pls 1-4.

--------- 1966b. Additional morphographic information on some characteristic acritarchs of the San Pedro and Furada formations (Silurian Devonian boundary) in Leon and Asturias, Spain. *Instituto Geologico y Minero de España, notas y comunicaciones*, **83**, p. 27-48, pls 1-5.

--------- 1966c. *Hoegispheres* and other microfossils *incertae sedis* of the San Pedro Formation (Siluro-Devonian boundary) near Valporquero, Leon, NW Spain. *Instituto Geologico y Minero de España, notas y comunicaciones*, **86**, 75-94, pls 1-2.

--------- 1968a. Palynologic microfossils of the Middle Silurian Maplewood Shale in New York. *Revue de micropaléontologie*, **11**, (2), 61-70, pl. 1.

--------- 1968b. Considérations paléogéographiques à propos d'une association de microplanctontes de la série gothlandienne de Birmingham (Alabama, USA.). *Bulletin de la Société géologique de France, 7e sér.*, no. 10, 126-131.

--------- 1969a. Possible implications for Silurian paleogeography from phytoplancton assemblages of the Rose Hill and Tuscarora formations of Pennsylvania. *Journal of Palaeontology*, **43**, (2), 485-91, pl. 1.

---------- 1969b. Consideraciones sobre la palinología y las paleolatitudes silúricas a proposito del microplancton silúrico de las Montañas Cantábricas del Noroeste de España. *Comunicacoes dos Servicos geologicos de Portugal*, **53**, 67-94, pls 1-11.

--------- 1970a. Distribution of selected Silurian acritarchs. An account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa. *Revista Española de Micropaleontologia, numero extraordinerio*, 1-203, pls 1-23.

--------- 1970b. Acritarchs and chitinozoans from the Silurian Ross Brook Formation, Nova Scotia. *Journal of Geology*, **78**, 745-749.

--------- 1971. Implications from Middle Paleozoic palynofacies transgressions for the rate of crustal movement, especially during the Wenlockian. *Anais da Academia brasileira de ciências*, **43**, 51-66, pls 1-4.

--------- & DIEZ, M. del C. R. 1968. Consideraciones taxonómicas sobre las acritarcas del Silúrico Medio y Superior del Norte de España. *Instituto Geológico y Minero de España, Boletín*, **79**, (6), 541-574, pls 1-21.

--------- --------- 1970. Acritarchs from the Lower Silurian Neahga Formation, Niagara Peninsula, North America. *Canadian Journal of Earth Sciences*, **7**, 1077-1085.

--------- --------- 1972. North American Silurian palynofacies and their spatial arrangement: Acritarchs. Palaeontographica Abt. B. **138**, (5-6), 107-180, pls 31-36.

--------- --------- 1976. Acritarchs from the La Vid Shales (Emsian to lower Couvinian) at Colle, Léon, Spain. *Palaeontographica, Abt. B*, **158**, (1-4), p. 72-103, pls 1-7.

--------- --------- 1977. Late Arenigian (Ordovician) acritarchs from Cis-Saharan Morocco. *Micropaleontology*, **23**, (3), 339-360, pls 1-6.

--------- --------- 1979. Lower Paleozoic acritarchs (Acritarcos del Paleozoici Inferior). *Instituto de Investigaciones Palinológicas, Apartado 244, Léon, España*, 17-160.

--------- --------- & CUERDA, A. J. 1974. Late Silurian chitinozoans and acritarchs from Cochabamba, Bolivia. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, 1-12.

--------- --------- & RODRIGUEZ, R. M. & FOMBELLA, M. A. 1976. Acritarcos de la Formacion San Pedro (Silurico Superior) de Torrestio, Provincia de Leon, España. *Revista Española de Micropaleontología*, **8**, (3), 439-452, pls 1-2.

--------- --------- & KJELLSTRÖM, G. 1979. Acritarchs. In: JAANUSSON, V., LAUFELD, S. & SKOGLUND, R. (eds.). Lower Wenlock faunal and floral dynamics - Vattenfallet Section, Gotland. *Sveriges Geologiska Underskökning, serie C, no. 762*, 39-53, figs 16-19.

DEFLANDRE, G. 1935. Considérations biologiques sur les microorganismes d'origine planctonique conervés dans les silex de la craie. Bulletin biologique de la France et de la Belgique, 69, 213-244, pls 5-9.

--------- 1936. Les flagellés fossiles. Aperçu biologique et paléontologique. Rôle Géologique. *Actualités Scientifique et Industrielles*, No. 335, 1-97.

--------- 1937. Microfossiles des silex crétacés. Deuxième partie. Flagellés *incertae sedis*. Hystrichospaeridés. Sarcodinés. Organismes divers. *Annales de Paléontologie*, **26**, 51-103, pls 11-18.

--------- 1942. Sur les Hystrichospères des calcaires siluriens de la Montage Noire. *Comptes rendu des séances de l'Académie de sciences*, **215**, (20) 475-476.

--------- 1945. Microfossiles des calcaires siluriens de la Montagne Noire. *Annales de Paléontologie*, **31**, 41-75, pls 1-3.

--------- 1947. Le problème des hystrichosphères. *Bulletin de l'Institut océanographique (Monaco)*, No. 918, 1-23.

--------- 1954. Systématique des Hystrichosphaeridés: sur l'acception du genre *Cymatiosphaera* O. Wetzel. *Comptes rendu sommaire Société géologique de France*, **4**, (9-10), 257-259.

--------- & COOKSON, I. C. 1955. Fossil microplankton from Australian Late Mesozoic and Tertiary sediments. *Australian Journal of Marine and Freshwater Research*, **6**, (2), 242-313, pls 1-9.

--------- DEFLANDRE-RIGAUD, M. 1964. Notes sur les Acritarches. *Revue de Micropaléontology*, 7, (2), 111-4.

--------- --------- 1965. Fichier micropaléontologique général - Série 13. Acritarches II. Acanthomorphitae 1. Genre *Micrhystridium* Deflandre *sens. lat.* Archives originales, Centre de documentation, *centre national de la recherche scientifique.* No. 402, I-V, fiches 2176-2521.

DEUNFF, J. 1951. Sur la présence de microorganismes (Hystrichosphères) dans les schistes ordoviciens du Finistère. *Comptes rendu des seances de l'Académie de sciences*, **233**, (4), 321-323.

--------- 1954a. Sur un microplancton du Dévonien du Canada recélant des types nouveaux d'Hystrichosphaeridés. *Comptes rendu des séances de l'Académie des sciences*, **239**, (17), 1064-1066.

--------- 1954b. *Veryhachium*, genre nouveau d'Hystrichosphères du Primaire. *Comptes rendu sommaire des séances de la société géologique de France, no. 13*, 305-307.

--------- 1955. Un microplancton fossile Dévonien a Hystrichosphères du Continent Nord-Américain. *Bulletin de la microscopie applquée, sér. 2*, **5**, (11-12). 138-149, pls 1-4.

--------- 1957. Microorganismes nouveaux (Hystrichosphères) du Dévonien de l'Amerique du Nord. *Bulletin de la Société géologique et mineralogique de Bretagne, nouvelle sér, no. 2*, 5-14.

--------- 1959. Microorganismes planctoniques du primaire Armoricain. I.- Ordovicien du Veryhac'h (Presqu'île de Crozon). *Bulletin de la Société géologique et mineralogique de Bretagne, nouvelle sér., no. 2*, 1-41, pls 1-12.

--------- 1961. Quelques précisions concernant les Hystrichospaeridées du Dévonien du Canada. *Comptes rendu des séances de l'Académie de sciences*, **233**, (4), 321-323.

--------- 1964. Le genre *Duvernaysphaera* Staplin. *Grana Palynologica*, **5**, (2), 210-5.

--------- 1966. Acritarches du Dévonien de Tunisie. *Comptes rendu sommaire des séances de la Société géologique de France*, No. 1, p. 22-23.

--------- 1967a. Présence d'Acritarches dans une série dévonienne du lac Huron (Canada). *Compte rendu sommaire des séances de la société géologique de France, no. 6*, 258-260, 1 pl.

--------- 1967b. Recherches sur les microplanctons du Devonien (Acritarches et Dinophyceae). *Bulletin de la Société géologique et mineralogique de Bretagne, nouvelle series*, 17-25.

---------- 1971. Le genre *Polyedrixium* Deunff. Révision et observations. In: JARDINÉ, S. (ed.). Microfissiles organiques du Paleozoique, 3. Acritarches. Commission Internationale de

Microflore du Paléozoique (C.I.M.P.), *Editions du Centre National de la Recherche Scientifique, Paris*. 17-49, pls 1-8.

--------- 1976. Les Acritarches. In: LARDEAUX, H. (ed.). Les Schistes et Calcaires Eodevoniens de Saint-Ceneré (Massif Armoricain, France): sédimentologie, paleontologie, stratigraphie. *Mémoire de la Société géologique et mineralogique de Bretagne, no. 19*, 59-77, pls 10-16.

--------- 1978. *Lanveocia* et *Candelasphaeridium*, genres nouveaux d'Acritarches des Grès de Landévennec (Gédinnien inférieur de la Rade de Brest-Finistère). *Geobios*, **11**, (1), 113-117, pl. 1.

--------- & EVITT, W. R. 1968. *Tunisphaeridium*, a new acritarch genus from the Silurian and Devonian. *Stanford University Publications, Geological Sciences*, **12**, (1), 1-13, pl. 1.

---------- LEFORT, J-. P. & PARIS, F. 1971. Le microplancton Ludlovien des Formations Immergees des Minquiers (Manche) et sa place dans la distribution du paleoplancton Silurien. *Bulletin de la Société géologique et mineralogique de Bretagne, sér C*, **3**, (1), 9-28, pls 1-4.

--------- GÓRKA, H. & RAUSCHER, R. 1974. Observations nouvelles et précisions sur les Acritarches a large ouveture polaire du Paleozoique inférieur. *Geobios*, **7**, (1), 5-18, pls 1-4.

DIEZ, M. del. C. R. & CRAMER, F. H. 1974. Range chart of selected Lower Paleozoic acritarch taxa. *Review of Palaeobotany and Palynology*, 18, 155-170.

--------- --------- 1976. Acritarches et miospores du Ludlovien de Corniero, Province de León, Espagne. *Revue de Micropaléontologie*, **19**, (3), 121-133.

DORNING, K. J. 1981a. Silurian acritarchs from the type Wenlock and Ludlow of Shropshire, England. *Review of Palaeobotany and Palynology*, **34**, 175-203, 3 pls.

--------- 1981b. Silurian Chitinozoa from the type Wenlock and Ludlow of Shropshire, England. *Review of Palaeobotany and Palynology*, **34**, 175-203.

--------- 1981c. Silurian acritarch distribution in the Ludlovian shelf sea of South Wales and the Welsh Borderland, 31-36. In: NEALE, J. W. & BRASIER, M. D. (eds.). *Microfossils from recent and fossil shelf seas*, Ellis Harwood, Chichester.

--------- 1982. Early Wenlock acritarchs from the Knockgardner and Straiton Grit formations of Knockgardner, Ayrshire. *Scottish Journal of Geology*, **18**, (4), 267-273, pls 1-2.

--------- 1983. Palynology and stratigraphy of the Much Wenlock Limestone Formation of Dudley, Central England. *Mercian Geologist*, **9**, (1), 31-40, pls 5-7.

--------- & ALDRIDGE, R. J. 1982. A preliminary investigation of palynological assemblages from the early Silurian of Ringerike. *Paleontological Contributions from the University of Oslo, no. 278*, 105-108.

--------- & BELL, D. G. 1987. The Silurian carbonate shelf microflora: acritarch distribution in the Much Wenlock Limestone Formation. In: HART, M. B. (ed.). *Micropalaeontology of carbonate environments*, 266-287.

DOWNIE, C. 1958. An assemblage of microplanckton from the Shineton Shales (Tremadocian). *Proceedings of the Yorkshire Geological Society*, **31**, 331-350, pls 16-17.

--------- 1959. Hystrichospheres from the Silurian Wenlock Shale of England. *Palaeontology*, **2**, (1), 56-71, pls 10-12.

--------- 1963. 'Hystrichospheres' (acritarchs) and spores of the Wenlock Shales (Silurian) of Wenlock, England. *Palaeontology*, **6**, (4), 625-52, pls 91-92.

--------- 1973. Observations on the nature of the acritarchs. *Palaeontology*, **16**, (2), 239-259, 4 pls.

--------- 1984. Acritarchs in British stratigraphy. *Geological Society of London, Special Report, no. 17*, 1-26.

--------- & SARJEANT, W. A. S. 1963. On the interpretation and status of some hystrichosphere genera. *Palaeontology*, **6**, (1), 83-96.

--------- --------- 1965. Bibliography and index of fossil dinoflagellates and acritarchs. *Geological Society of America, Memoir*, No. 94, pp. 180. (cover date 1964, issue date 1965).

--------- EVITT, W. R. & SARJEANT, W. A. S. 1963. Dinoflagellates, hystrichospheres and the classification of the acritarchs. *Stanford University Publications, Geological Sciences*, **7**, (3), 3-16.

--------- WILLIAMS, G. L. & SARJEANT, W. A. S. 1961. Classification of fossil microplancton. *Nature*. **192**, 471.

DUFFIELD, S. L. & LEGAULT, J. A. 1981. Acritarch biostratigraphy of Upper Ordovician-Lower Silurian rocks, Anticosti Island, Québec: preliminary results. In: LESPERANCE, P. J. (ed.). *Subcommission on Silurian Stratigraphy, Ordovician - Silurian boundary Working Group. II*, 91-99, Quebec.

EDWARDS, D., DUCKETT, J. G. & RICHARDSON, J. B. 1995. Hepatic characters in the earliest land plants. *Nature*, **374**, 635-636, 1 pl.

EISENACK, A. 1931. Neue Mikrofossilien des baltischen Silurs. 1. *Palaeontologische Zeitschrift*, **13**, (1-2), 74-118, pls 1-5.

--------- 1934. Neue Mikrofossilien des baltischen Silura III und neue Mikrofossilien des böhmischen Silurs I. *Palaeontologische Zeitschrift*, **16**, (1-2), 52-76, pls 4-5.

--------- 1938. Hystrichosphaerideen und verwandte Formen im baltischen Silur. *Zeitschrift für Geschiebeforschung und Flachlandsgeologie*, **14**, 1-30, pls 1-4.

--------- 1954. Hystrichosphären aus dem baltischen Gotlandium. *Senckenbergiana Lethaea*, **34**, (4-6), 205-211, pl. 1.

--------- 1955. Chitinozoen, Hystrichosphären und andere Mikrofossilien aus dem *Beyrichia*-Kalk. *Senckenbergiana Lethaea*, **36**, (1-2), 157-188, pls 1-5.

--------- 1958a. *Tasmanites* Newton 1875 und *Leiosphaeridia* n.g. als Gattungen der Hystrichosphaeriea. *Palaeontographica. Abt. A*, **110**, (1-3), 1-19, pls 1-2.

--------- 1958b. Mikroplankton aus dem norddeutschen Apt nebst einigen Bemerkungen über fossile Dinoflagellaten. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **106**, (3), 383-422, pls 21-7.

--------- 1959. Neotypen baltischer Silur-Hystrichospären und neue Arten. *Palaeontographica, Abt. A*, **112**, (5-6), 193-211, pls 15-17.

--------- 1963a. Hystrichosphären. *Biological Reviews (and Proceedings) of the Cambridge Biological Society*, **38**, 107-39.

--------- 1963b. Mitteilungen zur Biologie der Hystrichosphären and üder neue Arten. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **118**, (2), 207-16, pls 19, 20.

--------- 1965a. Mikrofossilien aus dem Silur Gotlands. Hystrichospären, Problematika. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **122**, (3), 257-274, pls 21-24.

--------- 1965b. Die Mikrofauna der Ostseekalke. 1. Chitinozoen, Hystrichospären. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **123**, (2) 115-148, pls 9-13.

--------- 1968a. Über die Firtpflanzung paläozoischer Hystrichosphären. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **131**, (1), 1-22, pls 1-3.

--------- 1968b. Mikrofossilien eines Geschiebes der Borkholmer Stufe, baltischens Ordovizium, F2. *Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg, no. 37*, 81-94, pls 23-25.

--------- 1969. Zur Systematik einiger paläozoischer Hystrichospären (Acritarcha) des baltischen Gebietes. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **133**, 245-266.

--------- 1972. Kritische Bemerkung zur Gattung *Pterospermopsis* (Chlorophyta, Prasinophyceae). *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, **10**, 596-601.

--------- 1977. Mikrofossilien in organischer Substanz aus den Middle Nodular Beds (Wenlock) von Dudley, England. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte, no. 1*, 25-35, 3 pls.

--------- CRAMER, F. H. & DIEZ, M. del C. R. 1973. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band III Acritarcha 1. Teil. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 1104.

--------- --------- --------- 1976. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band IV Acritarcha 2. Teil. E. Schweizertbart'sche Verlagsbuchhandlung, Stuttgart, pp. 863.

--------- --------- --------- 1979a. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band V Acritarcha 2. Teil. E. Schweizertbart'sche Verlagsbuchhandlung, Stuttgart, pp. 529.

--------- --------- --------- 1979b. Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien. Band VI Acritarcha 2. Teil. E. Schweizertbart'sche Verlagsbuchhandlung, Stuttgart, pp. 531.

EISERHARDT, K. H. 1986. *Palaeohystrichosphaeridium wimani* (Eisenack 1968), n.g. - ein ordovizischer Dinoflagellat? *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, no. 3*, p. 175-191.

---------- 1989. Baltisphären aus Gotländer Öjlemyrtlint (Acritarcha, Oberordoviz, Gescheibe, Scweeden). *Mitteilungen aus dem Geologisch-Päläontologischen Institut der Universität Hamburg*, **68**, 79-129.

ELLES, G. L. & WOOD, E. M. R. 1901-1918. A monograph of British graptolites. *Palaeontographical Society [Monograph]*, i-clxxi, 1-539.

ERKMEN, U. & BOZDOGAN, N. 1979. Acritarchs from the Dadas Formation in Southeast Turkey. *Géobios*, **12**, 445-449.

EVITT, W. R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres and acritarchs. *Proceedings of the National Academy of Science USA*, **49**, 158-164.

FAURE, G. 1986. Principles of isotope geology. John Wiley & Sons.

FENSOME, R. A., WILLIAMS, G. L., BARSS, M. S., FREEMAN, J. M., & HILL, J. M. 1990. Acritarchs and fossil prasinophytes: An index to genera, species and intraspecific taxa. *American Association of Stratigraphic Palynologists, Contribution Series*, No. 25, pp. 771.

FISHER, D. W. 1953. A microflora in the Maplewood and Neahga Shales. *Bulletin of the Buffalo Society of Natural Sciene*, 21, (2), 13-18, pl. 7.

FOMBELLA, M. A. 1977. Acritarchos de edad Cámbrico medio-inferior de la Provincia de León, España. *Revista Española de Micropaleontología*, **9**, (1), 115-124.

GAADER, K. R. 1954. Coccolithineae, Silicoflagellatae, Pterospermataceae and other forms from the «Michael Sars» North Atlantic deep sea expedition 1910. *Report on the science results of the «Michael Sars» North Atlantic deep sea expedition 1910.* **2**, (4), 1-20.

GALLOWAY, W. E. 1989. Genetic stratigraphic sequences in basin analysis I: Architecture and genesis of flooding-surface bounded depositional units. *American Association of Petroleum Geologists Bulletin*, **73**, 125-142.

GARDINER, P. R. R. & VANGUESTAINE, M. 1971. Cambrian and Ordovician microfossils from South-east Ireland and their implications. *Geological survey of Ireland, Bulletin*, **1**, (20, 163-210, pls 1-2.

GÓRKA, H. 1969. Mikroorganismes de l'Ordovicien de Pologne. *Palaeontologia Polonica, no. 22*, 1-102. pls 1-31.

GRAHN, Y. 1982. Chitinozoophoran palaeoecology in the Ordovician of Öland. *Sveriges Geologiska Undersøokning, Ser. C*, **792**, 1-17.

GRAY, J. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970-1984. *Philosophical Transactions of the Royal Society, London, B*, **309**, 167-195.

--------- & BOUCOT, A. J. 1989. Is *Moyeria* a Euglenoid? *Lethaia*, **22**, 447-456.

HABIB, D. & KNAPP, S. D. 1982. Stratigraphic utility of Cretaceous small acritarchs. *Micropaleontology*, **28**, (4), p. 335-371, pls 1-11.

HILL, P. J. 1974. Stratigraphic palynology of acritarchs from the type area of the Llandovery and the Welsh Borderland. *Review of Palaeobotany and Palynology*, **18**, (1-2), 11-23.

--------- 1978. A review of *Cymbosphaeridium pilar* and comparison with *Multiplicisphaeridium pachymurum* sp. nov. from the Llandovery and Wenlock of Shropshire, Great Britain. *Palynology*, **2**, 181-185, 1 pl.

--------- & DORNING, K, J. 1984. The Llandovery Series of the type area. Appendix I. Acritarchs. In: COCKS, L. R. M., WOODCOCK, N. H., RICKARDS, R. B., TEMPLE, J. T. & LANE, P. D. The Llandovery Series of the type area. *Bulletin of the British Museum of Natural History (Geology)*, **38**, (3), 174-176.

--------- & MOLYNEUX, S. G. 1988. Biostratigraphy, palynofacies and provincialism of Late Ordovician - Early Silurian acritarchs from northeast Libya. In: EL-ARNAUTI, A *et al.* (eds.). *Subsurface Palynostratigraphy of Northeast Libya*, 27-43, pls 5-7.

HOLLAND, C. H. 1980. Silurian series and stages: decisions concerning chronostratigraphy. *Lethaia*, **13**, 238.

HOLLAND, C. H. & BASSETT, M. G. 1989. (eds.). A Global Standard for the Silurian System. 325. National Museum of Wales, Geological Series No. 9, Cardiff.

--------- LAWSON, J. D. & WALMSLEY, V. G. 1963. The Silurian rocks of the Ludlow District, Shropshire. *Bulletin of the British Museum (Natural History)*, **8**, (3), 95-171, 7 pls.

--------- RICKARDS, R. B. & WARREN, P. T. 1969. The Wenlock graptolites of the Ludlow District, Shropshire, and their stratigraphical significance. *Palaeontology*, **12**, (4), 663-683, pl. 1.

--------- LAWSON, J. D., WALMSLEY, V. G. & WHITE, D. E. 1980. Ludlow stages. *Lethaia*, **13**, 268.

HU YUNXU. 1986. Micropalaeoflora from the Early Ordovician in Gaoqiao Region of Shaanxi and its stratigraphic significance. Bulletin of the Xian institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, **14**, 199-239, pls 1-20. (Chinese with English summary).

JABLONSKI, D. 1986. Causes and consequences of mass extinctions: A comparative approach. In: ELLIOTT, D. K. (ed.). *Dynamics of Extinction*, 183-229.

JACOBSON, S. R. & ACHAB, A. 1985. Acritarch biostratigraphy of the *Dicellograptus complanatus* graptolite Zone from the Vaureal Formation (Ashgillian), Anticosti Island, Quebec, Canada. *Palynology*, **9**, 165-198, pls 1-9.

JARDINÉ, S. & YAPAUDJIAN, L. 1968. Lithostratigraphie et palynologie du Dévonien - Gothlandien Gréseux du Bassin de Polignac (Sahara). *Revue de l'Institut français du pétrole*, **43**, (4), 439-468, pls 1-6.

--------- & COMBAZ, A., MAGLOIRE, L., PENIGUEL, G. & VACHEY, G. 1972. Acritarches du Silurien terminal et du Dévonien du Sahara Algérien. *Comptes rendus 7e Congrès international de stratigraphie et de géologie du Carbonifère, Krefeld, August 1971*, **1**, 295-311, pls 1-3.

--------- --------- --------- --------- --------- 1974. Distribution stratigraphique des Acritarches dans le Paléozoïque du Sahara Algérien. *Review of Palaeobotany and Palynology*, **18**, (1-2), 99-129, pls 1-3.

JEPPSSON, L. 1983. Silurian conodont faunas from Gotland. *Fossils and Strata*, **15**, 121-144.

--------- 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. *Journal of the Geological Society of London*, **147**, 663-674.

--------- ALDRIDGE, R. J. & DORNING, K. J. 1995. Wenlock (Silurian) oceanic episodes and events. *Journal of the Geological Society, London*, **152**, 487-498.

JOHNSON, M. E., KALJO, D. & RONG, J-Y. 1991. Silurian eustasy. In: BASSETT, M. G., LANE, P. D. & EDWARDS, D. (eds.). The Murchison symposium: Proceedings of an international conference on the Silurian System. *Special Papers in Palaeontology*, **44**, 145-163.

--------- & McKERROW, W. S. 1991. Sea level and faunal changes during the latest Llandovery and earliest Ludlow (Silurian). *Historical Biology*, **5** 153-169.

JUX, U. 1975. Phytoplankton aus dem mittleren Oberdevon (Nehden-Stufe) des Südwestlichen bergischen Landes (rheinisches Schiefergebirge). *Palaeontographica, Abt. B*, **149**, (5-6), p. 113-138, pls 1-6.

KEEGAN, J. B., RASUL, S. M. & SHAHEEN, Y. 1990. Palynostratigraphy of the Lower Palaeozoic, Cambrian to Silurian, sediments of the Hashemite Kingdom of Jordan. *Review of Palaeobotany and Palynology*, **66**, 167-180, pls 1-3.

KEMP, A. S. 1991. Mid Silurian pelagic and hemipelagic sedimentation and palaeoceanography, *Special Papers in Palaeontology*, **44**, 261-299, pls 1-3.

KIRYANOV, V. V. 1974. Novye akritarkhi iz kembriyskikh otlozheniy Volyni. *Paleontologicheskii Zhurnal, no. 2*, 117-129, pls 7-8. English translation: *Paleontological Journal*, **8**, 225-236.

--------- 1978. Akritarkhi siluria Volyno-Podolii. *Akademiya Nauk Ukrainskoi* SSR, *Institut Geologicheskikh Nauk, Kiev, Naukova Dumka*, pp. 116, pls 1-20. [In Russian].

KJELLSTRÖM, G. 1971. Ordovician microplankton (baltisphaerids) from the Grötlingo Borehole No. 1 in Gotland, Sweden. *Sveriges Geologiska Undersökning, ser. C, no. 655*, **65**, (1), 1-75, pls 1-4.

KRÍZ, J. 1989. The Pridoli Series in the Prague Basin (Barrandian area, Bohemia). In: HOLLAND, C. H. & BASSETT, M. G. (eds.). A Global Standard for the Silurian System, 90-100. National Museum of Wales, Geological Series No. 9, Cardiff.

LAPWORTH, C. 1880. On new British graptolites. *Ann. Mag. nat. hist. (Series 5)*, **5**, 149-178.

LAWSON, J. D. 1960. The succession of shelly faunas in the British Ludlovian. *C. r. 21st Int. Geol. Congr., Norden*, **7**, 114-125.

--------- 1973a. Facies and faunal changes in the Ludlovian rocks of Aymestry, Herefordshire. *Geological Journal*, **8**, (2), 247-278.

--------- 1973b. New exposures on forestry roads near Ludlow. *Geological Journal*, **8**, (2), 279-284.

--------- 1975. Ludlow benthonic assemblages. *Palaeontology*, **18**, (3), 509-525.

--------- & WHITE, D. E. 1989. Standard Ludlow Series. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). *A Global Standard for the Silurian System*, 73-90. National Museum of Wales, Geological Series No. 9, Cardiff.

LEFORT, J. P. & DEUNFF, J. 1974. Etude du socle antémésozïque de la partie septentrionale du golfe normano-breton. *Bulletin du B.R.G.M.* **4**, 73-83.

LEGAULT, J. A. 1973. Chitinozoa and Acritarcha of the Hamilton Formation (Middle Devonian), Southwestern Ontario. *Bulletin of the Geological Survey of Canada*, 221, 1-101.

LE HÉRISSÉ, A. 1984. Microplancton a paroi organique du Silurien de Gotland (Suede): Observations au microscope electronique de structures de desenkystement. *Review of Palaeobotany and Palynology*, **43**, 217-236, pls 1-3.

--------- 1989. Acritarches et kystes d'algues Prasinophycées du Silurien de Gotland, Suède. *Palaeontographica Italica*, **76**, 57-302, pls 1-30.

--------- & DEUNFF, J. 1988. Acritarches et Prasinophycées (Givétian supérieur - Frasnien moyen) de Ferques (Boulonnais, France). In: BRICE, D. (ed.). Le Dévonien de Ferques, Bas-Boulonnais (Nord de la France). *Biostratigraphie du Paléozoïque 7, Brest.*

LISTER, T. R. 1970. A monograph of the acritarchs and chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope areas, Shropshire. *Palaeontographical Society [Monograph]*: (1), 1-100, pls 1-13.

--------- & DOWNIE, C. 1967. New evidence for the age of a primitive echinoid *Myriastiches gigas*. *Palaeontology*, **10**, (2), 171-174, pl. 23.

--------- --------- 1974. The stratigraphic distribution of the acritarchs in the Ludlow succession at Ludlow. *Review of Palaeobotany and Palynology*, **18**, 25-27.

LOEBLICH, A. R. Jr. 1970. Morphology, ultrastructure and distribution of Paleozoic acritarchs. *Proceedings of the North American Paeontological Convention, Chicago, 1969, part G*, **2**, 705-788.

---------- & DRUGG, W. S. 1968. New acritarchs from the Early Devonian (Late Gedinnian) Haragan Formation of Oklahoma, USA. *Tulane Studies in Geology*, **6**, (4), 129-137, pls 1-4.

---------- & WICANDER, R. 1976. Organic-walled microplancton from the Lower Devonian, Late Gedinnian Haragan and Bois d'Arc Formations of Oklahoma, USA., Part 1. *Palaeontographica. Abt. B*, **159**, (1-3), 1-39, pls 1-12.

--------- & TAPPAN, H. 1978. Some Middle and Late Ordovician microphytoplankton from Central North America. *Journal of Paleontology*, **52**, (6), 1233-1287.

LUNDIN, R. F., PETERSEN, L. E. & SIVETER, DAVID J. 1991. Nonpalaeocope ostracod biostratigraphy of the type Wenlock Series, Silurian, of the Welsh Borderland. *Journal of Micropalaeontology*, **9**, (2), 173-189, pls 1-2.

LU LICHANG & WICANDER, R. 1988. Upper Devonian acritarchs and spores from the Hongguleleng Formation, Hefeng District in Xinjiang, China. *Revista Española de Micropaleontologia*, **20**, 109-148, pls 1-5.

MABILLARD, J. E & ALDRIDGE, R. J. 1985. Microfossil distribution across the base of the Wenlock Series in the type area. *Palaeontology*, **28**, (1), 89-100.

MÄDLER, K. A. 1963. III. Die figurierten organischen Bestondteile der Posidonienschefer. *Geologisches Jahrbuch Beihefte*, **58**, 287-406, pls 15-30.

MAGLORE, L. 1968. Étude stratigraphique, par la palynologie, des dépôts argilo-gréseux du silurien et du Dévonien inférieur, dans la région d Grande Erg Occidental (Sahara Algérien). *International Symposium on the Devonian System, Calgary, 1967*, **2**, 473-492.

MAHER, L. J. Jr. 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, **32**, 153-191.

MARTIN, F. 1966a. Les Acritarches du sondage de la brasserie Lust, à Kortrijk (Courtrai) (Silurien belge). *Bulletin de la Société belge de geologie, de paléontologie et d'hyrologie*, **74**, (2), 354-400, 1 pl.

--------- 1966b. Les Acritarches de Sart-Bernard (Ordovicien belge). *Bulletin de la Société belge de geologie, de paléontologie et d'hydrologie*, **74**, (2), 423-444.

--------- 1967. Les Acritarches du parc de Neuville-sous-Huy (Silurian belge). *Bulletin de la Société belge de Géologie, de Paléontologie et d'hydrologie*, **75**, (3), 306-35, pl. 1.

--------- 1969. Les Acritarches de l'Ordovicien et du Silurien Belges. Détermination et valeur stratigraphique. *Institut royal des sciences naturelles de Belgique, Mémoire no. 160*, 1-175, pls 1-8 (Cover date 1968, Issue date 1969).

--------- 1978. Sur quelques Acritarches Llandoveriens de Cellon (Alpes Carniques Centrales, Autriche). *Geologische Bundesanstalt, Verhandlungen*, **2**, 3-42, pls 1-2.

--------- 1981. Acritarches du Famennien inférieur a Villers-sur-Lesse (Belgique). *Intstitut royal des sciences naturalles de Belgique, sciences de la terre, Bulletin*, **52**, (2), 1-55, pls 1-6.

--------- 1989. Acritarchs. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). *A Global Standard for the Silurian System*, 207-215. National Museum of Wales, Geological Series No. 9, Cardiff.

--------- 1993. Acritarchs: A review. *Biological Reviews of the Cambridge Philosophical Society*, **68**, (4), 475-538, pls 1-3.

MARTINEZ-MACCHIAVELLO, J. C. 1968. Quelques Acritarches d'un échantillan du Dévonien inférieur (Cordobés) de Blanquillo, Départment de Durazno, Uraguay. *Revue de Micropaléontologie*, **11**, (2), 77-84, pl. 1.

MATTHEWS, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16**, (4), 713-719.

McKERROW, W. S. 1979. Ordovician and Silurian changes in sea level. *Journal of the Geological Society, London*, **136**, 137-145.

MILLER, C. G. 1995. Ostracode and conodont distribution across the Ludlow/Prídolí boundary of Wales and the Welsh Borderland. *Palaeontology*, **38**, (2), 341-384.

MILLER, M. A. & EAMES, L. E. 1982. Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, USA. *Palynology*, **6**, 221-254, pls 1-6.

MOCZYDLOWSKA, M. 1991. Acritarch biostratigraphy of the Lower Cambrian and the Precambrian-Cambrian boundary in southeastern Poland. *Fossils and Strata*, **29**, 1-127.

--------- & VIDAL, G. 1988. Early Cambrian acritarchs from Scandinavia and Poland. *Palynology*, **12**, 1-10, pls 1-2.

MOLDOWAN, M. J., DAHL, J., JACOBSON, S. R., HUIZINGA, B. J., FAGO, F. J., WATT, D. S. & PETERS, K. E. 1996. Chemostratigraphic reconstruction of biofacies: Molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology*, **24**, (2), 159-162.

MOREAU-BENOÎT, A. 1974. Recherches de Palynologie et de Planctologie. Sur le Dévonien et quelques formations siluriennes dans le Sud-Est du Massif Armoricain. *Mémoires de la société géologique et mineralogique de Bretagne*, **no. 18**, p. 1-248, pls 1-15.

--------- & PONCET, J. 1982. Les Schistes et Calcaires éodévoniens de Néhou dans la coupe de Barnville (nord-est du Massif Armoricain). Sédimentologie, palynologie, planctologie, stratigraphie. *Bulletin du Bureau de Recherches Géologiques et Minières, section 1*, (1-2), 81-114, pls 1-5.

NEWTON, E. T. 1875. On 'Tasmanite' and Australian 'white coal'. *Geological Magazine*, **12**, (8), 337-342, pl. 10.

PARIS, F. 1981. Les Chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe (Cadre géologique-Étude systématique-Biostratigraphie). *Mémoires de la Société Géologique et Minéralogique de Bretagne*, **26**, 1-412.

--------- & DEUNFF, J. 1970. Le paleoplancton Llanvirinien de la Roche-au-Merle (Commone de Vieux-Vy-sur-Couesnon, Ille-et-Vilaine). *Bulletin de la Société géologique et mineralogique de Bretagne, sér. C*, **2**, (1), 25-43, pls 1-3.

PARKE, M., BOALCH, G. T., JOWELT, R. & HARBOUR, D. S. 1978. The genus *Pterosperma* (Prasinophyceae) species with a single equatorial ala. *Journal of the Marine Biological Association*. **58**, 239-276, pls

PECK, R. 1974. A comparison of four absolute pollen preparation techniques. *New Phytologist*, **73**, 567-587.

PIROZYNSKI, K. A. 1976. Fungal spores in fossil record. *Palaeopalynology*, **4**, *Biol. Mem.* 1 (1/2): 104-120.

PISKUN, L. V. 1974. Paleontologicheskaya kharakteristika siluriiskikh otlozhenii Brestskoi vpadiny. In: Microfossilii SSSR (Microfosiils of the USSR). *Academy of sciences of USSR, Siberian Branch, Transactions of the Institute of Geology and Geophysics, Novosibirsk*, **81**, 30-36. [In Russian.]

PLAYFORD, G. 1977. Lower to Middle Devonian acritarchs from the Moose River Basin, Ontario. *Geological Survey of Canada, Bulletin*, **279**, 1-87, pls 1-20.

---------- & DRING, R. S. 1981. Late Devonian acritarchs from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology*, **no. 27**, p. 1-78, pl. 1-19.

PÖTHÉ DE BALDIS, E. D. 1971. Microplancton del Silurico superior de la Provincia de Santiago del Estero, Republica Argentina. *Ameghiniana*, **8**, (3-4), 282-290.

--------- 1974a. Microplancton adicional del Silurico superior de Santiago del Estero, Republica Argentina. *Revista de la Asiciación Paleontológica Argentina*, **11**, (4), 313-327, pls 1-4.

---------- 1974b. El microplancton del Devonico medio de Paraguay. *Revista Española de Micropaleontologia*, **6**, (3), 367-79. pls 1-3.

---------- 1975. Microplancton del Wenlockiano de la Precordillera Argentina. *Revista Española de Micropaleontología*, 7, (3), 489-505. pls 1-5.

---------- 1981. Paleomicroplanton y mioesporas del Ludloviano inferior de la Formacion Los Espejos en el perfil los azulejitos en la Provincia de San Juan, Republica Argentina. *Revista Española de Micropaleontología*, **13**, (2), 231-265, pls 1-8.

PRIEWALDER, H. 1987. Acritarchen aus dem Silur des Cellon-Profils (Karnische Alpen, Österreich). *Abhandlungen der Geologischen Bundesanstalt*, **40**, 1-121, pls 1-24.

RAUSCHER, R. 1973. Recherches micropaléontologiques et stratigraphiques dans l'Ordovicien et le Silurian en France. Étude des acritarches, des chitinozoaires et des spores. *Sciences Géologiques, Université Louis Pasteur de Strasbourg, Institut de géologie, Mémoire 38*, 1-224, pls 1-12.

--------- & ROBARDET, M. 1975. Les microfossiles (Acritarches, Chitinozoaires et spores) des couches de passage du Silurien au Dévonien dans le Cotentin (Normandie). *Annales de la Société Géologique du Nord*, XCV, 2, 81-92, pls 9-11.

RICHARDSON, J. B. 1984. Mid-Palaeozoic palynology, facies and correlation. *Proceedings of the 27th International Geological Congress*, **1**, 341-365.

--------- & IOANNIDES, N. 1973. Silurian palynomorphs from the Tanezzuft and Acacus Formations, Tripolitania, North Africa. *Micropalaeontology*, **19**, (3), 257-307, pls 1-13.

--------- & LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201-252, pls 37-43.

---------- & MCGREGOR, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Bulletin of the Geological Survey of Canada*, **364**, 1-79, pls 1-21.

--------- & RASUL, S. M. 1990. Palynofacies in a late Silurian regressive sequence in the Welsh Borderland and Wales. *Journal of the Geological Society of London*, **147**, 675-686.

RICKARDS, R. B. 1976. The sequence of Silurian graptolite zones in the British Isles. *Geological Journal*, **11**, 153-188.

--------- 1989. Exploitation of graptoloid cladogenesis in Silurian Stratigraphy. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). *A Global Standard for the Silurian System*, 267-274. National Museum of Wales, Geological Series No. 9, Cardiff.

--------- 1995. Utility and precision of Silurian graptolite biozones. *Lethaia*, **28**, 129-137.

RUBINSTEIN, C. V. 1993. Acritarchs from the upper Silurian of San Juan, Argentina: biostratigraphy and palaeobiogeography. *Special Papers in Palaeontology, No. 48*, 67-78, 1 pl.

SARJEANT, W. A. S. 1961. Microplankton from the Kellaways Rock and Oxford Clay of Yorkshire. *Palaeontology*, **4**, (1), 90-118, pls 13-15.

--------- 1976. English Jurassic dinoflagellate cysts and acritarchs: a re-examination of some type and figured specimens. *Geoscience and Man*, 15, 1-24, pls 1-7.

--------- 1984. A restudy of some dinoflagellate cyst holotypes in the University of Keil Collections. V. The Danian (Palaeocene) holotypes of Walter Wetzel (1952, 1955). *Meyniana*, **36**, 121-171, pls 1-8.

--------- & STANCLIFFE, R. P. W. 1994. The *Micrhystridium* and *Veryhachium* complexes (Acritarcha: Acanthomorphitae and Polygonomorphitae): a taxonomic reconsideration. *Micropaleontology*, **40**, (1), 1-77, pl. 1.

SCHAARSCHMIDT, F. 1963. Sporen und Hystrichospaerideen aus dem Zechstein von Büdingen in der Waterau. *Palaeontogrphica Abt. B*, **113**, (1-4), 38-91, pls 11-20.

SCHULTZ, G. 1967. Mikrofossilien des oberen Llandovery von Dalarne (Schweden). *Kölner Geologische Hefte*, **13**, p. 175-187, pl. 1.

SHERGOLD, J. H. & BASSETT, M. G. 1970. Facies and faunas at the Wenlock/Ludlow boundary of Wenlock Edge, Shropshire. *Lethaia*, **3**, (2), 113-142.

--------- & SHIRLEY, J. 1968. The faunal stratigraphy of the Ludlovian rocks between Craven Arms and Bourton, near Much Wenlock, Shropshire. *Geological Journal*, **6**, (1), 119-138.

SHESHAGOVA, L. I. 1984. Akritarkhi silura severa Sibirskoi platformy. *Izdatestvo Nauka, Sibirskoe Otdelenie, Novosibirsk*, 1-172, 24 pls.

SIVETER, DAVID J. 1978. The Silurian. In: BATE, R & ROBINSON, E. (eds.). A stratigraphic index of British Ostracoda. *Geological Journal Special Issue*, **8**, 57-100.

---------- 1980. British Silurian Beyrichiacea (Ostracoda). *Palaeontographical Society Monographs*, (1), 1-76, pls 1-27.

--------- 1984. Habits and mode of life of Silurian ostracodes. In: BASSETT, M. G. & LAWSON, J. D. (eds.). Autecology of Silurian organisms. *Special papers in Palaeontology*, **32**, 71-85, 2 pls.

--------- 1989. Ostracodes. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). A Global Standard for the Silurian System. *A Global Standard for the Silurian System*, 252-264. National Museum of Wales, Geological Series No. 9, Cardiff.

---------- OWENS, R. M & THOMAS, A. T. 1989. Silurian Field Excursions. *A geotraverse across Wales and the Welsh Borderland.* National Museum of Wales, Geological Series No. 10, Cardiff. 1-133, pls 1-3.

SMELROR, M. 1987. Early Silurian acritarchs and Prasinophycean algae from the Ringerike District, Oslo Region (Norway). *Review of Palaeobotany and Palynology*, **52**, 137-159, pls 1-5.

SOPER, N. J. & WOODCOCK, N. H. 1990. Silurian collision and sediment dispersal patterns in southern Britain. *Geological Magazine*, **127**, (6), 527-542.

STANCLIFFE & SARJEANT, W. A. S. 1994. The acritarch genus *Veryhachium* Deunff 1954, emend. Sarjeant and Stancliffe 1994: a taxonomic restudy and a reassessment of its constituent species. *Micropaleontology*, **40**, (3), 223-241.

STAPLIN, F. L. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, **4**, (3), 392-424, pls 48-51.

---------- JANSONIUS, J. & POCOCK, S. A. J. 1965. Evaluation of some Acritarchous Hystrichosphere Genera. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **123**, (2), 167-201, pls 18-20.

STOCKMANS, F. W. & WILLIÈRE, Y. 1960. Hystrichospères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). *Senckenbergiana Lethaea*, **41**, (1-6), 1-11, pls 1-2.

---------- ---------- 1962a. Hystrichosphères du Dévonien belge (Sondage de l'Asile d'aliénés à Tournai). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **71**, (1), 41-77, pls 1-2.

--------- --------- 1962b. Description de trois Hystrichosphères trouvés dans les schistes de l'horizon marin de petit buisson. In: LECKWIJK, W. P. & CHESAUX, C. H. (eds.). Étude de l'Horizon Marin de Petit Buisson dans la Partie Occidentale du Massif du Borinage. In: *Observations sur la Paléontologie, la Lithologie et la Stratigraphie du Westphalien B et C dans la Partie Occidentale du Massif du Borinage (District du Couchant de Mons).* Centre national de géologie houillère (Belgium), No. 5, 11-30.

--------- --------- 1963. Les Hystrichosphères ou mieux les Acritarches du Silurien Belge. Sondage de la Brasserie Lust à Courtrai (Kortrijk). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **71**, (3), 450-81, pls 1-3.

--------- --------- 1966. Les Acritarches du Dinantien du sondage de Vieux Leuze à Leuze (Hainaut, Belgique). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **75**, (2), 233-242.

--------- --------- 1969. Acritarches du Famannien Inférieur. *Académie royale de Belgique, memoires de la classe des sciences*, **38**, (6), p. 1-63, pls 1-3.

--------- --------- 1974. Acritarches de la «Tranchée de Senzeille» (Frasnian supérieur et Famannien inférieur). *Académie royale de Belgique, memoires de la classe des sciences*, **41**, p. 1-79, pls 1-4.

STOCKMARR, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, **13**, 616-621.

--------- 1973. Determination of spore concentration with an electronic particle counter. *Geological Society of Denmark, Yearbook, 1972*, 87-89.

SUTHERLAND, S. J. E. 1994. Ludlow chitinozoans from the type area and adjacent regions. *Palaeontological Society Monograph, London*, **148**, 1-104.

--------- & DORNING, K. J. 1994. Ludlow chitinozoan biozonation of the Welsh Basin. *Contributions to the CIMP conference on palynology, palaeoenvironments and stratigraphy 6-10 September, 1994, University of Sheffield.* p. 13-14.

SWAN, A. & SANDILANDS. M. H. 1995. *Introduction to Geological data analysis.* Blackwell Science.

SWIRE, P. H. 1993. The palynology of the lower Wenlock of the Wenlock type area, Shropshire, England. *Special Papers in Palaeontology, No. 48*, 97-109, 1 pl.

TAPPAN , H. 1980. *Palaeobiology of plant protists.* Freeman, 1-1028, San Francisco.

--------- LOEBLICH, A. R. Jr. 1971. Surface sculpture of the wall in Lower Paleozoic acritarchs. *Micropalaeontology*, **17**, (4), 385-410, pls 1-11.

THUSU, B. 1973a. Acritarchs from the Middle Silurian Rochester Formation of Southern Ontario. *Palaeontology*, **16**, (4), 799-826, pls 104-106.

--------- 1973b. Acritarchs provenant de l'Ilion Shale (Wenlockien) Utica, New York. *Micropaléontologie*, **16**, (2), 137-146, pls 1-2.

TIMOFEEV, B. V. 1959. Drevneishaya flora Pribaltiki i ee stratigraficheskoe znachenie. *Vsesoyuznyi Neftyanoi Nauchno-Issledovatelskii Geologorazvedochnyi Institut, Leningrad (VNIGRI), Trudy*, No. 129. pp. 136, pls 1-24.

---------- 1962. Teodolitnyi paleontologicheskii stolik (novyi metod issledovaniya iskopaemogo mikroplanktona) obshchie zamechaniya. *Vsesoyuznyi Neftyanoi Nauchno-Issledovatelskii Geologorazvedochnyi Institut, Leningrad (VNIGRI),Trudy*, No. 196, 601-47, pls 1-20.

--------- 1969. Sferomorfidy proterozoya. *Akademiya Nauk SSSR, Leningradskoe Otdelenie Izdatelstva Nauka, Leningrad*, 1-145, pls 1-39.

TURNER, N., SPINNER, E. & DORNING, K. J. 1995. A palynological study of the Lower Carboniferous Lydebrook Sandstone and adjacent late Wenlock and Langsettian strata, Shropshire, England. *Review of Palaeobotany and Palynology*, **84**, 305-329, pls 1-5

TURNER, R. E. 1984. Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England. *Palaeontographica, Abt. B*, **190**, (4-6), 87-157, pls 1-14.

TRAVERSE, A. 1978. Supplementary palynological information from site reports for DSDP leg 42B. 3. Site 379. In: ROSS, D. A., NEPROCHNOV, Y. P. *et al.* (eds). *Initial Reports of the Deep Sea Drilling Project*, **42,** (2), p. 41.

UTTING, J. 1987. Palynology of the Lower Carboniferous Windsor Group and Windsor - Canso boundary beds of Nova Scotia, and their equivalents in Quebec, New Brunswick and Newfoundland. *Bulletin of the Geological Survey of Canada*, **374** p. 1-93, pls 1-6.

VALENSI, L. 1947. Note preliminaire à une étude des microfossiles des silex jurassiques de la région de Poitiers. *Comptes rendu des séances de l'Académie des sciences, Paris*, **225**, 816-8.

VAVRDOVÁ, M. 1965. Ordovician acritarchs from central Bohemia. *Vestnik Ustredniho Ustavu Geologickeho*, **40**, (5), 351-357, pls 1-4.

--------- 1966. Palaeozoic microplankton from central Bohemia. *Casopis pro Mineralogii a Geologii*, **11**, (4), 409-414, pls 1-3.

--------- 1972. Acritarchs from Klabava Shales (Arenig). *Vestnik Ustredniho Ustavu Geologickeho,* **47**, 79-86, 2 pls.

VANGUESTAINE, M. 1979. Remaniements d'Acritarches dans le siegenien et l'Emsien (Devonien inferiur) du Synclinorium de Dinant (Belgique). *Annales de la Société Géologique de Belgique*, **101**, 243-267, pls 1-4. (cover date 1978, issue date 1979).

VERNIERS, J., NESTOR, V., PARIS, F., DUFKA, P., SUTHERLAND, S. & VAN GROOTEL, G. 1995. A global Chitinozoa biozonation for the Silurian. *Geological Magazine*, **132**, (6), 651-666, 2 pls.

VOLKOVA, N. A., KIRYANOV, V. V., PISKUN, L. V., PASKEVICIENE, L. T. & YANKAUSKAS, T. V. 1979. Rastitelnye mikrofossilii. In: VOLKOVA, N. A. *et al.*

Paleontologiya verkhnedokembriiskikh i kembriiskikh otlozhenii vostochno-Evropeiskoi platformy. *Akademiya Nauk SSSR, Ordena Trudovogo Krasnogo Znameni Geologicheskii Institut, Izdatelstvo Nauka, Moskova.* 4-38.

WALL, D. 1965. Microplankton, pollen, and spores from the Lower Jurassic in Britain. *Micropaleontology*, **11**, 151-190.

--------- & DOWNIE, C. 1963. Permian hystrichospheres from Britain. *Palaeontology*, **5**, (4), 770-784, pls 112-114.

WALLISER, O. H. 1962. Conodontenchronologie des Silurs (= Gotlandiums) und des tieferen Devons mit besanderer Berücksichtigung der Formations Grenze. *Symposium Silur/Devon - Grenze, Bonn-Bruxelles (1960)*, 281-287.

---------- 1964. Conodonten des Silurs. *Abh. hess. Landesamit. Bodenforsh. Wiesbaden*, **41**, 1-106, pls 1-32.

--------- 1971. Conodont biostratigraphy of the Silurian of Europe. In: SWEET, W. C. & BERGSTRÖM, S. M. (eds.). Symposium on conodont biostratigraphy. *Memoire of the Geological Society of America*, **127**, 195-206.

WATKINS, R. 1979. Benthic community organisation in the Ludlow Series of the Welsh Borderland. *Bulletin of the British Museum of Natural History (Geology)*, **31**, 175-280.

WELLMAN, C. H. & RICHARDSON, J. B. 1993. Terrestrial plant microfossils from the Silurian inliers of the Midland Valley of Scotland. *Palaeontology*, **36**, 155-193.

WETZEL, O. 1933a. Die in organischer Substanz erhaltenen Mikrofossilien des baltischen Kreide-Feuersteins mit einem sediment-petrographischen und stratigraphischen Anhang. *Palaeontographica*, Abt. A, **77**, 141-188.

1933. Die in organischer Substanz erhaltenen Mikrofossilien des baltischen Kreide-Feuersteins mit einem sediment-petrographischen und stratigraphischen Anhang. *Palaeontographica*, Abt. A, **78**, 1-110, pls 1-7.

WETZEL, W. 1952. Beitrag zur Kenntnis des dan-zeitlichen Meeres-planktons. *Geologisches Jahrbuch, Hannover*, **66**, 391-419, pl. A.

WHITAKER, J. H. McD. 1962. The Geology of the area around Leintwardine, Herefordshire. *Quarterly Journal of the Geological Society, London*, **118**, 319-351, 14 pls.

--------- 1994. Silurian basin slope sedimentation and mass movement in the Wigmore Rolls area, central Welsh Borderland. *Journal of the Geological Society, London*, **151**, 27-40.

WHITE, D. E. 1974. The boundary between the Wenlock and Ludlow series. *Geological Magazine*, **111**, 448-449.

--------- 1981. The base of the Ludlow Series in the graptolitic facies. *Geological Magazine*, **118**, 566.

--------- & LAWSON, J. D. 1978. The stratigraphy of new sections in the Ludlow Series of the type area, Ludlow, Salop, England. *Reports of the Institute of Geological Sciences*, **78/30**, 1-10.

--------- --------- 1989. The Pridoli Series in the Welsh Borderland and south-central Wales. In: HOLLAND, C. H. & BASSETT, M. G. (eds.). A Global Standard for the Silurian System, 131-141. National Museum of Wales, Geological Series No. 9, Cardiff.

WHITE, J. M. 1989. Methodology of the exotic spike: differential settling of palynomorphs during sample preparation. *Pollen et Spores*, **30**, (1), 131-148.

WICANDER, E. R. 1974. Upper Devonian-Lower Mississippian acritarchs and prasinophycean algae from Ohio, U.S.A. *Palaeontographica, Abt. B*, **148**, (1-3), 9-43, pls 5-19.

---------- 1983. A catolog and biostratigraphic distribution of North American Devonian acritarchs. *American Association of Stratigraphic Palynologists, Contribution Series*, No. 10, 1-133.

--------- 1986. Lower Devonian (Gedinnian) acritarchs from the Haragan Formation, Oklahoma, USA. *Review of Palaeobotany and Palynology*, **47**, 327-365.

---------- & WOOD, G. D. 1981. Systematics and biostratigraphy of the organic-walled microphytoplankton from the Middle Devonian (Givetian) Silica Formation, Ohio, U.S.A. *American Association of Stratigraphic Palynologists, Contribution Series*, no. 8, 1-137, pls 1-17.

--------- & WRIGHT, R. P. 1983. Organic walled microphytoplancton abundance and stratigraphic distribution from the Middle Devonian Columbus and Delaware Limestones of the Hamilton Quarry, Marion County, Ohio. *Ohio Journal of Science*, **83**, (1), 2-13.

WOOD, E. M. R. 1900. The Lower Ludlow Formation and its graptolite-fauna. *Quarterly Journal of the Geological Society, London*, **56**, 415-492.

WOODCOCK, N. H. 1984. Early Palaeozoic sedimentation and tectonics in Wales. *Proceedings of the Geological Association of London*, **95**, (4), 323-335.

--------- 1990. Sequence stratigraphy of the Palaeozoic Welsh Basin. *Journal of the Geological Society, London*, **147**, 537-547.

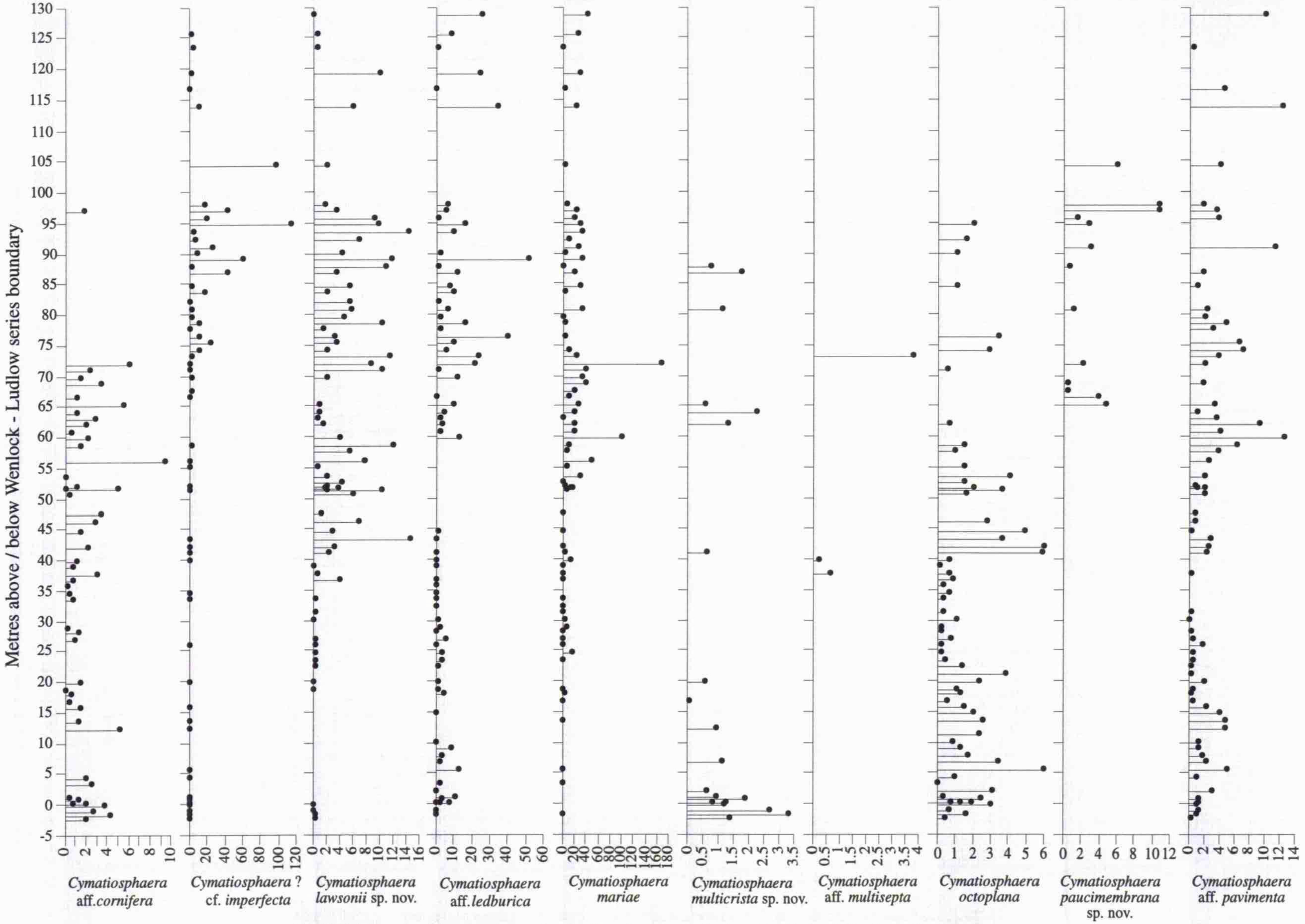
--------- & GIBBONS, W. 1988. Is the Welsh Borderland Fault System a terrane boundary? *Journal of the Geological Society, London*, **145**, 915-923.

YANKAUSKAS, T. V & VAITEKUNENE, G. K. 1972. Akritarkhi iz silura Pribaltiki. *Paleontologicheskii Zhurnal*, **no. 2**, p. 113-121, pl. 7.

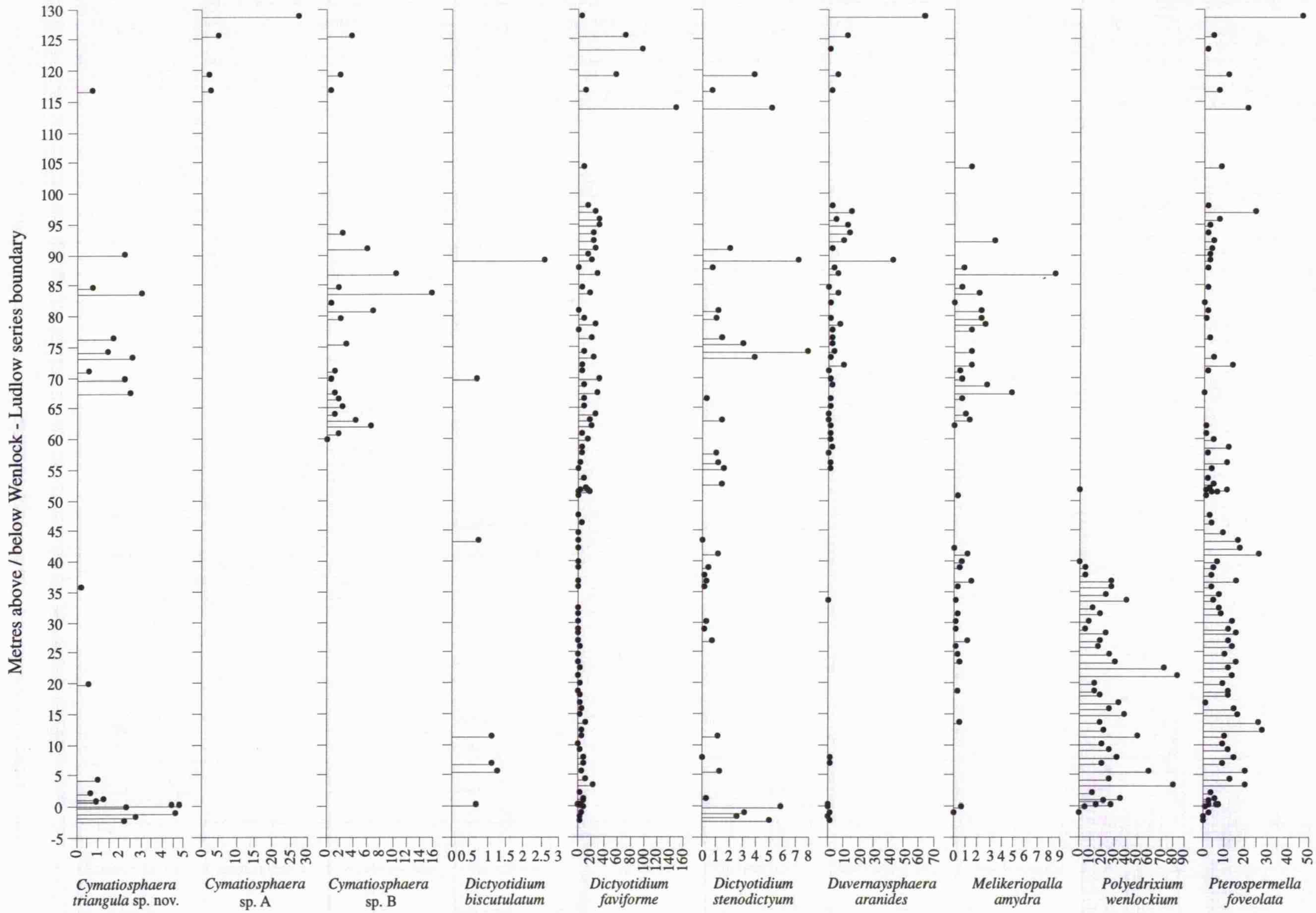
ZIEGLER, A. M., COCKS, L. R. M. & MCKERROW, W. S. 1968. The Llandovery transgression of the Welsh Borderland. *Palaeontology*, **11**, 736-782.

APPENDIX 1

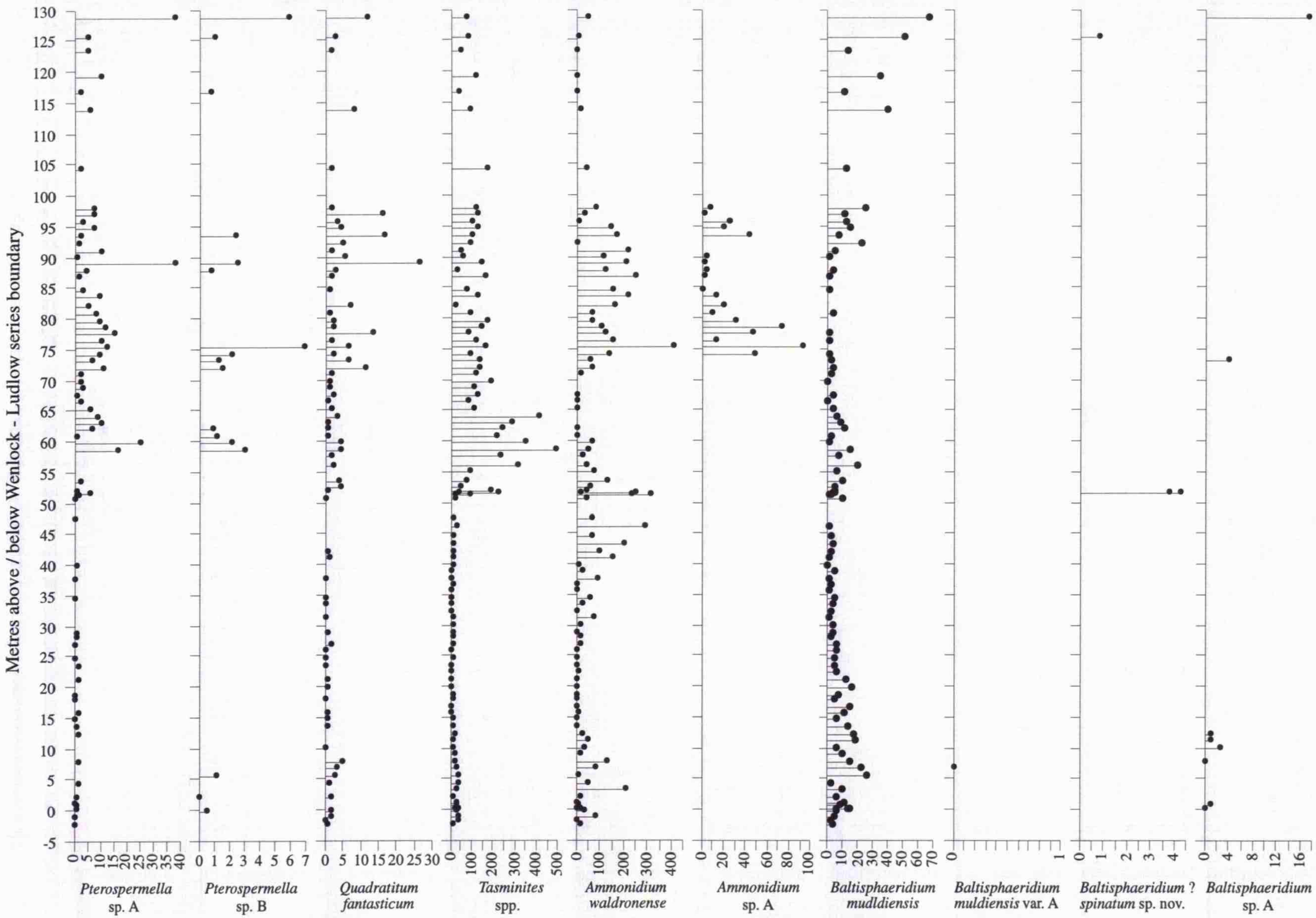
ABSOLUTE ABUNDANCE OF ACRITARCHS AND
PRASINOPHYTE ALGAE, GOGGIN ROAD, MORTIMER FOREST, LUDLOW.



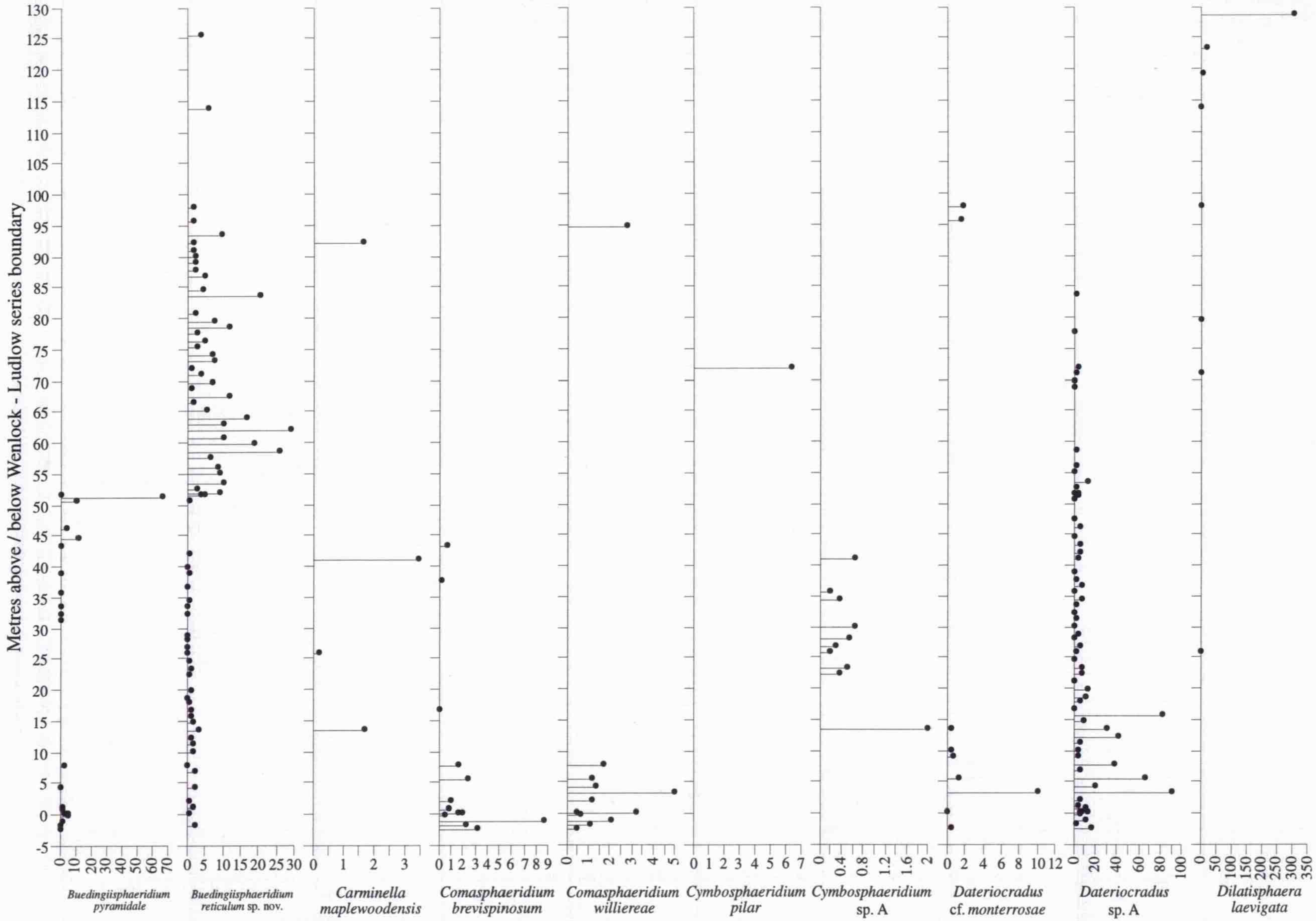
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



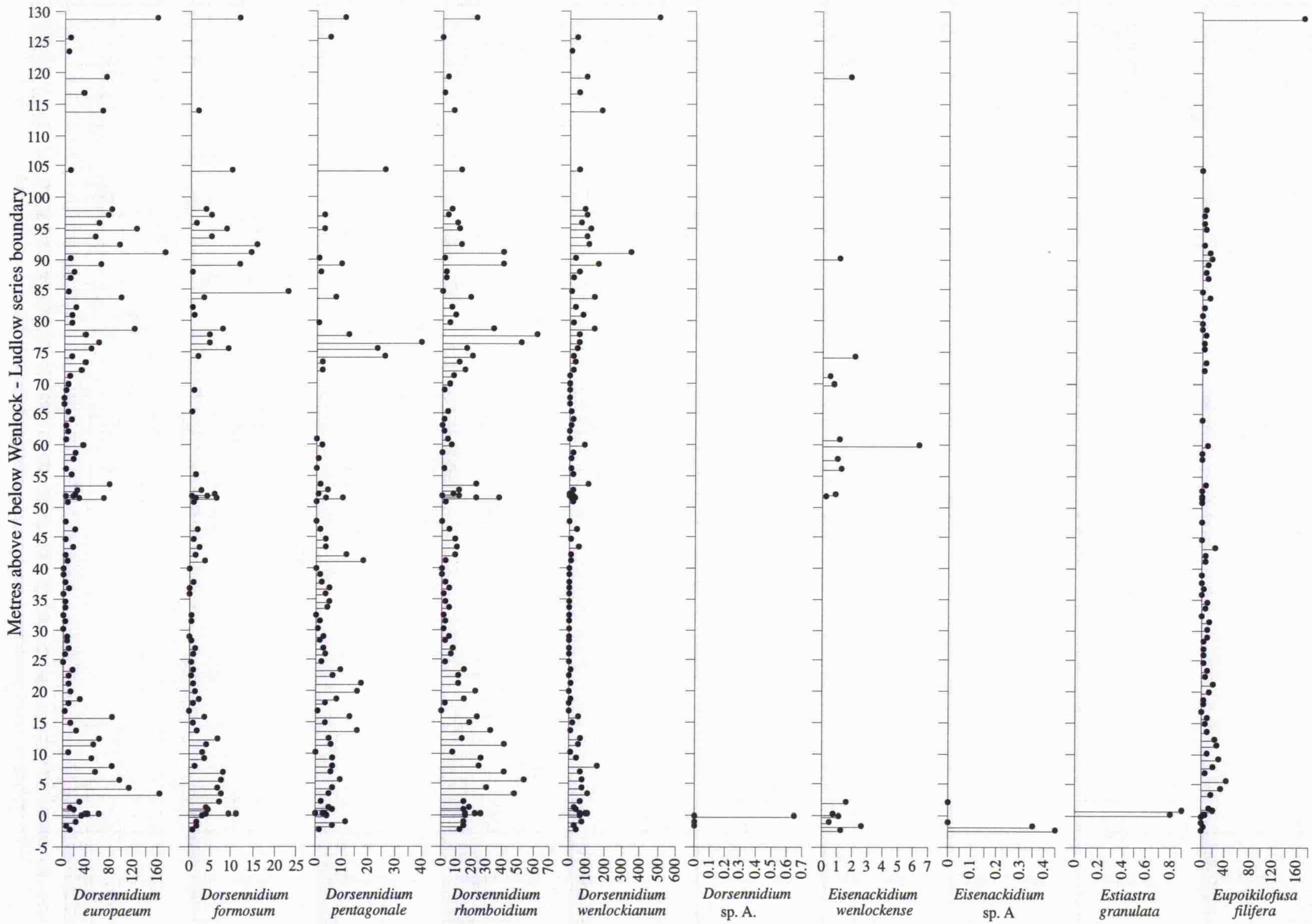
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



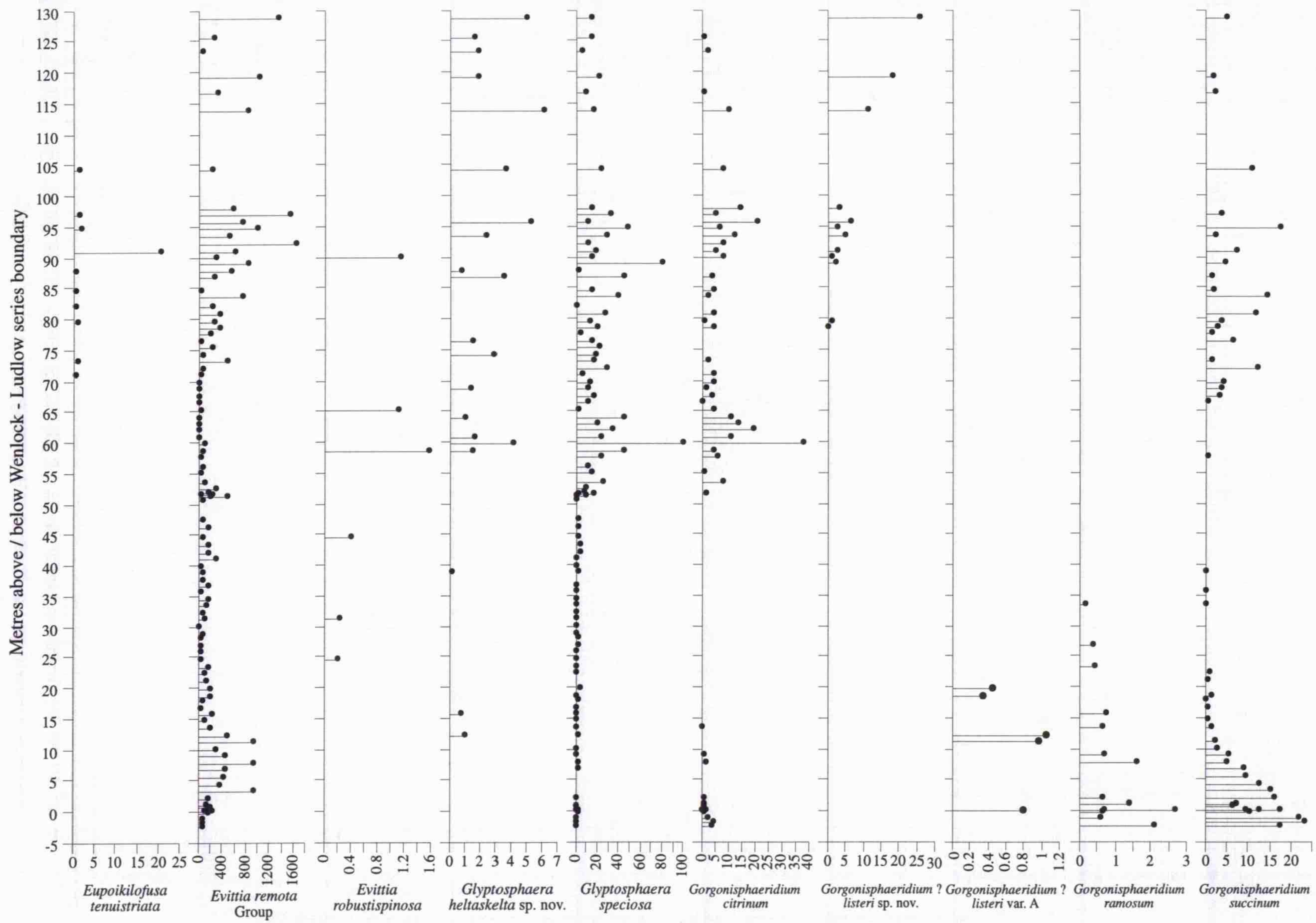
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



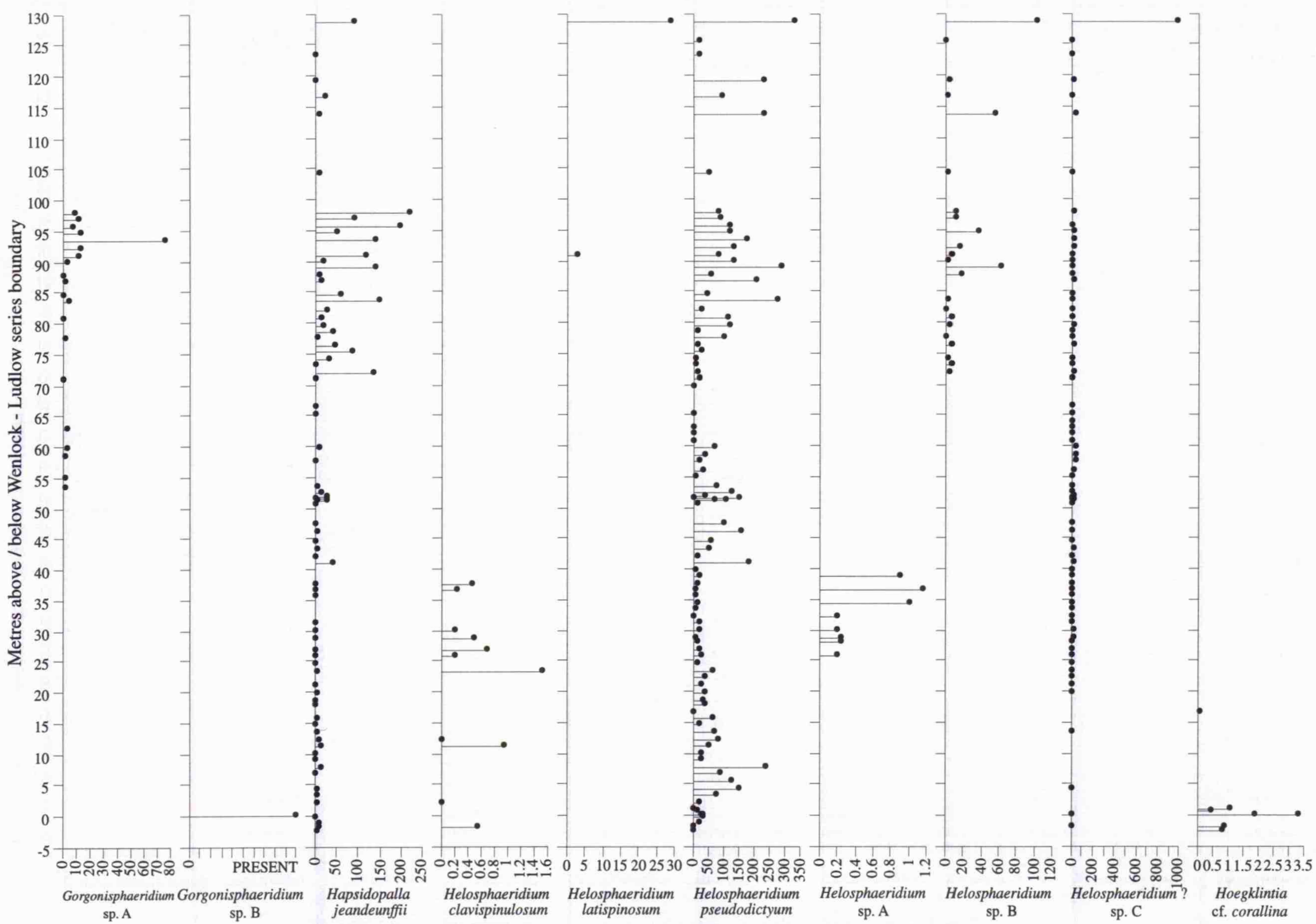
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



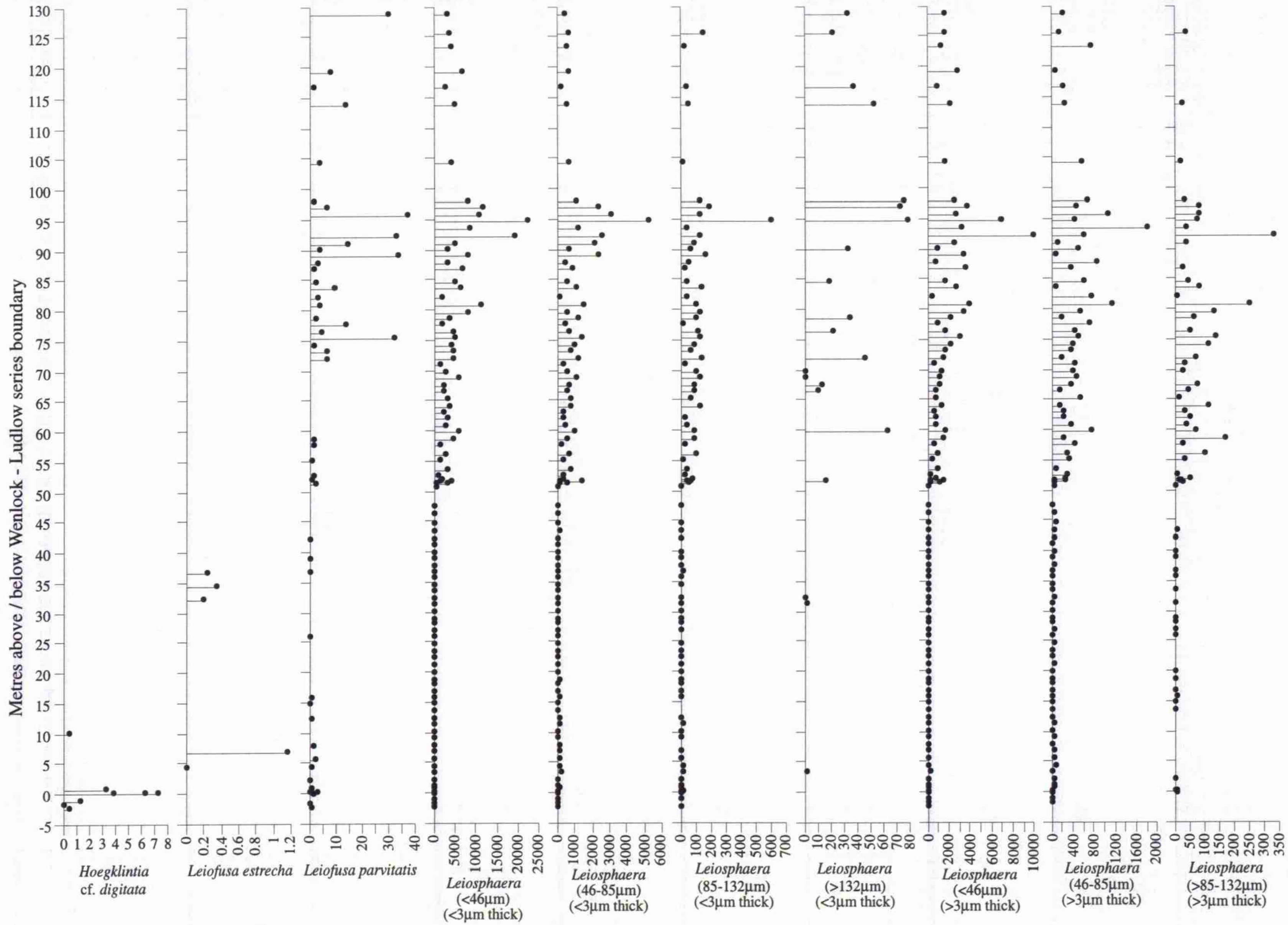
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



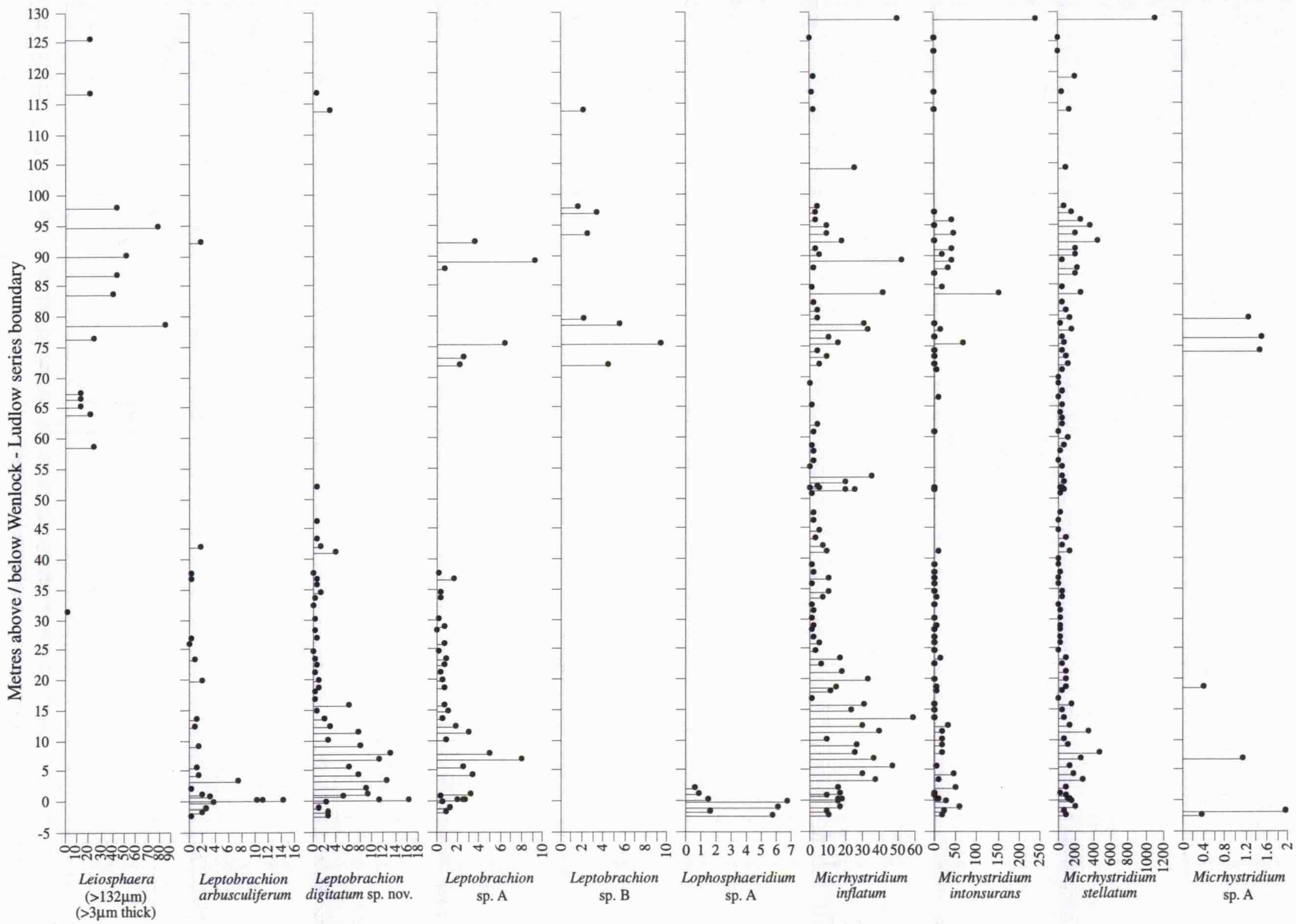
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



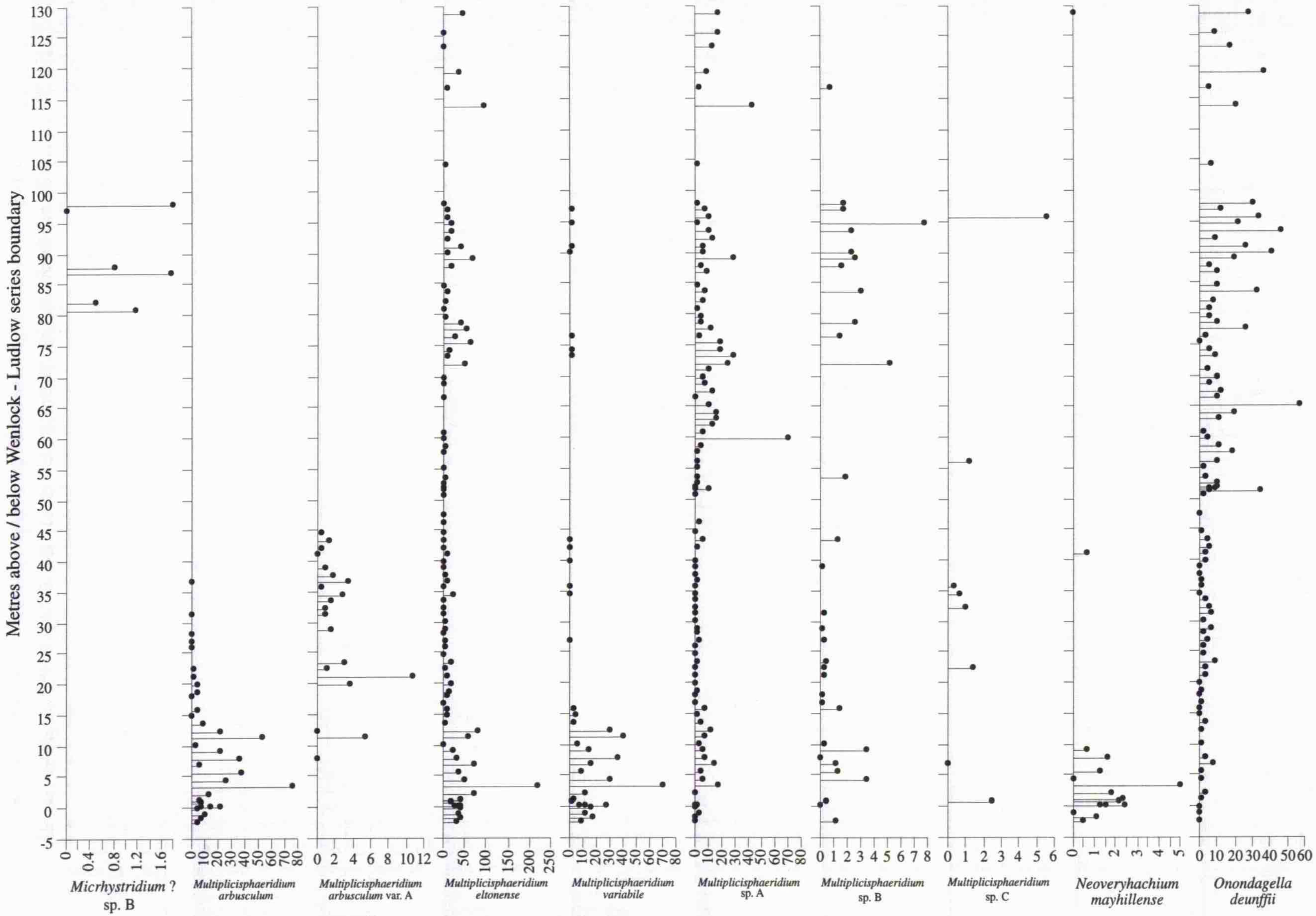
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



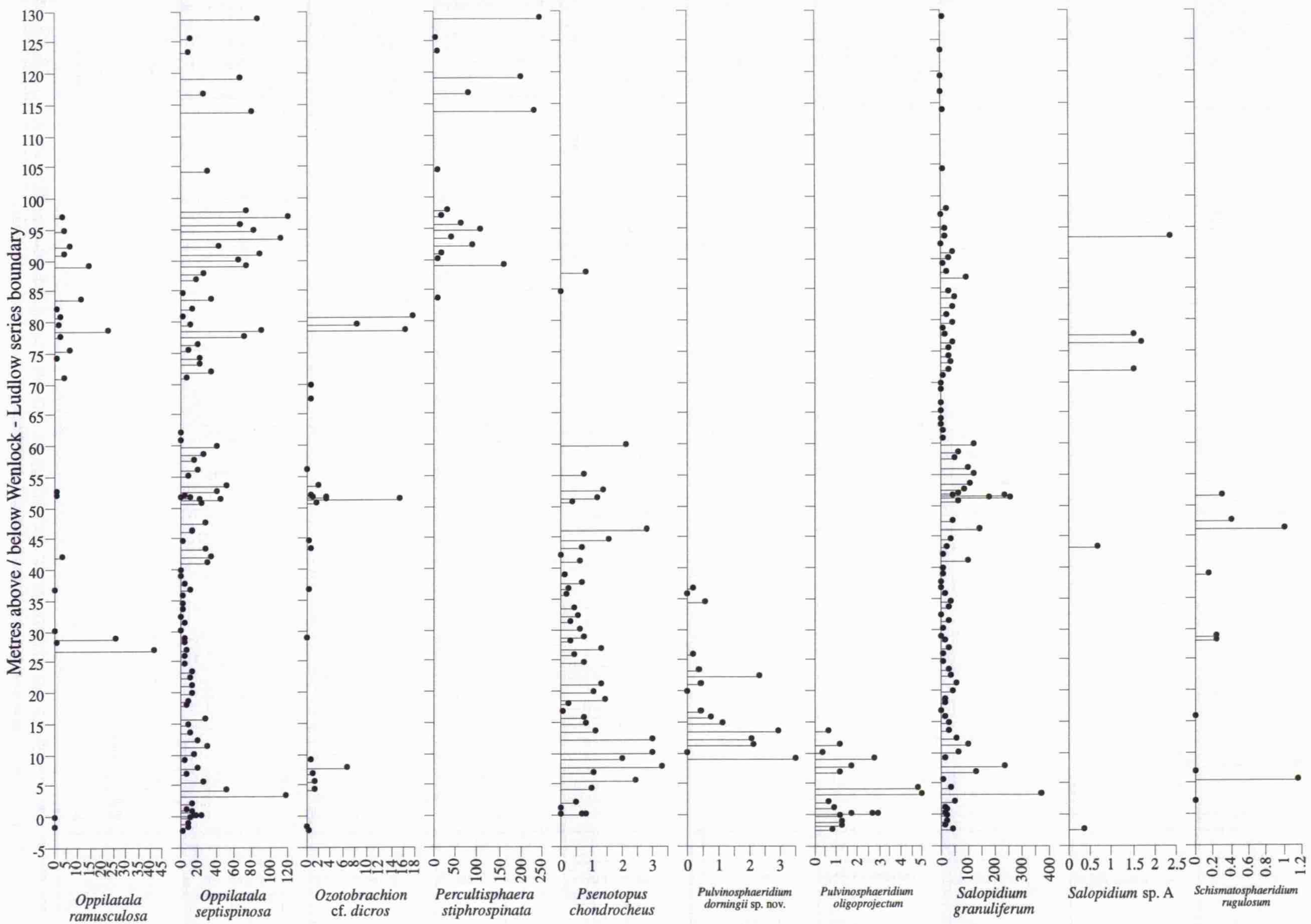
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



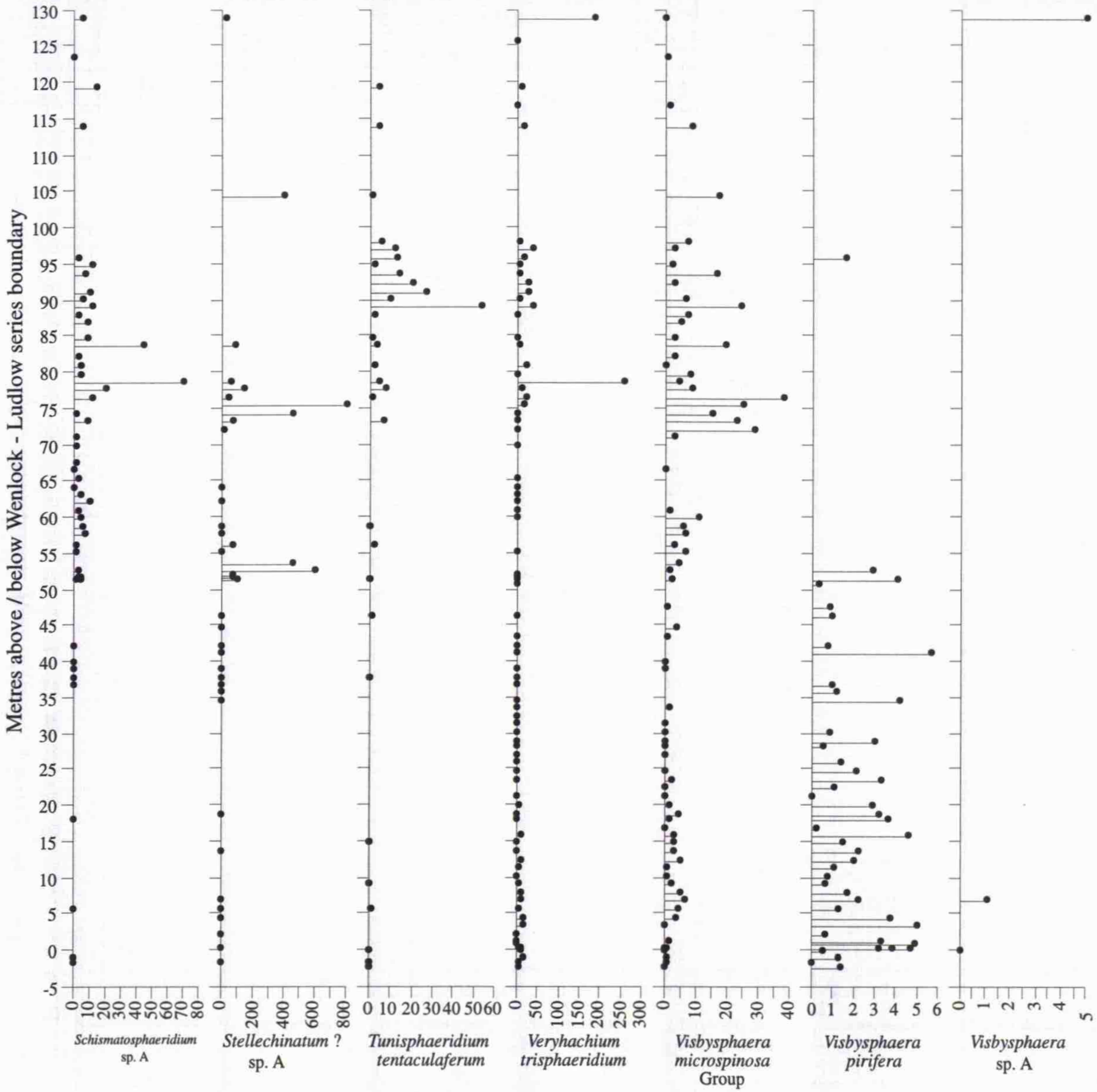
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



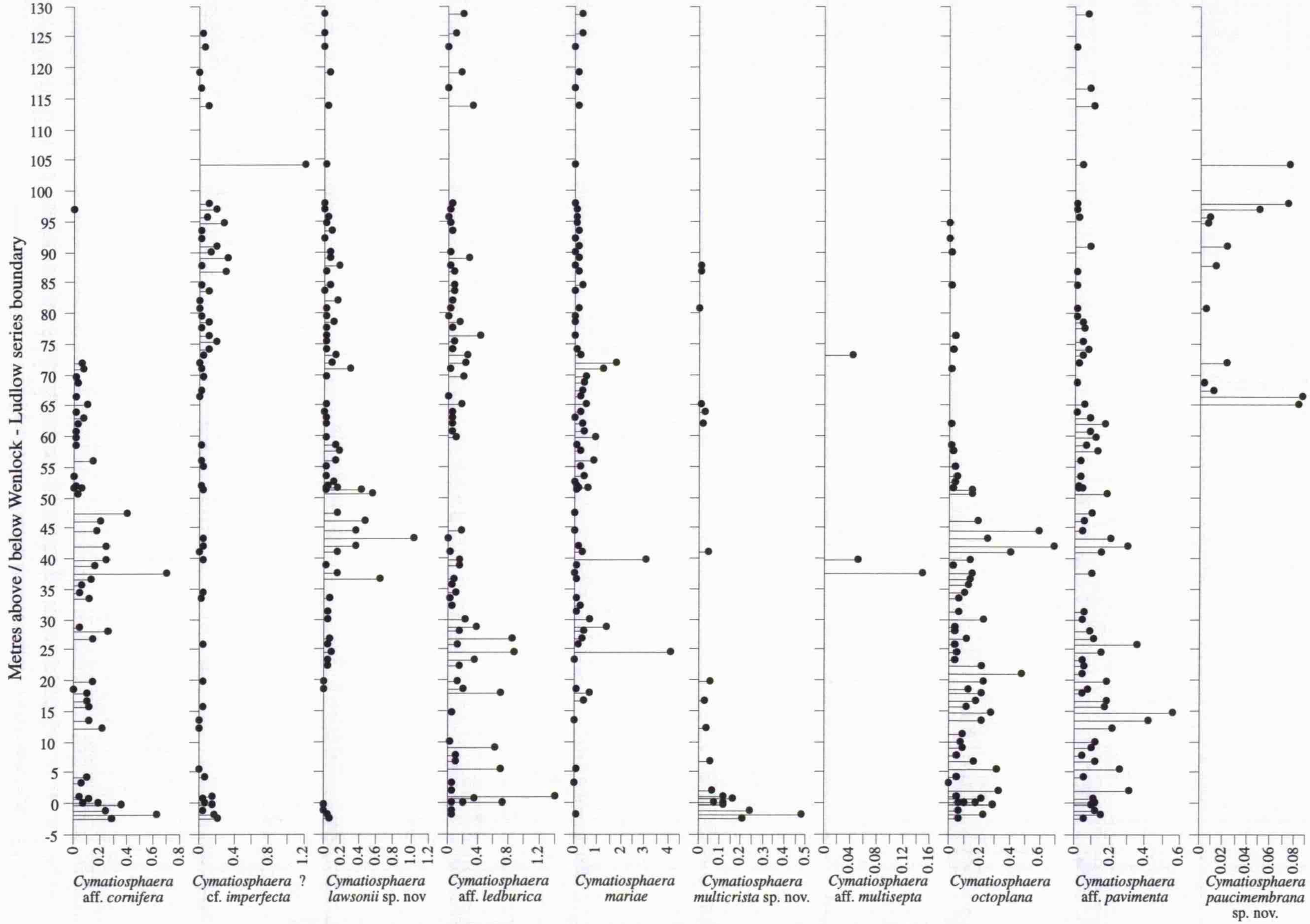
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



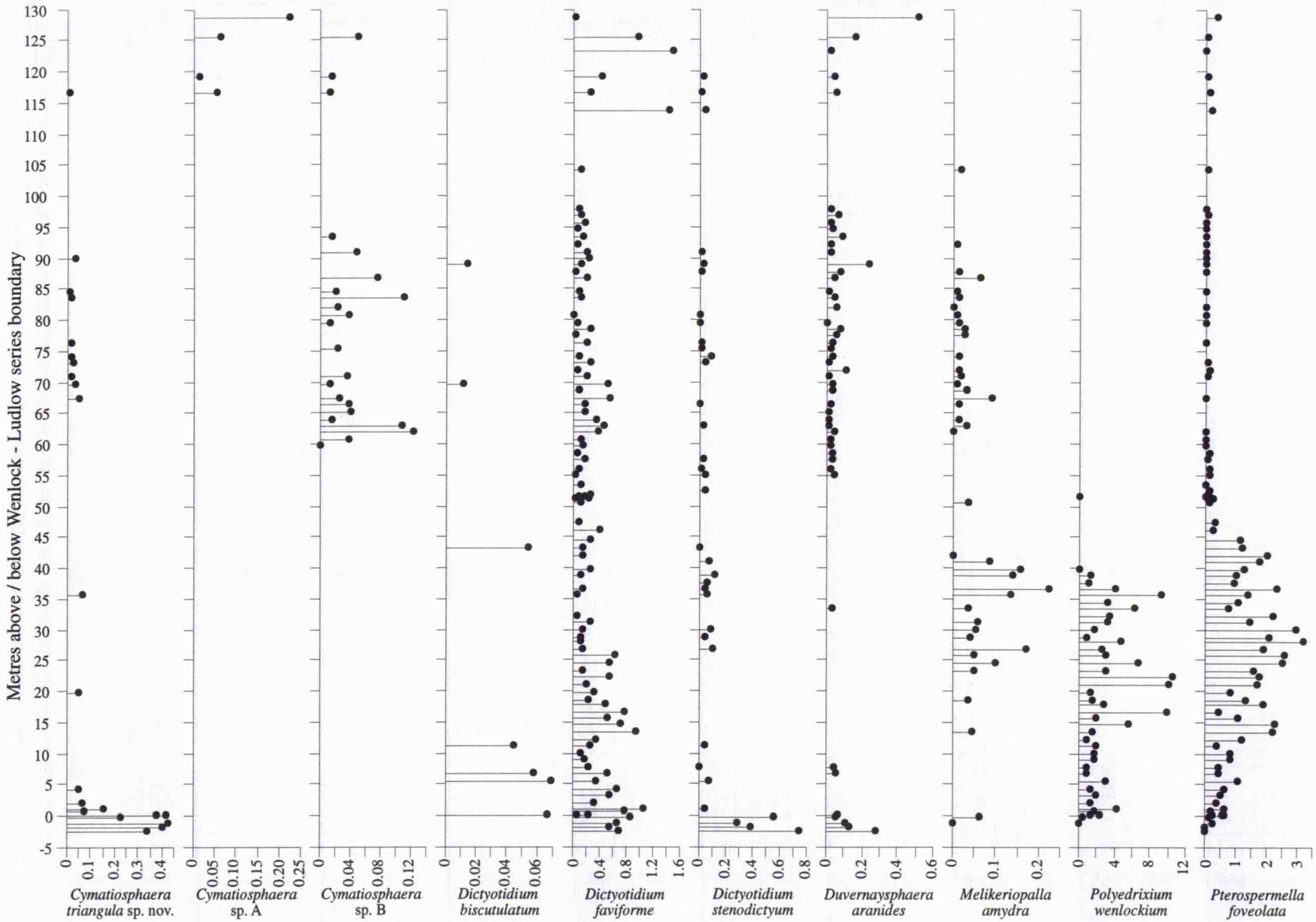
APPENDIX 1: Absolute anbundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.

APPENDIX 2

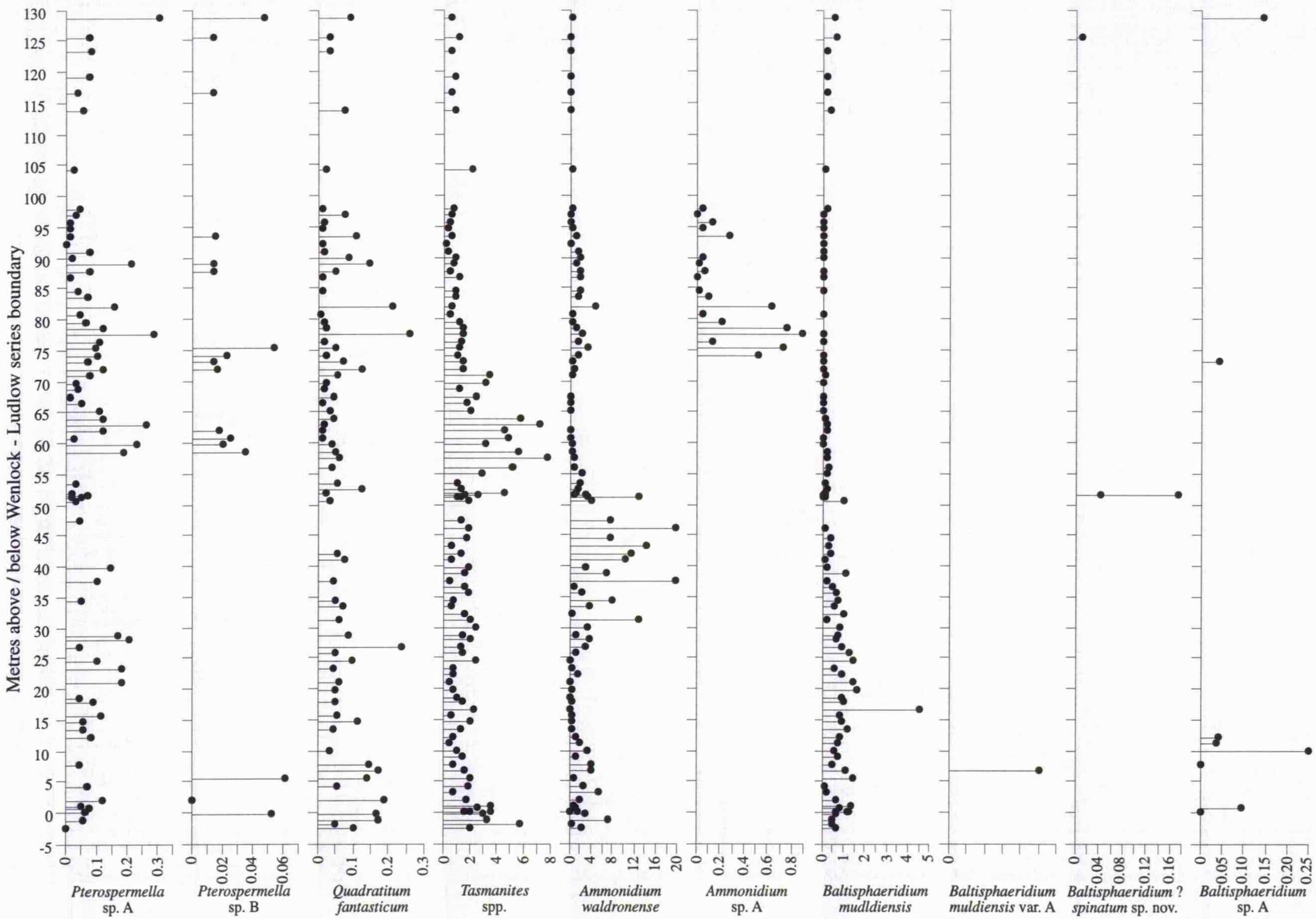
RELATIVE ABUNDANCE OF ACRITARCHS AND PRASINOPHYTE ALGAE, GOGGIN ROAD, MORTIMER FOREST, LUDLOW.



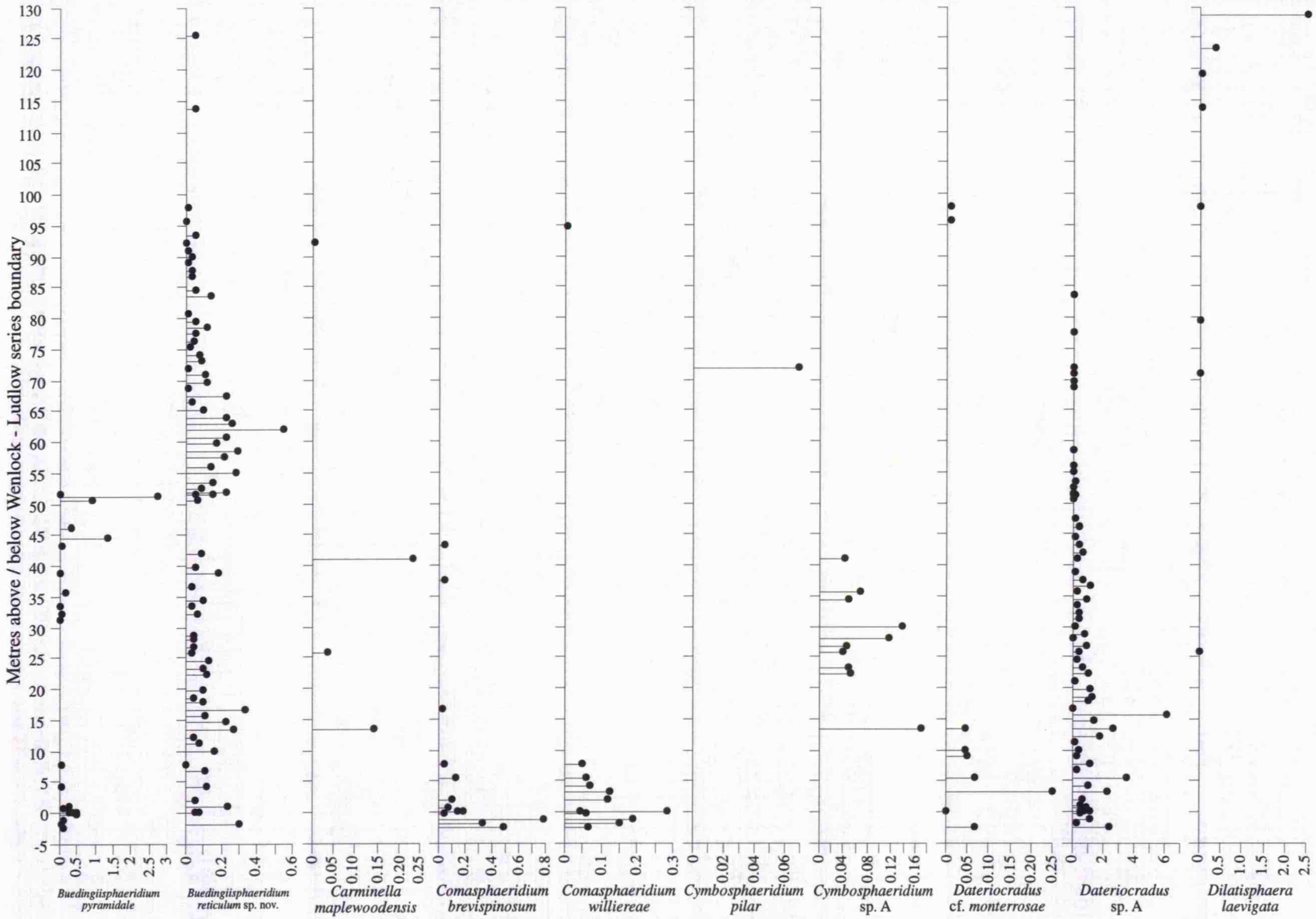
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



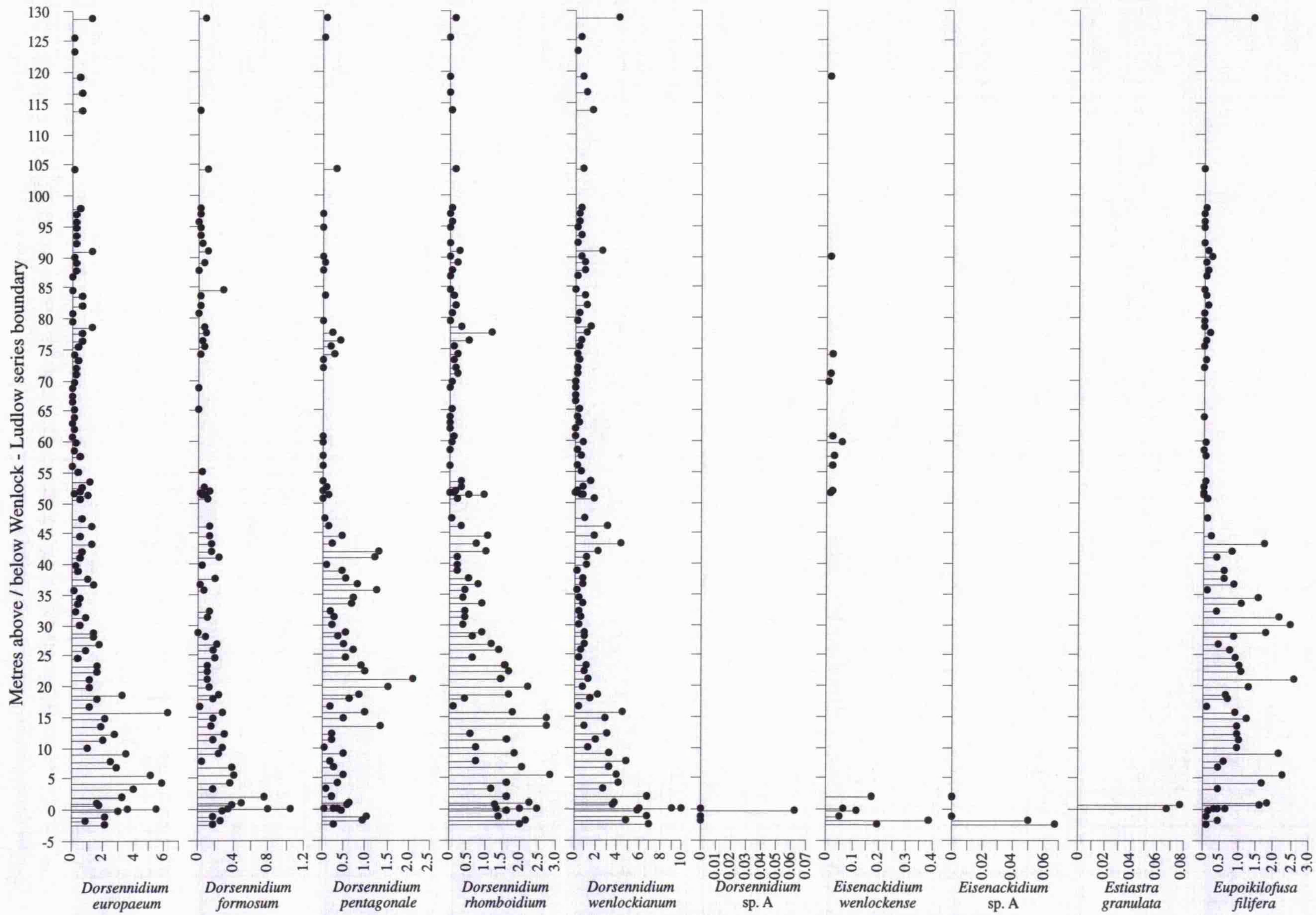
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



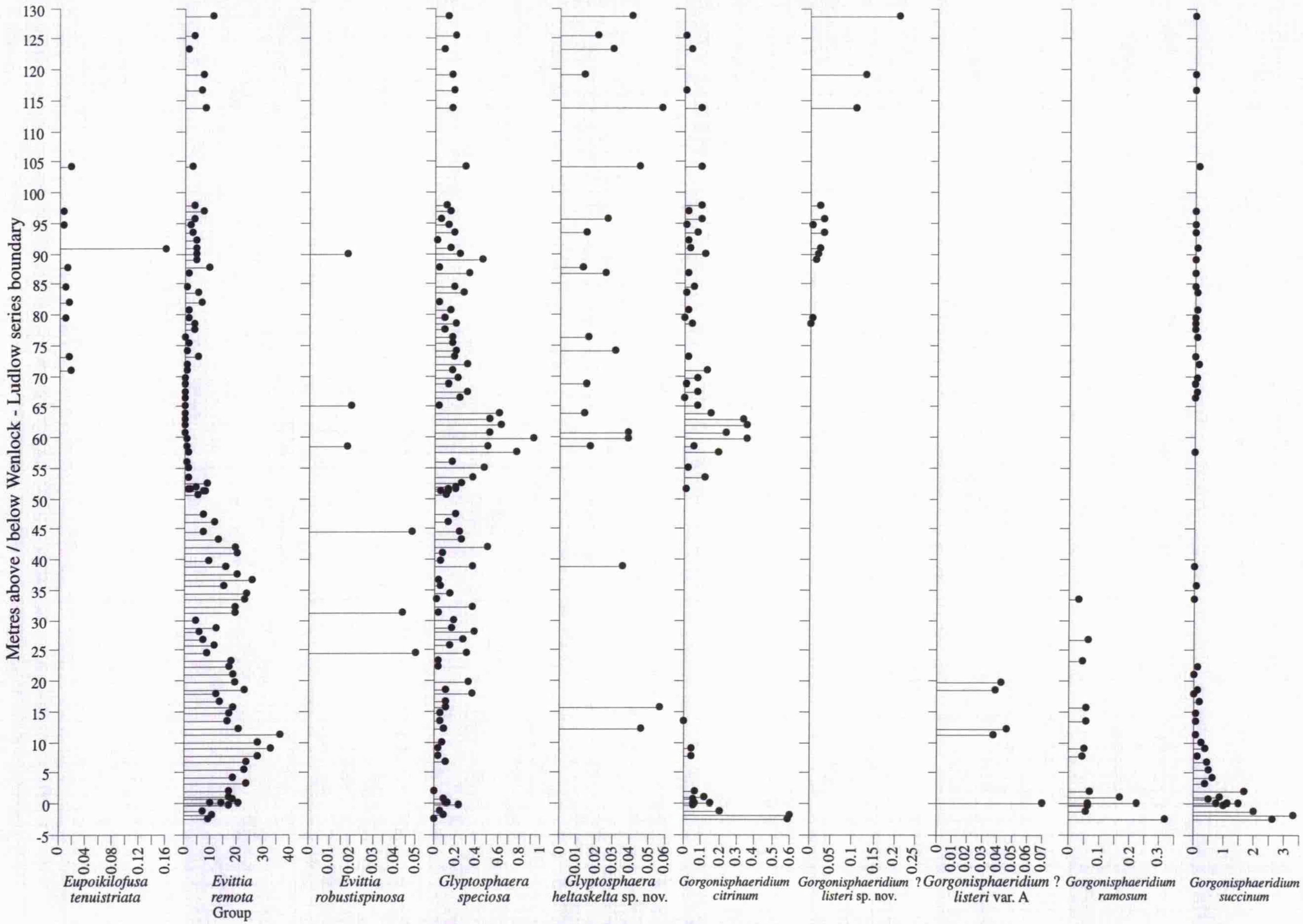
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



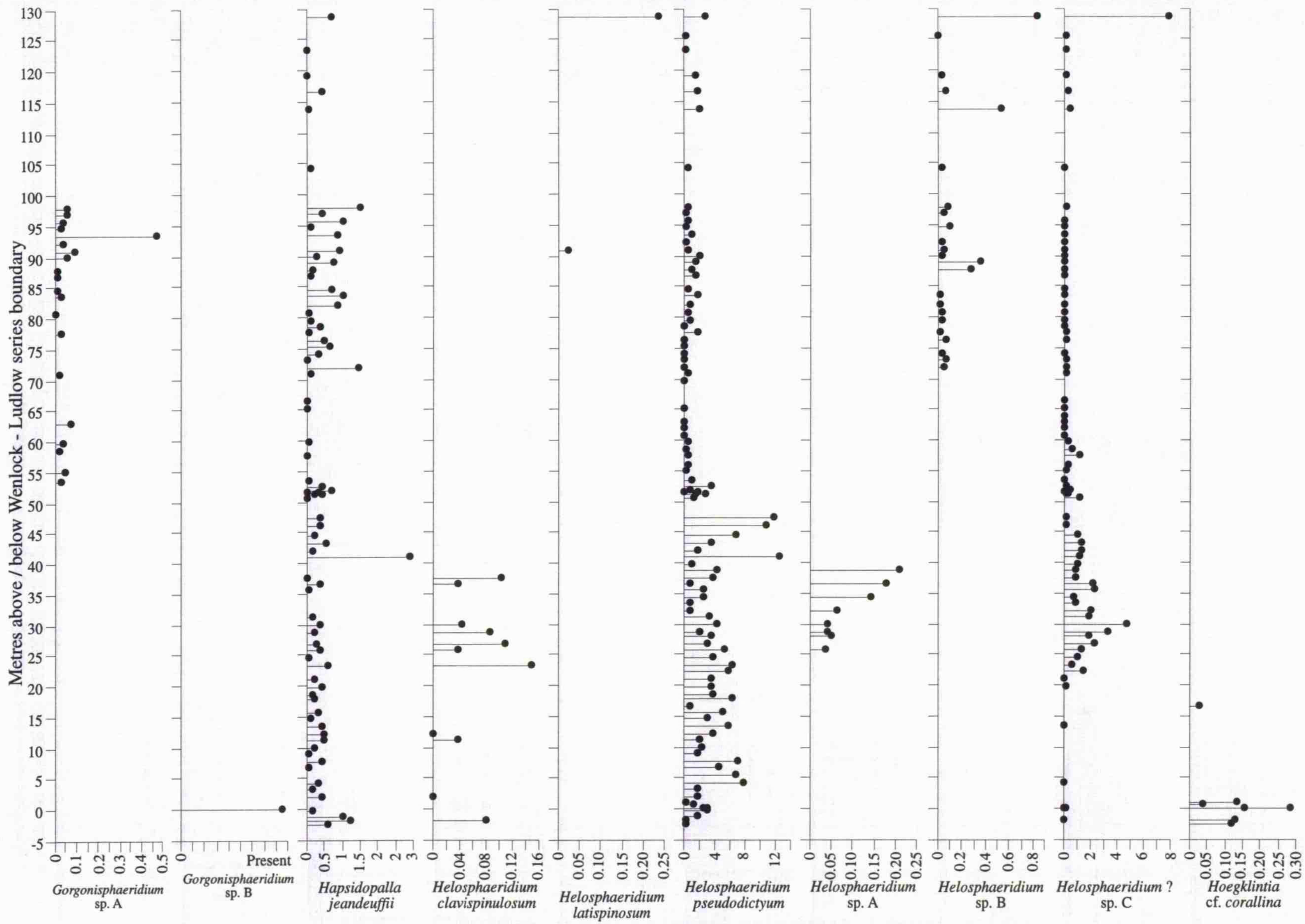
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



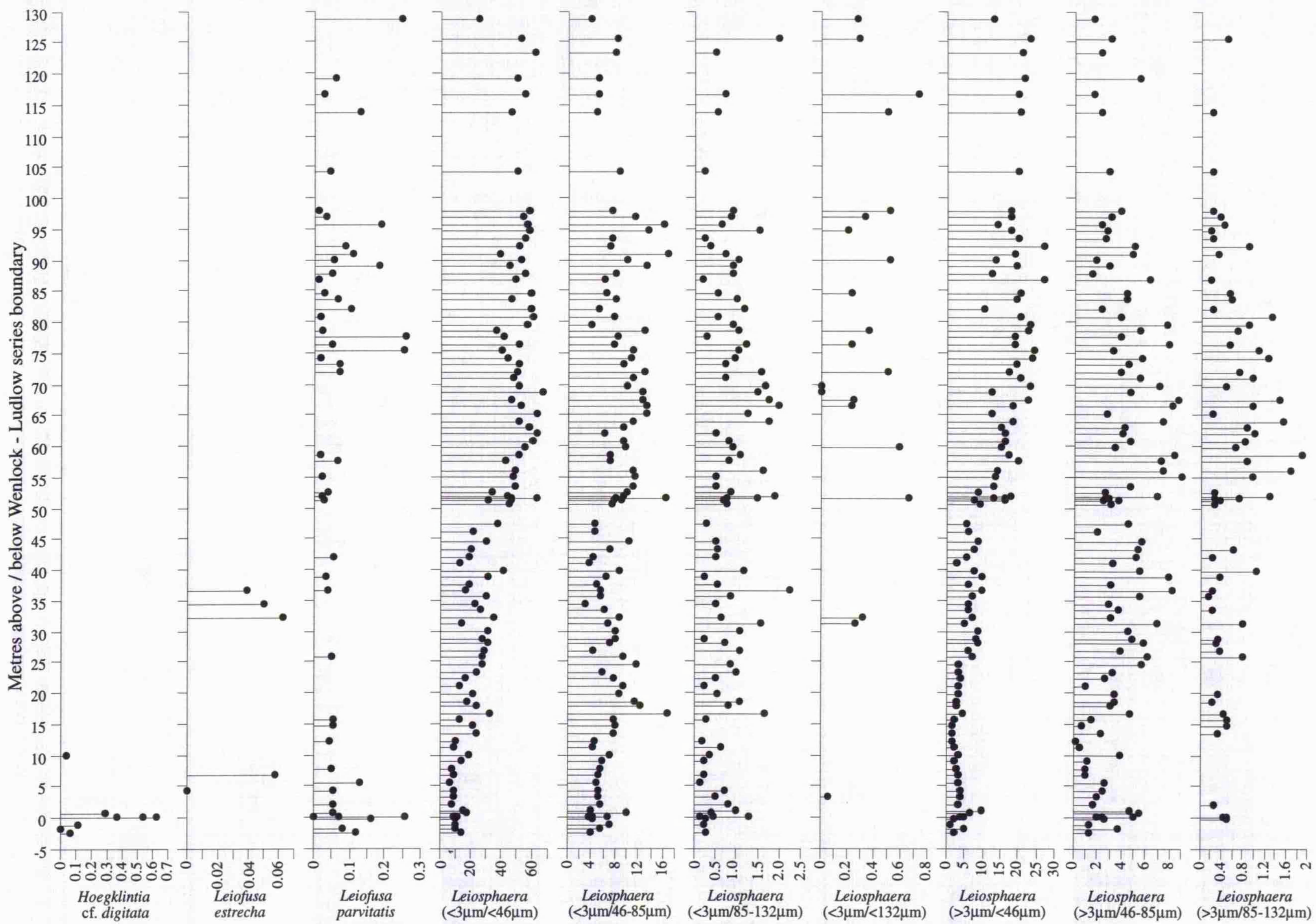
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



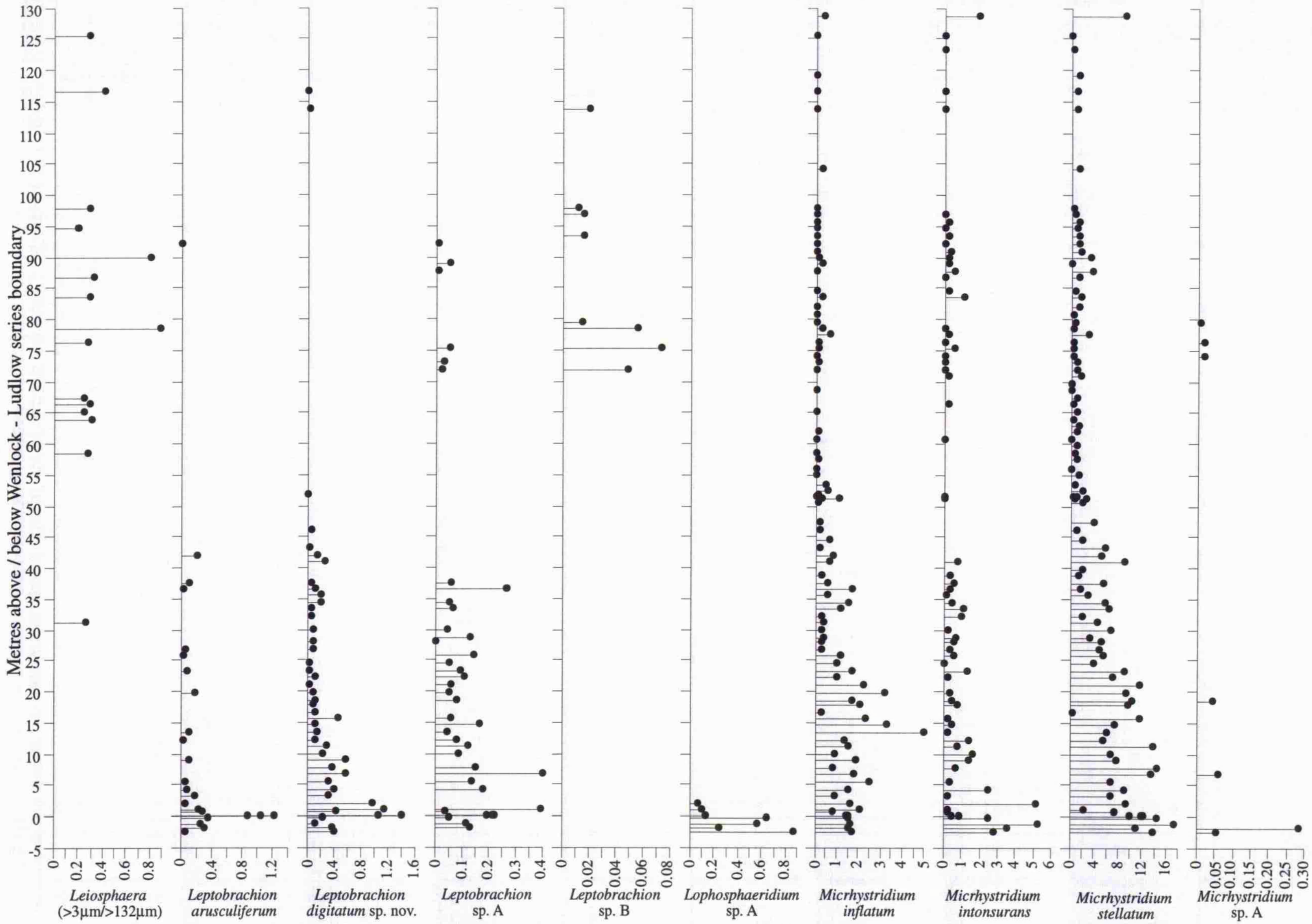
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



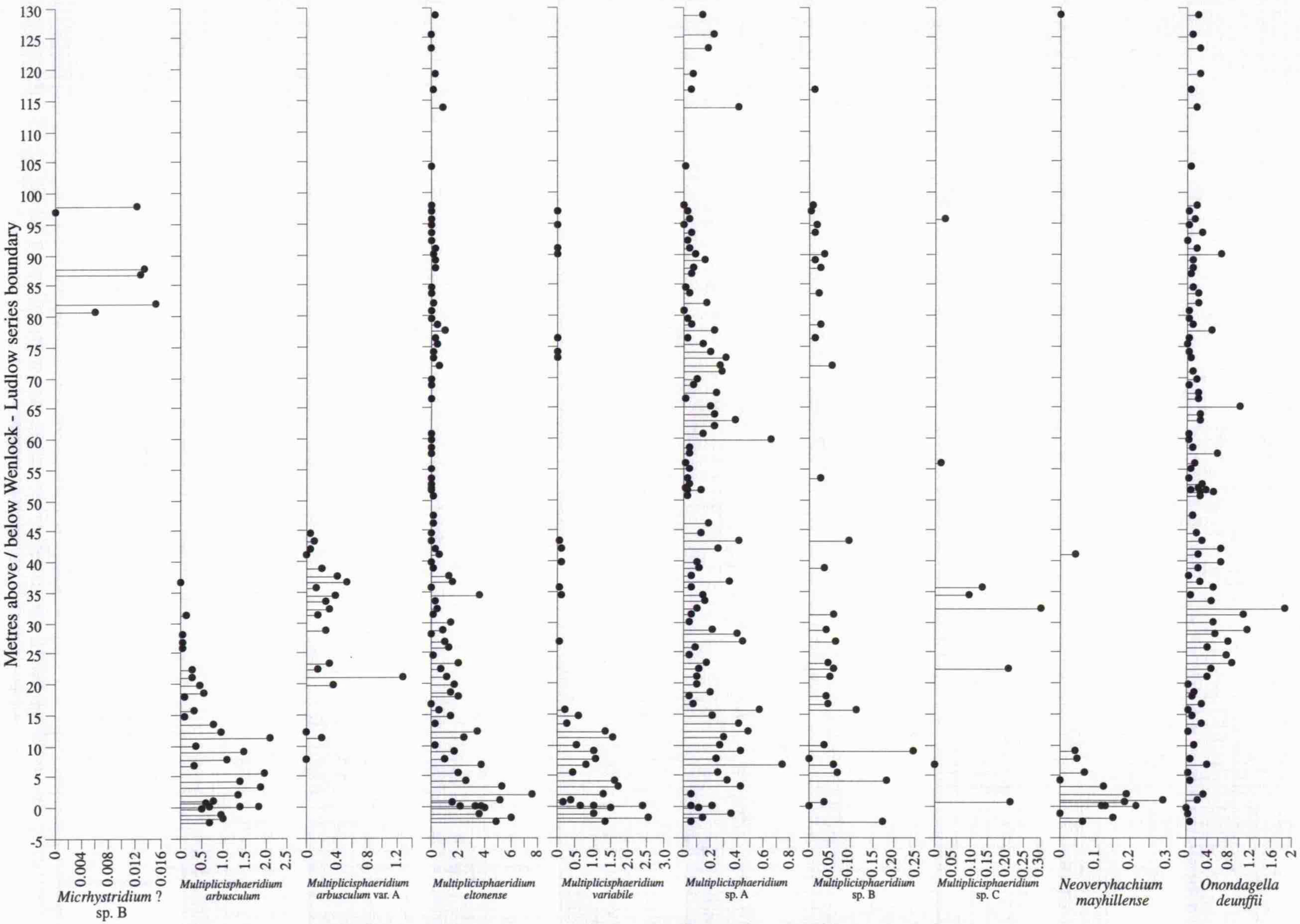
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



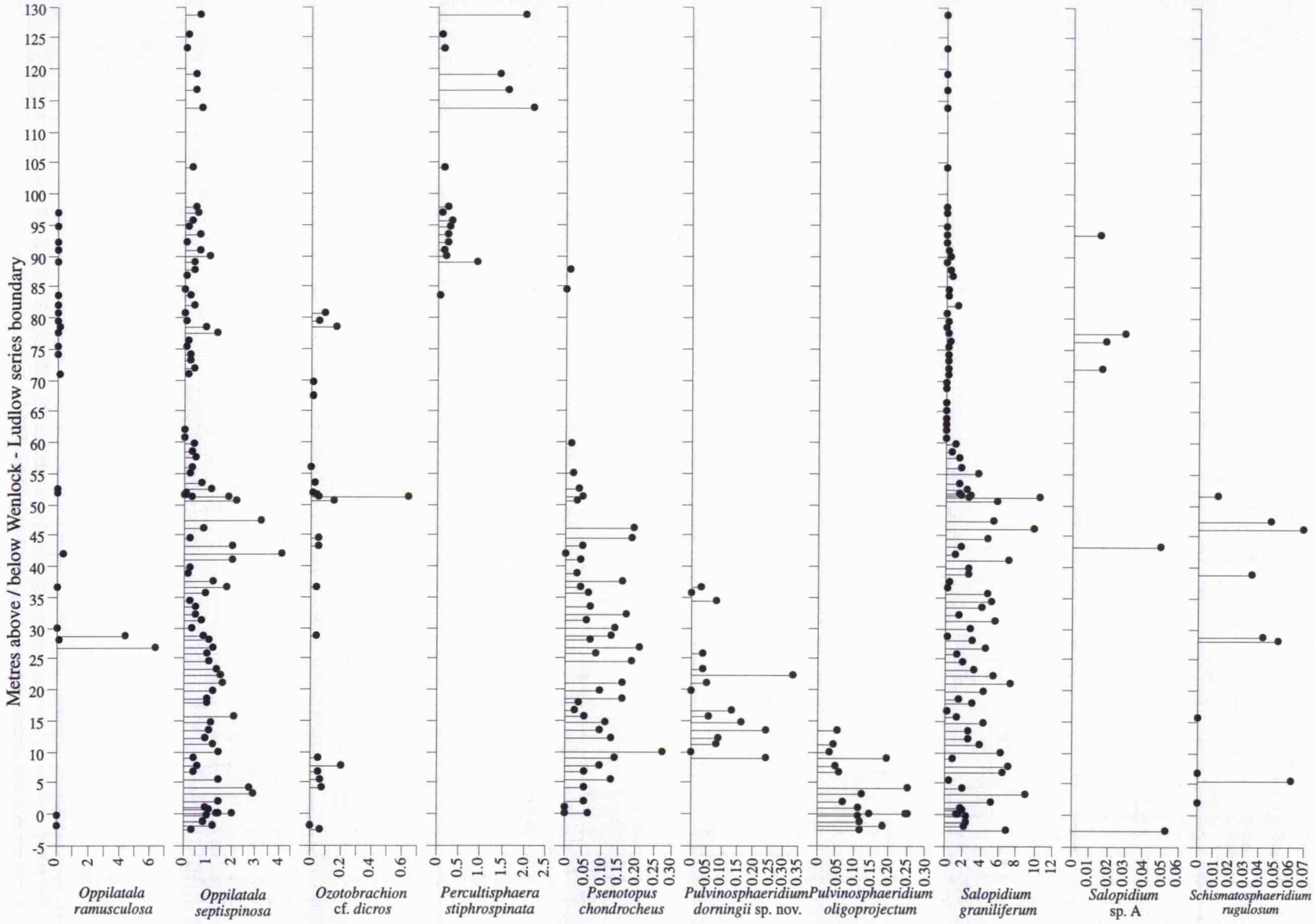
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



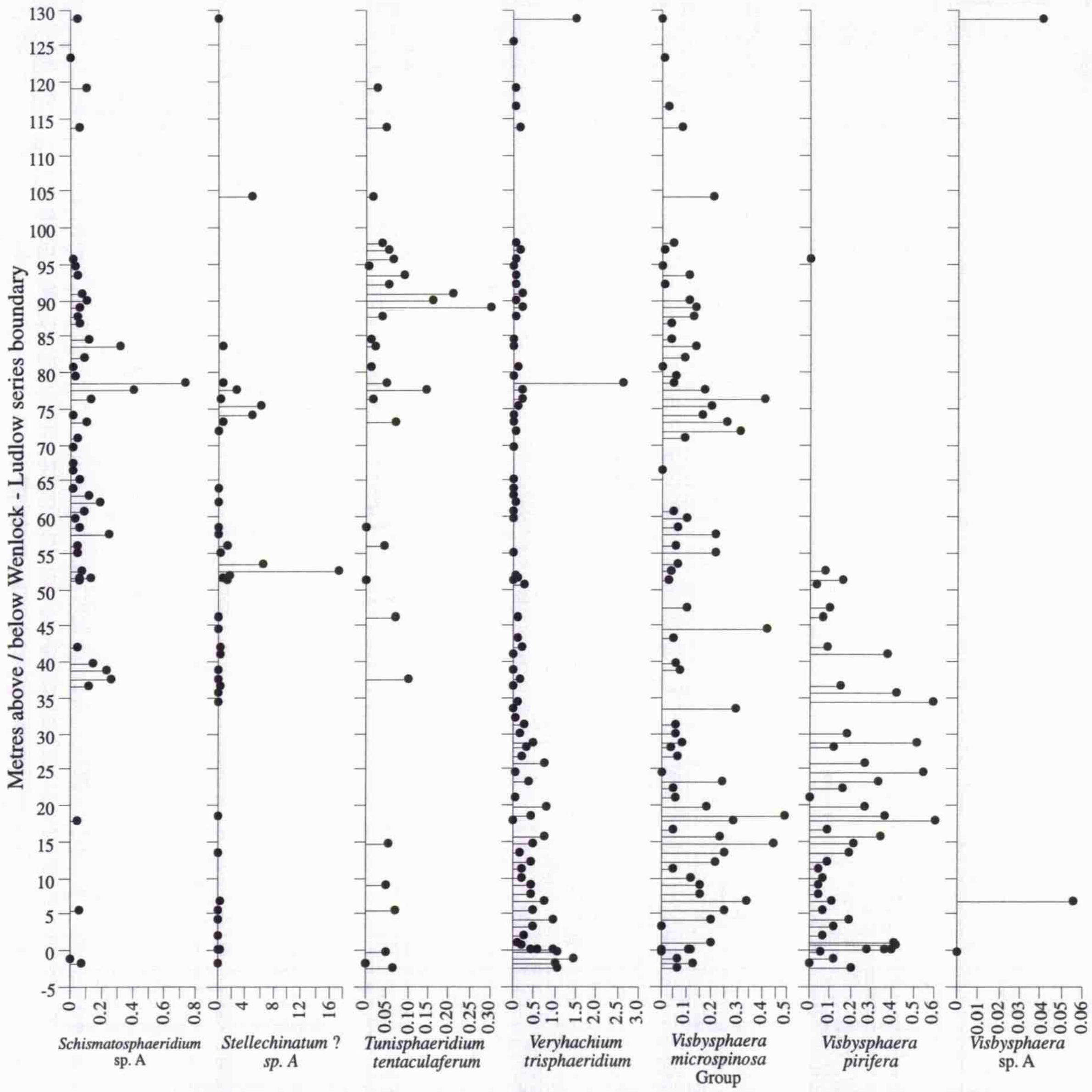
APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.



APPENDIX 2: Relative abundance of acritarchs and prasinophyte algae, Goggin Road, Mortimer Forest, Ludlow.

APPENDIX 3

ACRITARCHS AND PRASINOPHYTE ALGAE - ABUNDANCE PER GRAM AT GOGGIN ROAD.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Lycopodium spores	Cymatiosphaera spp.	Cymatiosphaera aff. cornifera	Cymatiosphaera ? cf. imperfecta	Cymatiosphaera lawsonii	Cymatiosphaera aff. ledburica	Cymatiosphaera mariae	Cymatiosphaera mulicrista	Cymatiosphaera aff. multisepta	Cymatiosphaera octoplana	Cymatiosphaera paucimembrana	Cymatiosphaera aff. pavimenta	Cymatiosphaera triangula	Cymatiosphaera sp. A	Cymatiosphaera sp. B
GOG1/2-C	-2.56	1254.5	0.7	1.95	1.5	0.45			1.4		0.45		0.35	2.25		
GOG1/5-C	-1.8	1568.5	3.45	4.35	1.25	0.35	0.35	0.55	3.3		1.6		1.05	2.8		
GOG1/7-C	-1.12	791	2.65	2.65	0.65	PRESENT	0.7		2.65		0.7		1.3	4.6		
TRENCH1/9-C	-0.39	918	5.8	3.7	1.65	PRESENT			1.2		3		1.1	2.35		
TRENCH1/10-A	-0.015	477	3.3	0.8	0.85		2.5		0.85		0.8			4.8		
TRENCH1/11-A	0.015	648.5	5.3		0.8		0.8				1.3			4.45		
TRENCH1/12-A	0.145	624.5	5.3	2.05	0.7		7.65		1.25		1.95		1.3			
TRENCH1/14-A	0.54	783.5	7.2	1.35	0.65		4.1		1.9		2.5		1.25	0.9		
TRENCH1/17-A	0.85	860	5.45	0.4	1.25		11.45		0.95		0.4			1.25		
TRENCH1/23-A	1.92	772.5	2.3				0.65		0.65		3.1		2.95	0.65		
TRENCH1/29-A	3.13	166	22.6	2.5			2.5	2.5			PRESENT					
GOG2/34-A	4.23	348	1.4	2.05	1.4						1		1	1		
GOG2/37-A	5.275	330.5	36.7		PRESENT		13.1	2.45			5.95		4.95			
GOG2/42-A	6.65	358.5	5.65				2.25		1.15		3.4		2.3			
GOG2/47-A	7.73	251.5	10				3.3				1.7		1.7			
GOG2/50-A	8.825	609	12.8				8.9				1.3		1.45			
GOG2/55-A	9.99	957	6.3				0.5				0.9		1.35			
GOG2/62-A	11.15	380	4.25								2.35					
GOG2/65-A	12.15	406.5	8.1	5.1	PRESENT				0.95				4.85			
GOG2/69-A	13.37	655	3.35	1.35	PRESENT			0.65			2.55		4.9			
GOG2/72-A	14.49	1059	2.35				0.4				2		3.95			
GOG2/75-A	15.56	506	3.05	1.5	0.75						1.5		2.3			
GOG2/77-A*	16.62	2934	2.25	0.35				1.5	0.1		0.6		0.6			
GOG2/81-A	17.67	1498.5	2.7	0.6			4.2	4.25			1.3		0.3			
TRENCH2/83-A	18.55	1107	6.2	PRESENT		PRESENT	1.8	0.75			1.1		0.7			
TRENCH2/88-A	19.85	860.5	2.9	1.5	0.45	PRESENT	1.45		0.55		2.35		1.95	0.55		
TRENCH2/90-A	20.985	908.5	1.35								3.9		0.4			
TRENCH2/94-A	22.2	1129.5	1.1			0.35	1.15				1.45		0.4			
TRENCH2/96-A	23.315	864.5	5.75			0.5	3.45	0.5			0.45		0.5			
GOG3/98-A	24.44	2083.5	10.3			0.4	3.55	16.6			0.2		0.6			
GOG3/100-A	25.63	1745	1.85		0.25	0.25	0.7	0.95			0.2		1.85			
GOG3/103-A	26.68	1242	6.6	1		0.4	5.6	2.45			0.75		0.7			
GOG3/106-A	27.83	1748	3.15	1.25			0.7	1.9			0.2		0.45			
GOG3/108-A	28.76	1614.5	9.6	0.25			2.25	8			0.25					
GOG3/111-A	29.95	1939	2.05			0.2	1.1	2.95			1.05		0.2			
GOG3/113-A	31.01	1400	2.35			0.35		0.5			0.35		0.35			
GOG3/116-A*	32.095	2525	1.9				0.2	0.95								
GOG3/119-A	33.21	1762.5	2.55	0.8	0.2	0.45	0.2	0.75			0.4					
GOG3/122-A	34.35	1073.5	2.4	0.35	0.35		0.7				0.7					
GOG3/124-A*	35.47	1964	1.05	0.2			0.2				0.4			0.2		
GOG3/127-A	36.415	1552.5	3.2	0.85		4.1	0.6	0.75			0.9					
GOG3/131-A	37.545	1697	1.8	3.1		0.65		0.2		0.65	0.65		0.45			
GOG3/135-A	38.67	2780.5	2.75	0.7		0.15	0.65	0.6			0.15					
TRENCH3/141-A**	39.71	1681	17.7	1.2	0.25		0.75	14.6		0.25	0.7					
TRENCH3/144-A	40.89	538	15.95		PRESENT	2.3	0.65	4.7	0.65		5.85		2.25			
TRENCH3/147-A	42.04	919	12.9	2.15	0.5	3.15		1.3			6		2.65			
TRENCH3/151-A	43.17	546.5	7.8		0.75	14.4	PRESENT				3.6		2.85			
TRENCH3/154-A	44.37	1094	6.45	1.5		3.05	1.5	0.4			4.9		0.4			
TRENCH3/156-A	46.05	430	12.3	2.95		6.9					2.8		0.9			
TRENCH3/160-A	47.23	973	8	3.45		1.25		0.4					0.85			
TRENCH4/163-A	50.43	1101.5	8.5	0.4		6.05					1.65		2.05			
TRENCH4/165-A	51.03	325	28.65		1.2	10.25					3.6					
TRENCH4/LE2-A	51.25	1200	22.6	PRESENT		3.85		14.15					1.05			
TRENCH4/ LE1-A	51.465	254.5	35.95			2.1		6.2								
TRENCH4/ ME1-A(a+b)	51.605	223.5	51.2	5.05		1.7		15.95			2.05		2.05			
TRENCH4/ME2-A(a+b)	51.805	410	15.05	1.05	0.85	2.05		5.15					0.85			
TRENCH4/167-A	52.27	285	16.1			4.2		1.4			1.5					
TRENCH4/170-A	53.35	199	48.2	PRESENT		1.95		28.9			4.05		2.1			
TRENCH4/174-A	54.8	522	32.35		1.55	0.75		8.5			1.5					
TRENCH4/176-A	55.92	311	62.4	9.35	1.25	7.8		47.95					2.5			
TRENCH4/180-A	57.37	486	21.55			5.45		8.95			1		3.9			
TRENCH4/183-A	58.37	268	9.15	1.5	3.05	12.05		9.15			1.55		6.15			
TRENCH4/187-A	59.64	197	60.6	2.15		4.15	12.75	100.3					12.5			PRESENT
TRENCH4/189-A	60.76	733	7.9	0.6			2.25	20.35					3.95			1.7
TRENCH4/192-A	61.81	530.5	12.9	1.95		1.6	3.55	20.65	1.3		0.65		9.35			6.55
TRENCH4/195-A	62.87	573.5	4.65	2.9		0.8	2.85	2.2					3.45			4.35
TRENCH4/197-A	63.98	387	15	1.1		1.05	4.3	19.2	2.25				1.1			1.1
TRENCH4/200-A	65.18	701	26.9	5.5		1.05	9.9	26.4	0.6			4.65	3.4			2.3

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Lycopodium spores	Cymatiosphaera spp.	Cymatiosphaera aff. cornifera	Cymatiosphaera ? cf. imperfecta	Cymatiosphaera lawsonii	Cymatiosphaera aff. ledburica	Cymatiosphaera mariae	Cymatiosphaera mulicrista	Cymatiosphaera aff. multisepta	Cymatiosphaera octoplana	Cymatiosphaera paucimembrana	Cymatiosphaera aff. pavimenta	Cymatiosphaera triangula	Cymatiosphaera sp. A	Cymatiosphaera sp. B
GOG4/204-A	66.31	1213	7.45	1.05	0.35		0.7	11.4				3.9				1.7
GOG4/207-A	67.465	877	23		2			19.15				0.6		2.5		1.35
GOG4/209-A	68.545	887	40.4	3.5				38				0.4	1.7			
GOG4/212-A	69.595	543	50.2	1.45	2.95	2.15	11.7	31.55						2.2		0.75
GOG4/214-A	70.715	649	36.55	2.4	1.2	10.35	1.2	40.2			0.6			0.6		1.2
GOG4/216-A	71.835	273.5	102.85	6	1.5	8.7	21.9	165.85				2.1	2.1			
GOG4/218-A	72.955	326.5	62.4		3.85	11.45	24.2	24.4		3.8			3.85	2.55		
GOG4/220-A	74.075	233.5	29.9		11.3	2.1	5.65	10.6			2.9		7.1	1.45		
TRENCH5/222-A	75.195	129.5	32.05		24.65	3.45	9.8						6.4			2.95
TRENCH5/225-A	76.315	233	30.45		10.95	3.2	39.7	3			3.45			1.7		
TRENCH5/228-A	77.435	273.5	8.95		1.5	1.5	3						3			
GOG5/232-A	78.435	178	31.85		11.75	10.4	16.2	4.2					4.7			
GOG5/234-A	79.545	371.5	16.15		3.5	4.75	3	1.25					2			2
GOG5/236-A	80.665	340.5	68.85		3.45	5.85	7	32.7	1.15			1.15	2.3			7
GOG5/238-A	81.785	625.5	10.05		0.5	5.35	1.8									0.75
GOG5/241-A	83.465	161	27.3		17.35	2.15	10.4	3.05						3.05		15.6
GOG5/243-A	84.585	479.5	61.45		2.1	5.4	7.3	30.05			1.05		1.05	0.75		1.8
GOG6/252-A	86.555	231	41.2		42.6	3.45	11.95	20.55	1.75				1.7			10.2
GOG6/254-A	87.675	501	15.05		2.25	10.75	1.45	0.8	0.75			0.75				
GOG6/256-A	88.81	124.5	75.8		60.05	11.7	50.9	33.6								
GOG6/259-A	89.835	367.5	30.3		8.95	4.45	2.2	4.4			1.15			2.25		
GOG6/263-A	90.95	170	24.2		26.2			28.15				3.05	11.2			6.1
GOG6/266-A	92.09	230	25.4		6.95	6.85		11.55			1.65					
GOG6/269-A	93.49	166	136.3		4.85	14.3	9.5	31.7								2.35
GOG6/271-A	94.61	163.5	77.1		112.9	9.8	16.8	28.75			2.1	2.8				
GOG6/273-A	95.73	236.5	44.05		19.35	9.15	1.95	19.95				1.65	3.9			
GOG6/275-A	96.85	207.5	17.55	1.8	43.7	3.4	5.3	23.2				10.6	3.5			
GOG6/277-A	97.97	222.5	27.95		17.4	1.8	6.85	9.05				10.75	1.7			
GOG7/282-A	104.19	207.5	23.25		97	2.05		3.6				6.1	4.05			
GOG8/288-A	113.715	158.5	37.7		11.15	6.05	33.75	23.5					12.1			
GOG9/292-A	116.505	518	15		1.45		0.75	2.95					4.5	0.75	2.95	0.75
GOG10/294-A	119.21	262	65.85		2.1	9.95	24.35	30.15							2.1	2.1
GOG11/298-A**	123.315	591	6.6		4	0.65	1.2	0.65					0.65			
GOG11/300-A*	125.405	437.5	38.4		3.1	0.8	9	27.35							4.75	3.7
GOG12/302-A	128.58	74.5	140.55			PRESENT	25.85	42.45					10		27.4	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Dictyotidium spp.	Dictyotidium biscutulatum	Dictyotidium faviforme	Dictyotidium stenodictyum	Duvernaysphaera aranides	Melikeriopalla amydra	Polyedrixium wenlockium	Pterospermella spp.	Pterospermella foveolata	Pterospermella sp. A	Pterospermella sp. B	Quadratitum fantasticum	Tasminites spp.	Ammonidium waldronense	Ammonidium sp. A
GOG1/2-C	-2.56			4.6	4.95	1.85			0.7	PRESENT	PRESENT		0.7	13.55	15.55	
GOG1/5-C	-1.8			3.8	2.65	0.9			0.35	PRESENT			0.35	39.05	3.8	
GOG1/7-C	-1.12	0.6		7.3	3.1	1.2	PRESENT	1.2		2.65	0.6		1.9	35.6	79.95	
TRENCH1/9-C	-0.39			8.95	5.85	0.65	0.65	4.8	0.65	1.3		0.55	1.75	32.25	32.85	
TRENCH1/10-A	-0.015	0.85						15.3		3.25				41.9	19.1	
TRENCH1/11-A	0.015			2.85				28.1	0.5	6.9				24.5	0.5	
TRENCH1/12-A	0.145		0.7	0.7		0.7		14.55		7.1	0.7			17.15	1.85	
TRENCH1/14-A	0.54			9				21.75	1.1	2.6	0.9			31.25	13.6	
TRENCH1/17-A	0.85			8.6	0.4			35.2	0.4	5.4	0.4			29.2	6.75	
TRENCH1/23-A	1.92			3.05				12.2		3.85	1.15	PRESENT	1.8	16.15	17.5	
TRENCH1/29-A	3.13			22.55				80.2		20.05				32.6	213.25	
GOG2/34-A	4.23			12.75				26.35		12.75	1.4		1	36.05	47.2	
GOG2/37-A	5.275		1.3	6.55	1.3			58.65		20.1		1.15	2.6	38.6	13.55	
GOG2/42-A	6.65		1.15	10.15		1.1		20.3		9			3.4	32.7	80.15	
GOG2/47-A	7.73			8.25	PRESENT	1.6		32.65		14.7	1.6		4.9	24.8	130.3	
GOG2/50-A	8.825			2.7				25.35		11.55				21.1	17.85	
GOG2/55-A	9.99			1.35				19.25		9.45			0.4	11.8	36.95	
GOG2/62-A	11.15		1.15	6.55	1.15			49.2		9.9				12.25	48.3	
GOG2/65-A	12.15			8.05				21.55		28	1.9			18.8	24.55	
GOG2/69-A	13.37			11.05			0.55	17.5		25.5	0.65		0.55	16	4.05	
GOG2/72-A	14.49			5.15				39.15		16.1	0.4		0.8	14.15	4.35	
GOG2/75-A	15.56			6.85				26.75		14.5	1.55		0.75	7.65	8.4	
GOG2/77-A*	16.62			2.55				33.15		1.45				7.7	0.25	
GOG2/81-A	17.67			3				17.35		11.45	0.55		0.3	9.15	2.1	
TRENCH2/83-A	18.55			2.2			0.35	13.95		12.05	0.4			9.15	0.4	
TRENCH2/88-A	19.85			3.35				13.55		8.95			0.55	7.6	4.5	
TRENCH2/90-A	20.985			1.75				83.5		13.85	1.5		0.5	4.1	1.35	
TRENCH2/94-A	22.2			3.75				72.6		12				5.45	10.6	
TRENCH2/96-A	23.315			1.4			0.5	31.2		15.55	1.8		0.45	7.4	5.4	
GOG3/98-A	24.44			2.2			0.4	26.4		10	0.4		0.4	9.85	0.8	
GOG3/100-A	25.63			3.3			0.25	16.25		13.35			0.25	7.25	5.75	
GOG3/103-A	26.68			1	0.7		1.1	17.3		12.15	0.3		1.55	8.3	20.25	
GOG3/106-A	27.83			0.65				23.1		15.35	1			9.75	17.5	
GOG3/108-A	28.76			0.75	0.25		0.25	5.35		11.95	1		0.5	8.6	6.85	
GOG3/111-A	29.95			0.7	0.4		0.25	8.65		13.85				11.2	16.2	
GOG3/113-A	31.01			1.5			0.35	18.8		8.5			0.35	12.15	73.65	
GOG3/116-A*	32.095			0.2				11		6.95				5.3	1.9	
GOG3/119-A	33.21					0.25	0.25	39.85		5			0.45	3.8	23.85	
GOG3/122-A	34.35							22.3		7.55	0.35		0.35	5.5	56.55	
GOG3/124-A*	35.47			0.2	0.2		0.4	27.75		4.05				5.5	6.35	
GOG3/127-A	36.415			0.95	0.3		1.45	27.25		15.1				10.55	5.05	
GOG3/131-A	37.545				0.25			5.35		4.25	0.45		0.2	2.05	86.35	
GOG3/135-A	38.67			0.5	0.5		0.6	5.4		4.3				6.6	29.25	
TRENCH3/141-A**	39.71			1.2			0.75	0.25		6.1	0.7			8.7	14.3	
TRENCH3/144-A	40.89				1.15		1.25			25.6			1.15	9.65	153.65	
TRENCH3/147-A	42.04	0.8		1.4			PRESENT			17.35			0.5	11.6	99.3	
TRENCH3/151-A	43.17		0.75	2.05	PRESENT					16.6				8.45	199.9	
TRENCH3/154-A	44.37			2.3						9.55				14.8	63.35	
TRENCH3/156-A	46.05			5.85						3.85				26.9	285.7	
TRENCH3/160-A	47.23			0.9						3	0.4			11.45	65.1	
TRENCH4/163-A	50.43			1.25			0.4			1.4	0.4		0.4	20.15	45.95	
TRENCH4/165-A	51.03			1.2						6.65	1.2			24.55	310.3	
TRENCH4/LE2-A	51.25	0.3		2.5				0.3		1.1				37.95	19.65	
TRENCH4/ LE1-A	51.465			16.6					2.1	4.2	1.35			93.15	229.95	
TRENCH4/ ME1-A(a+b)	51.605			15.45						10.5	5.85			228.15	249.6	
TRENCH4/ME2-A(a+b)	51.805			11.25					2.75	3.4	0.85		0.85	185.1	44.05	
TRENCH4/167-A	52.27				1.5					4.45			4.3	45.8	59.6	
TRENCH4/170-A	53.35			8.3						1.95	2.1		3.85	75.55	133.8	
TRENCH4/174-A	54.8			1.55	1.55	1.55				3.85				93.9	76.25	
TRENCH4/176-A	55.92			5.15	1.25	1.4				10.75			2.5	312.9	40.8	
TRENCH4/180-A	57.37	1		5.45	1	1				2.2			1.75	232.8	23.2	
TRENCH4/183-A	58.37			6.1		3.05				12.05	16.5	3.05	4.55	488.5	51.4	
TRENCH4/187-A	59.64			16.55		2.15				4.3	24.9	2.15	4.3	344.7	64.35	
TRENCH4/189-A	60.76			5.7		1.15				1.15	1.15	1.1	0.55	214.75	2.25	
TRENCH4/192-A	61.81			20.3		2.25	PRESENT			0.95	6.45	0.95	0.65	243.4	2.6	
TRENCH4/195-A	62.87			18.55	1.45	0.8	1.3		0.8		10.45		0.65	287.85		
TRENCH4/197-A	63.98			25.6		1.05	1.05				8.65		3.3	413.35		
TRENCH4/200-A	65.18			10.75		1.1					5.85		1.75	113.3	4.05	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Dictyotidium spp.	Dictyotidium biscutulatum	Dictyotidium faviforme	Dictyotidium stenodictyum	Duvernaysphaera aranides	Melikeriopalla amydra	Polyedrixium wenlockium	Pterospermella spp.	Pterospermella foveolata	Pterospermella sp. A	Pterospermella sp. B	Quadratitum fantasticum	Tasminites spp.	Ammonidium waldronense	Ammonidium sp. A
GOG4/204-A	66.31			8.8	0.35	1.35	0.7				2.4		0.65	80.05	1.4	
GOG4/207-A	67.465			29.5			4.85			0.4	0.75		2.4	130.85	0.6	
GOG4/209-A	68.545			8.15		2.7	2.7				3.4		1.4	107.75		
GOG4/212-A	69.595		0.7	31.25		2.2	0.7				2.15		1.45	185.4		
GOG4/214-A	70.715			6.8		0.6	0.6			2.4	2.45		1.85	115.7	18.25	
GOG4/216-A	71.835			6.6		9.9	1.5			13.5	11.1	1.5	11.4	138.55	66.9	
GOG4/218-A	72.955	1.25		24.2	3.85	1.3			3.2	5.15	6.4	1.3	6.35	135.05	57.4	
GOG4/220-A	74.075			9.95	7.75	3.55	1.45				9.2	2.1	2.1	90.6	141.75	48.1
TRENCH5/222-A	75.195				2.95	2.95			2.95		12.35	6.85	6.4	159.65	405.4	91.7
TRENCH5/225-A	76.315	1.7		19.5	1.5	3.2				3	9.8		1.7	122.35	153	12.85
TRENCH5/228-A	77.435			1.5		3	1.5		1.5		14.85		13.4	79.05	119.25	46.15
GOG5/232-A	78.435			25.05		7.3	2.6				11.5		2.1	148.65	109.75	73.65
GOG5/234-A	79.545	1.25		8.7	1	1.25	2.25			1.25	9.2		2.5	174.55	69.55	30.3
GOG5/236-A	80.665			2.3	1.15		2.35			2.3	8.2		1.15	87.6	64.15	9.3
GOG5/238-A	81.785					1.8	PRESENT			0.5	5.15		6.95	21.35	159.15	20.85
GOG5/241-A	83.465			16.85		6.05	2.15				9.55			122.6	218.75	13.45
GOG5/243-A	84.585			7.85		1.05	0.75			2.15	3.25		1.05	70.95	150.95	1.45
GOG6/252-A	86.555	1.7		29		6.8	8.55				1.75		1.55	158.9	248.05	1.75
GOG6/254-A	87.675			1.55	0.8	4.55	0.8			2.25	4.55	0.8	3	32.35	122.95	3.8
GOG6/256-A	88.81		2.55	21.4	7.15	42.25				2.55	37.7	2.55	25.95	142	206.15	2.55
GOG6/259-A	89.835			14.5						3.3	1.15		5.55	54.15	113.85	3.35
GOG6/263-A	90.95			25.25	2	3.05				4	10.1		2	51.45	219.55	
GOG6/266-A	92.09			22.35		10.4	3.4		1.75	5.15	1.65		4.9	93.45	5.05	
GOG6/269-A	93.49			24.3		14.65				2.5	2.5	2.35	16.8	96.4	167.55	43.4
GOG6/271-A	94.61			31.55		12.6				2.8	7		4.2	128.35	149.4	20.3
GOG6/273-A	95.73			33.15		4.95				7.5	3.3		3.6	103.25	12.75	25.75
GOG6/275-A	96.85			26.35		15.65				24.25	7.1		15.9	129.3	35.25	1.7
GOG6/277-A	97.97			14.1		3.5				1.8	7		1.8	118.3	80.8	7.25
GOG7/282-A	104.19			9.2			1.55			8.25	2.05		2.05	172.7	41.6	
GOG8/288-A	113.715			148.85	5.1					20.2	6.05		8.15	88.3	20.25	
GOG9/292-A	116.505			13.5	0.75	3				7.35	2.2	0.75		34.55	5.15	
GOG10/294-A	119.21			58.15	3.85	6.1				12.05	10.15			115.9	3.85	
GOG11/298-A**	123.315			95.75		1.3				2	5.25		2	44.2	2	
GOG11/300-A*	125.405			71.75		12.5				5.15	5.55	1.05	2.7	84.1	6.95	
GOG12/302-A	128.58			5.8		63.25				45.9	37.45	5.8	11.6	74.9	46.65	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m).	Baltisphaeridium	Baltisphaeridium	Baltisphaeridium	Baltisphaeridium ?	Baltisphaeridium	Buedingiisphaeridium	Buedingiisphaeridium	Buedingiisphaeridium	Carminella	Comasphaeridium	Comasphaeridium	Cymbosphaeridium	Cymbosphaeridium	Dateriocradus	Dateriocradus
	(above/below Wenlock-	spp.	muldiensis	muldiensis var. A	spinatum	sp. A	spp.	pyramidale	retuculum	mapplewoodensis	brevispinosum	williereae	pilar	sp. A	cf. monterrosae	sp. A
	Ludlow boundary)															
GOG1/2-C	-2.56	5.65	4.25					0.9			3.2	0.45			0.45	16.05
GOG1/5-C	-1.8	0.9	3.45					0.55	2.1		2.3	1.05				1.75
GOG1/7-C	-1.12	0.6	5.2				0.7	1.3			8.6	2.05				12.05
TRENCH1/9-C	-0.39	0.65	6.65					5.3			0.55	0.65				6
TRENCH1/10-A	-0.015	3.3	13.85					5.7	0.85		1.65	3.25			PRESENT	13.2
TRENCH1/11-A	0.015	1.55	14.8					3.4				0.5			PRESENT	6.15
TRENCH1/12-A	0.145	6.8	7.15			PRESENT		4	0.6		2					7.95
TRENCH1/14-A	0.54	6.4	9.25			1.1		1.7			0.9					11.05
TRENCH1/17-A	0.85	0.85	11.05					2.25	1.95							4.95
TRENCH1/23-A	1.92	0.65	6.05						0.5		1	1.15				5.8
TRENCH1/29-A	3.13		10									5			10.05	90.4
GOG2/34-A	4.23		2.75					1	2.4			1.4				20.35
GOG2/37-A	5.275	7.45	26.65								2.45	1.15			1.3	65.5
GOG2/42-A	6.65	4.55	22.6	PRESENT					2.25							5.65
GOG2/47-A	7.73	4.95	14.95			PRESENT		3.3	PRESENT		1.6	1.7				38.05
GOG2/50-A	8.825		10.15												0.7	4.1
GOG2/55-A	9.99	2.9	6.5			2.75			1.85						0.5	4.7
GOG2/62-A	11.15	3.05	19.3			0.95			1.9							5.65
GOG2/65-A	12.15	1.05	18			0.95			1.05							40.9
GOG2/69-A	13.37		14.2						3.2	1.7				2	0.55	30.6
GOG2/72-A	14.49		6.7						1.6							10.25
GOG2/75-A	15.56		11.5						1.5							81.75
GOG2/77-A*	16.62		15.2						1.1		0.1					0.1
GOG2/81-A	17.67		5.95						0.6							6.5
TRENCH2/83-A	18.55	0.75	8.4						0.4							11.55
TRENCH2/88-A	19.85		16.8						1							12.5
TRENCH2/90-A	20.985		12.2													0.9
TRENCH2/94-A	22.2	0.7	6.45						0.8					0.35		7.25
TRENCH2/96-A	23.315		5.65						1.05					0.5		6.95
GOG3/98-A	24.44		5.8						0.55							1.2
GOG3/100-A	25.63		6.35						0.2	0.2				0.2		2.35
GOG3/103-A	26.68	0.4	6.05						0.3					0.3		5.9
GOG3/106-A	27.83		3						0.2					0.55		0.45
GOG3/108-A	28.76		4.3				0.25		0.25							4.85
GOG3/111-A	29.95		3.7											0.65		0.85
GOG3/113-A	31.01		1.35					0.25								2.25
GOG3/116-A*	32.095		3.1					0.2	0.2							1.15
GOG3/119-A	33.21		3.9					0.25	0.2							2.05
GOG3/122-A	34.35		5.5						0.7					0.35		6.85
GOG3/124-A*	35.47		1.9					0.6						0.2		0.85
GOG3/127-A	36.415		3.2						0.25							7.35
GOG3/131-A	37.545		1.1								0.2					3.1
GOG3/135-A	38.67		4.85					0.15	0.8							0.9
TRENCH3/141-A**	39.71		0.95						0.25							
TRENCH3/144-A	40.89		2.25							3.4				0.65		4.55
TRENCH3/147-A	42.04		3.25						0.8							5.7
TRENCH3/151-A	43.17		3.7					0.7			0.75					6.55
TRENCH3/154-A	44.37		3.05					11								1.15
TRENCH3/156-A	46.05		1.8					4.75								6
TRENCH3/160-A	47.23															1.4
TRENCH4/163-A	50.43		10.75					10	0.8							0.8
TRENCH4/165-A	51.03		2.55					66.05								3.75
TRENCH4/LE2-A	51.25		1.75		4.2		0.3	0.65	3.75							0.3
TRENCH4/ LE1-A	51.465		5.55													2.1
TRENCH4/ ME1-A(a+b)	51.605		4.15		3.75				5.05							3.75
TRENCH4/ME2-A(a+b)	51.805		5						9.25							
TRENCH4/167-A	52.27		5.95						3.05							2.8
TRENCH4/170-A	53.35		9.85						10.2							12.3
TRENCH4/174-A	54.8	0.75	6.95						9.2							1.5
TRENCH4/176-A	55.92	5.15	19.9				2.8		8.9							2.65
TRENCH4/180-A	57.37	0.75	7.5						6.65							
TRENCH4/183-A	58.37		15.35						25.65							1.55
TRENCH4/187-A	59.64		2.15						18.7							
TRENCH4/189-A	60.76		3.4						10.2							
TRENCH4/192-A	61.81	0.95	11.95						29							
TRENCH4/195-A	62.87		8.6						10.5							
TRENCH4/197-A	63.98		6.55						16.5							
TRENCH4/200-A	65.18		3.6						5.7							

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Baltisphaeridium spp.	Baltisphaeridium muldiensis	Baltisphaeridium muldiensis var. A	Baltisphaeridium ? spinatum	Baltisphaeridium sp. A	Buedingiisphaeridium spp.	Buedingiisphaeridium pyramidale	Buedingiisphaeridium retuculum	Carminella mapplewoodensis	Comasphaeridium brevispinosum	Comasphaeridium williereae	Cymbosphaeridium pilar	Cymbosphaeridium sp. A	Dateriocradus cf. monterrosae	Dateriocradus sp. A
GOG4/204-A	66.31	0.35	0.65						1.7							
GOG4/207-A	67.465	0.4	4						11.85							
GOG4/209-A	68.545								1.35							0.4
GOG4/212-A	69.595		0.7						7.3							0.75
GOG4/214-A	70.715		3.05						3.65							3.05
GOG4/216-A	71.835	3	3.6						1.5				6.3			3.6
GOG4/218-A	72.955	5.1	2.5			3.85			7.65							
GOG4/220-A	74.075		1.45						7.1							
TRENCH5/222-A	75.195	6.4							2.95							
TRENCH5/225-A	76.315	1.5	1.7						4.7							
TRENCH5/228-A	77.435		1.5						2.95							1.5
GOG5/232-A	78.435								12							
GOG5/234-A	79.545								7.7							
GOG5/236-A	80.665	4.65	4.65						2.3							
GOG5/238-A	81.785															
GOG5/241-A	83.465								20.35							2.15
GOG5/243-A	84.585	0.75	1.8						4.3							
GOG6/252-A	86.555	1.7	1.7						5.05							
GOG6/254-A	87.675	1.45	4.55						2.25							
GOG6/256-A	88.81	2.55							2.55							
GOG6/259-A	89.835		1.1						2.3							
GOG6/263-A	90.95		5.05						2							
GOG6/266-A	92.09		22.6						1.65	1.65						
GOG6/269-A	93.49		7.3						9.8							
GOG6/271-A	94.61		14.7									2.8				
GOG6/273-A	95.73		12.55						1.65						1.65	
GOG6/275-A	96.85		12.15													
GOG6/277-A	97.97		24.6						1.7						1.8	
GOG7/282-A	104.19		12.85													
GOG8/288-A	113.715		39.8						6.05							
GOG9/292-A	116.505		12													
GOG10/294-A	119.21		34.9													
GOG11/298-A**	123.315		14.5													
GOG11/300-A*	125.405		51.35		0.8				4.1							
GOG12/302-A	128.58	5	67.2			17.4										

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Dilatisphaera laevigata	Dorsennidium spp.	Dorsennidium europaeum	Dorsennidium formosum	Dorsennidium pentagonale	Dorsennidium rhomboidium	Dorsennidium wenlockianum	Dorsennidium sp. A	Eisenackidium spp	Eisenackidium wenlockense	Eisenackidium sp. A	Estiastra granulata	Eupoikilofusa filifera	Eupoikilofusa tenuistriata	Evittia spp.
GOG1/2-C	-2.56		4.1	14.05	1.15	2	13.1	46.65			1.3	0.45		0.8		
GOG1/5-C	-1.8		1.75	6.25	1.75	6.6	14.85	33.5	PRESENT		2.65	0.35		3		
GOG1/7-C	-1.12		3.35	23.9	1.9	11.35	15	73.65	PRESENT		0.6	PRESENT		1.3		
TRENCH1/9-C	-0.39		6	31.6	3.05	4.8	16.95	62.35	0.65		1.2			1.85		
TRENCH1/10-A	-0.015		10.8	62.95	4	3.3	22.9	104.3	PRESENT		0.8			4.15		
TRENCH1/11-A	0.015		7.05	43.85	9.3	0.5	15.9	71.25					0.8	5.4		
TRENCH1/12-A	0.145		9.3	38.15	11.1	3.9	25.85	106.1						6.7		
TRENCH1/14-A	0.54		4.2	20.25	4.6	6.75	15.2	43.1					0.9	19.25		
TRENCH1/17-A	0.85		4.45	13.1	4.15	5.25	18.4	30.7						14.8		
TRENCH1/23-A	1.92		2.45	30.85	7.1	2.3	15.1	63.65			1.65	PRESENT				
TRENCH1/29-A	3.13		2.5	163.1	7.5	5	47.65	107.85						17.55		
GOG2/34-A	4.23		3.45	112.25	6.85	6.85	30.65	77.95						31.65		
GOG2/37-A	5.275		22.3	95.65	7.7	9.75	53.5	73.55						42.1		
GOG2/42-A	6.65		12.4	56.25	7.95	5.65	40.65	64.35						9		
GOG2/47-A	7.73		3.2	82.3	1.6	6.55	24.8	161.8						19.85		
GOG2/50-A	8.825		0.7	49.2	3.55	6.9	26.2	45						30.45		
GOG2/55-A	9.99		0.8	11.15	3.1	0.5	8.25	14.6						10.8		
GOG2/62-A	11.15		8.5	52.8	4.25	5.9	40.75	52.05						25.95		
GOG2/65-A	12.15		5	62.75	6.8	5	13.45	69.35						22.85		
GOG2/69-A	13.37		3.8	22.05	1.8	15.9	32.45	11.35						11.65		
GOG2/72-A	14.49		3.55	15	1.2	3.6	19.3	20.15						8.65		
GOG2/75-A	15.56		7.7	82.55	3.8	12.95	23.7	60.35						12.2		
GOG2/77-A*	16.62		0.1	3.7	0.1	0.7	0.4	1.35						0.35		
GOG2/81-A	17.67		0.85	9.95	1.05	3.8	2.7	9.1						4.45		
TRENCH2/83-A	18.55		4.7	29.65	2.2	7.8	14.7	19.8						5.8		
TRENCH2/88-A	19.85		4.5	12.8	1.5	16	23.15	8.45						13.45		
TRENCH2/90-A	20.985		4.45	9.95	0.9	17.2	11.9	10.7						21.25		
TRENCH2/94-A	22.2		3.2	11.1	0.8	6.85	11.35	6.5						7.3		
TRENCH2/96-A	23.315		4.15	17.15	1.05	9.2	15.45	10.9						10.3		
GOG3/98-A	24.44		0.4	1.6	0.8	2.2	2.55	1.8						3.65		
GOG3/100-A	25.63	PRESENT	1.4	4.7	0.9	3.7	7.1	3.5						4		
GOG3/103-A	26.68		2.5	11.3	1.5	3.35	7.7	5.75						3.05		
GOG3/106-A	27.83		2.25	6.55	0.45	1.75	3.05	4.5						4.2		
GOG3/108-A	28.76		3.55	8.35	PRESENT	3.25	5.35	5.85						10.15		
GOG3/111-A	29.95		1.5	2.65		1.1	1.75	2.35						11.65		
GOG3/113-A	31.01		0.25	5.25	0.6	1.6	2.7	3.5						12.5		
GOG3/116-A*	32.095		1.1	1.1	0.4	0.6	1.35	1.15						1.3		
GOG3/119-A	33.21		0.85	3		4.35	5.9	5.4						6.85		
GOG3/122-A	34.35			3.75		5.1	2.75	3.4						10.95		
GOG3/124-A*	35.47		0.4	0.45	0.2	3.8	1.25	0.85						0.45		
GOG3/127-A	36.415		1.65	9.15	0.25	5.2	5.15	5.4						5.5		
GOG3/131-A	37.545		1.75	4.7	0.9	2.45	2.45	3.3						2.65		
GOG3/135-A	38.67		0.5	1.55		1.95	1.05	1.25						2.65		
TRENCH3/141-A**	39.71		1.4	1.45	0.25	0.45	1	5.15								
TRENCH3/144-A	40.89			7.7	3.55	17.6	3.15	15.85						6.05		
TRENCH3/147-A	42.04		7.25	5.85	1.4	11.4	9.05	18.6						7.15		
TRENCH3/151-A	43.17		7.9	18.4	2.2	3.5	10.8	61.85						24.1		
TRENCH3/154-A	44.37		6.05	4.9	1.15	3.8	8.75	15.9						1.9		
TRENCH3/156-A	46.05		5.75	19.1	1.9	1.9	4.95	44.2								
TRENCH3/160-A	47.23		6.2	5.2		0.4	0.45	8.2						1.2		
TRENCH4/163-A	50.43		3.7	6.55	1.25	0.4	2.45	20.8						1.2		
TRENCH4/165-A	51.03		10.25	25.15	1.35	3.9	23.2	16.55								
TRENCH4/LE2-A	51.25		3.4	4.3	0.7		0.95	3.1			0.35					
TRENCH4/ LE1-A	51.465		7.55	68.6	6.3	10.4	38.05	35.35						1.35		
TRENCH4/ ME1-A(a+b)	51.605		4.15	18.35	4.15		12	22.5						1.7		
TRENCH4/ME2-A(a+b)	51.805		18.15	20.85	5.85	1.05	8.25	9.25			0.85					
TRENCH4/167-A	52.27		2.8	23.15	2.8	4.2	11.5	24.7						1.5		
TRENCH4/170-A	53.35		26.6	76.95		1.95	22.55	104.9						6.2		
TRENCH4/174-A	54.8		7.7	14.6	1.55			22.3								
TRENCH4/176-A	55.92		6.7	4.05		PRESENT	1.4	12.15			1.25					
TRENCH4/180-A	57.37		10.45	17.8		1		17.35			1			1.75		
TRENCH4/183-A	58.37		13.6	19.75			PRESENT	27.2						PRESENT		
TRENCH4/187-A	59.64		41.6	33.5		2.15	6.2	85.1			6.3			10.5		
TRENCH4/189-A	60.76		7.35	4.5		0.55	4.55	5.65			1.15					
TRENCH4/192-A	61.81		12.9	8.7			1.95	5.2								
TRENCH4/195-A	62.87		4.2	3.55			0.65	18.35								
TRENCH4/197-A	63.98		7.65	13			1.1	20.8						1.05		
TRENCH4/200-A	65.18		12.9	7.25	0.6		4.45	18.6		0.5						

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Dilatisphaera laevigata	Dorsennidium spp.	Dorsennidium europaeum	Dorsennidium formosum	Dorsennidium pentagonale	Dorsennidium rhomboidium	Dorsennidium wenlockianum	Dorsennidium sp. A	Eisenackidium spp	Eisenackidium wenlockense	Eisenackidium sp. A	Estiastra granulata	Eupoikilofusa filifera	Eupoikilofusa tenuistriata	Evittia spp.
GOG4/204-A	66.31		2.05	1.35				1.5								
GOG4/207-A	67.465		5.75	1.65				3.1								
GOG4/209-A	68.545		3.65	4.05	0.85		1.35	8								
GOG4/212-A	69.595		10.2	7.3			5.8	5.1			0.75					
GOG4/214-A	70.715	0.6	9.75	11.55			7.9	7.9			0.6				0.6	
GOG4/216-A	71.835		10.85	28.8		2.1	14.7	26.4						3.6		
GOG4/218-A	72.955		7.65	35.65		2.5	11.5	35.7						8.95	1.25	
GOG4/220-A	74.075		7.1	14.8	2.1	25.55	20.05	26.75			2.1					
TRENCH5/222-A	75.195		20.15	46.25	8.9	22.55	16.25	44.8						3.45		
TRENCH5/225-A	76.315		10.2	57.5	4.7	38.8	51.45	59.05						4.95		
TRENCH5/228-A	77.435		17.85	35.75	4.45	11.95	61	59.5						8.95		
GOG5/232-A	78.435		20.4	119.25	7.55		33.45	143.85						2.6		
GOG5/234-A	79.545	1.25	3.75	14.2		1.25	5.75	24.55						2.25	1.25	
GOG5/236-A	80.665		7	13.95	1.15		9.3	81.65						2.35		
GOG5/238-A	81.785		6.2	20.9	0.75		6.2	38.05						3.85	0.5	
GOG5/241-A	83.465		18.65	96.15	3.05	7.4	19.55	136.9						12.55		
GOG5/243-A	84.585		2.95	6.8	22.55		1.05	12.65						PRESENT	0.75	
GOG6/252-A	86.555		5.15	10.25			3.35	23.9						11.95		
GOG6/254-A	87.675		2.2	16.45	0.8	1.45	3	58.25						8.4	0.8	
GOG6/256-A	88.81		22.9	61.1	11.7	9.15	40.25	163.9						11.7		
GOG6/259-A	89.835		2.25	11.3		1.15	1.15	39.55			1.1			15.6		
GOG6/263-A	90.95		11.2	169.55	14.15		39.6	339.1		2				13.2	20.35	
GOG6/266-A	92.09		11.85	93.85	15.4		13.4	110.75						5.2		
GOG6/269-A	93.49		2.35	53	4.95			99								
GOG6/271-A	94.61		4.2	121.35	8.4	2.8	11.2	115.7						7	2.1	
GOG6/273-A	95.73		3.3	59.8	1.65		10.5	69.2		1.65				3.9		
GOG6/275-A	96.85			73.65	5.2	3.3	3.6	103.4						3.4	1.7	
GOG6/277-A	97.97	PRESENT	3.4	81.4	3.5		7	92.6						8.8		
GOG7/282-A	104.19			9.85	9.7	25.65	12.85	61.6						PRESENT	1.55	
GOG8/288-A	113.715	5.1		65.65	2.1		8.15	180.75								
GOG9/292-A	116.505			32.05			1.45	60.85								
GOG10/294-A	119.21	5.95	1.9	70.45			4.2	98.25			1.9					
GOG11/298-A**	123.315	22.45		7.85				14.6								
GOG11/300-A*	125.405			9.25		5.55	0.8	47.8								
GOG12/302-A	128.58	306.7		157.15	11.6	10.8	23.2	504.9						170.55		

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Evittia remota Group	Evittia robustispinosum	Glyptosphaera heltaskelta	Glyptosphaera speciosa	Gorgonisphaeridium spp	Gorgonisphaeridium citrinum	Gorgonisphaeridium ? listeri	Gorgonisphaeridium ? listeri var. A	Gorgonisphaeridium ramosum	Gorgonisphaeridium succinum	Gorgonisphaeridium sp. A	Gorgonisphaeridium sp. B	Hapsidopalla jeandeunffi	Helosphaeridium spp	Helosphaeridium clavispinulosum
GOG1/2-C	-2.56	64			PRESENT	0.35	3.9			2.1	17.55			3.9	0.35	
GOG1/5-C	-1.8	77			0.7	1.4	4.15				22.95			8.4		0.55
GOG1/7-C	-1.12	79.5			0.7		2.2			0.6	21.65			11.25		
TRENCH1/9-C	-0.39	183.5			2.5		0.65			0.65	10.4			1.85		
TRENCH1/10-A	-0.015	116.5			1.6		0.8		0.8		17.2				0.8	
TRENCH1/11-A	0.015	243			1.3	0.8	1.85			2.65	9.3		PRESENT		0.5	
TRENCH1/12-A	0.145	156					0.6			0.7	12.35				PRESENT	
TRENCH1/14-A	0.54	216.5			1.1		0.65				6.45					
TRENCH1/17-A	0.85	142					0.95			1.4	7.1					
TRENCH1/23-A	1.92	163.5			PRESENT	0.5	0.65			0.65	15.9			4		PRESENT
TRENCH1/29-A	3.13	944									15.15			7.5		
GOG2/34-A	4.23	355.5									12.4			6.2	2.05	
GOG2/37-A	5.275	429									9.6					
GOG2/42-A	6.65	466.5			2.3	2.3					9			1.15	2.25	
GOG2/47-A	7.73	938			1.6		1.6			1.6	4.9			14.6	1.6	
GOG2/50-A	8.825	465.5			0.65		0.65			0.7	5.5			1.35	0.7	
GOG2/55-A	9.99	308.5			0.8						2.9			2.6	0.4	
GOG2/62-A	11.15	917				0.95			0.95		2.35			12.75		0.95
GOG2/65-A	12.15	477.5		1.05	2				1.05					11.05		PRESENT
GOG2/69-A	13.37	197			0.65		PRESENT			0.65	1.35			5.4		
GOG2/72-A	14.49	122			0.4						0.8			0.8		
GOG2/75-A	15.56	245		0.75	1.5					0.75				4.6		
GOG2/77-A*	16.62	47			0.4						0.75				0.15	
GOG2/81-A	17.67	75.5			2.15						0.3			1.3		
TRENCH2/83-A	18.55	203			1.05				0.35		1.45			1.45		
TRENCH2/88-A	19.85	203.5			3.4				0.45					4.65		
TRENCH2/90-A	20.985	152									0.4			1.9	0.4	
TRENCH2/94-A	22.2	120.5			0.35						1.15					
TRENCH2/96-A	23.315	179			0.5					0.45				5.9		1.5
GOG3/98-A	24.44	35.5	0.2		1.25									0.4		
GOG3/100-A	25.63	58.5			0.75									2.1		0.2
GOG3/103-A	26.68	50			1.75					0.4				2		0.7
GOG3/106-A	27.83	30			1.8											
GOG3/108-A	28.76	71.5			1									1.25	0.25	0.5
GOG3/111-A	29.95	20.5			0.9									1.8		0.2
GOG3/113-A	31.01	112	0.25		0.25									1.1		
GOG3/116-A*	32.095	62.5			1.15										0.2	
GOG3/119-A	33.21	149.5			0.2					0.2	0.2					
GOG3/122-A	34.35	163.5			1											
GOG3/124-A*	35.47	44.5			0.2						0.2			0.2		
GOG3/127-A	36.415	164.5			0.25									2.65	0.25	0.25
GOG3/131-A	37.545	88												0.2		0.45
GOG3/135-A	38.67	66.5		0.15	1.55						0.15					
TRENCH3/141-A**	39.71	46.5			0.25										0.25	
TRENCH3/144-A	40.89	296			1.15									42.55		
TRENCH3/147-A	42.04	171			4.4									1.5		
TRENCH3/151-A	43.17	181.5			3.5									7.7		
TRENCH3/154-A	44.37	60	0.4		1.9									1.9		
TRENCH3/156-A	46.05	166			1.8									5.75		
TRENCH3/160-A	47.23	64			1.7									3.4	0.45	
TRENCH4/163-A	50.43	61			1.2									0.4	0.8	
TRENCH4/165-A	51.03	198			1.35									4.95		
TRENCH4/LE2-A	51.25	36			2.95									0.35	0.3	
TRENCH4/ LE1-A	51.465	493.5			9.05									29.1	1.35	
TRENCH4/ ME1-A(a+b)	51.605	226			17.05		1.7							28.3	2.05	
TRENCH4/ME2-A(a+b)	51.805	175			8.2	2.75								29.15	1.05	
TRENCH4/167-A	52.27	303			8.9									15.65	1.5	
TRENCH4/170-A	53.35	119			24.65		8.1					1.95		6.2		
TRENCH4/174-A	54.8	53.5			15.4		0.75					1.5				
TRENCH4/176-A	55.92	80			10.6											
TRENCH4/180-A	57.37	47.5			23		5.75				0.75			0.75		
TRENCH4/183-A	58.37	71.5	1.55	1.55	44		4.6					1.5			3.05	
TRENCH4/187-A	59.64	114.5		4.15	99.4		37.95					4.05		8.45		
TRENCH4/189-A	60.76	PRESENT		1.7	23.3		10.7									
TRENCH4/192-A	61.81	PRESENT			33.55		19.05									
TRENCH4/195-A	62.87	PRESENT			20.7		13.55					3				
TRENCH4/197-A	63.98	PRESENT		1.05	45		11.15									
TRENCH4/200-A	65.18	28	1.1		2.7		4.15							0.5		

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Evittia remota	Evittia robustispinosum	Glyptosphaera heltaskelta	Glyptosphaera speciosa	Gorgonisphaeridium spp	Gorgonisphaeridium citrinum	Gorgonisphaeridium ? listeri	Gorgonisphaeridium ? listeri var. A	Gorgonisphaeridium ramosum	Gorgonisphaeridium succinum	Gorgonisphaeridium sp. A	Gorgonisphaeridium sp. B	Hapsidopalla jeandeunffi	Helosphaeridium spp	Helosphaeridium clavispinulosum
GOG4/204-A	66.31	21			11.1	0.35	0.35				0.7			0.35	1.7	
GOG4/207-A	67.465	13			16.1		4.1				3.25				0.6	
GOG4/209-A	68.545	20.5		1.35	11.95	0.45	1.35				3.9					
GOG4/212-A	69.595	PRESENT			12.8		4.35				4.35					
GOG4/214-A	70.715	39.5			5.45		4.25					0.6		3.65	0.6	
GOG4/216-A	71.835	67.5			28.5						12			134.05	2.1	
GOG4/218-A	72.955	485			16.6		2.55				1.3			3.8		
GOG4/220-A	74.075	68.5		2.9	18.5									32.4	2.1	
TRENCH5/222-A	75.195	245.5			21.95									85.1		
TRENCH5/225-A	76.315	50		1.5	15.35						6.4			47.15	3.2	
TRENCH5/228-A	77.435	200			4.5						1.5	1.5		4.5		
GOG5/232-A	78.435	374			19.9		4.2	PRESENT			2.6			40.25		
GOG5/234-A	79.545	256			13.25		1	1			3.5			21.15	3.25	
GOG5/236-A	80.665	348			26.85		4.65				11.65	1.15		14	2.35	
GOG5/238-A	81.785	220			1.25									28.75		
GOG5/241-A	83.465	746			39.5		2.15				14.3	4.35		148.6		
GOG5/243-A	84.585	57			14.85		4.3				1.8	0.75		57.45	2.2	
GOG6/252-A	86.555	260		3.45	44.35		3.45				1.7	1.75		13.75	5.15	
GOG6/254-A	87.675	550		0.75	2.3							0.8		9.15		
GOG6/256-A	88.81	838			80.5			2.55			4.6			140	4.6	
GOG6/259-A	89.835	292.5	1.15		14.55		7.9	1.15				3.35		18.15		
GOG6/263-A	90.95	601.5			19.1		5.05	3.05			7.05	12.05		118.4		
GOG6/266-A	92.09	1631.5			11.75		8.2					13.25				
GOG6/269-A	93.49	529		2.35	29.4		11.95	4.85			2.35	75.35		140.5		
GOG6/271-A	94.61	995.5			48.35		6.3	2.8			17.55	12.6		51.9		
GOG6/273-A	95.73	733.5		5.25	10.5		20.5	6.6				6.9		197.2		
GOG6/275-A	96.85	1543			33.2		5.4				3.5	12.25		91.75	3.4	
GOG6/277-A	97.97	572			15.65		14.25	3.6				8.65		216.8		
GOG7/282-A	104.19	249.5		3.6	24.1		8.15				10.8			9.7		
GOG8/288-A	113.715	853		6.05	16.55		10.25	11.15						9.05		
GOG9/292-A	116.505	335.5			9.1		0.75				2.3			23.95		
GOG10/294-A	119.21	1025.5		1.9	22.45	2.1		18.05			1.9			1.9		
GOG11/298-A**	123.315	88.5		1.95	6.6		2.65							0.65		
GOG11/300-A*	125.405	272		1.65	15.15		0.8									
GOG12/302-A	128.58	1359.5		5	15			25.85			5			89.9	5.8	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Helosphaeridium. latispinosum	Helosphaeridium pseudodictyum	Helosphaeridium sp. A	Helosphaeridium sp. B	Helosphaeridium ? sp. C	Hoegklintia spp.	Hoegklintia cf. corallina	Hoegklintia cf. digitata	Leiofusa estrecha	Leiofusa parvitatis	(<3μm)Leiosphere <46μm	(<3μm)Leiosphere 46-85μm	(<3μm)Leiosphere 85-132μm	(<3μm)Leiosphere 132μm+	(>3μm)Leiosphere <46μm
GOG1/2-C	-2.56		1.65					0.8	0.45		0.8	97.5	26.5	2		16.5
GOG1/5-C	-1.8		2.3			PRESENT		0.9	PRESENT		0.55	73.5	37.5			34.5
GOG1/7-C	-1.12		19.4						1.3			119.5	76.5	2.5		14.5
TRENCH1/9-C	-0.39		32.55								1.7	106	45	3		25.5
TRENCH1/10-A	-0.015		30.3			1.65		3.3	7.25		0.85	124.5	49	1.5		42.5
TRENCH1/11-A	0.015		29.75			PRESENT	1.05	1.85	6.3		PRESENT	142.5	80.5	15.5		56
TRENCH1/12-A	0.145		32.3				2.65		3.9		2.75	95	40	5		54
TRENCH1/14-A	0.54		16.3				2.9	0.45	3.35		0.65	203.5	117.5	5		79.5
TRENCH1/17-A	0.85		3.5					1.1				128.5	32.5	8		78.5
TRENCH1/23-A	1.92		18.15								0.5	75	52.5	7.5		30
TRENCH1/29-A	3.13		77.8									360.5	206	21	2.5	164.5
GOG2/34-A	4.23		148.45			1.4				PRESENT	1	162.5	102	14		71
GOG2/37-A	5.275		128.4								2.45	128.5	93.5	3		60.5
GOG2/42-A	6.65		88.05							1.15		178.5	102.5	5		72
GOG2/47-A	7.73		235.9								1.7	262	180.5			89
GOG2/50-A	8.825		25.95									203.5	84	3.5		33.5
GOG2/55-A	9.99		25.35						0.5			213	80.5	4		35.5
GOG2/62-A	11.15		51.55									245.5	111	16.5		52.5
GOG2/65-A	12.15		85.1								1.05	243.5	101.5	4.5		36.5
GOG2/69-A	13.37		67.55			PRESENT						286	90.5			19
GOG2/72-A	14.49		21.3								0.4	151.5	57.5			12.5
GOG2/75-A	15.56		65.7								0.75	176.5	102	4		30
GOG2/77-A*	16.62		2.7					0.1				110.5	55.5	5.5		14
GOG2/81-A	17.67		37.5									148.5	73.5	5		17.5
TRENCH2/83-A	18.55		33.9									160.5	99.5	9.5		26
TRENCH2/88-A	19.85		37.8			2.8						229.5	92.5	6		33
TRENCH2/90-A	20.985		29.25			0.5						108	77.5	2		27.5
TRENCH2/94-A	22.2		39.3			9.85						116	53.5	3.5		25.5
TRENCH2/96-A	23.315		62.95			5.75						236	58	10		35.5
GOG3/98-A	24.44		14.85			4.45						113.5	46	3.5		14
GOG3/100-A	25.63		26.95	0.2		7.05					0.25	140.5	49			37
GOG3/103-A	26.68		19.35			14.75						189.5	28	7		41
GOG3/106-A	27.83		17.2	0.25		9.35						151	34.5	3.5		41
GOG3/108-A	28.76		11.4	0.25		19						163.5	47.5	1.5		47
GOG3/111-A	29.95		20.25	0.2		22.3						148	38	5		41.5
GOG3/113-A	31.01		19.65			11.05						81.5	39.5	9	1.5	28
GOG3/116-A*	32.095		2.8	0.2		6.5				0.2		113.5	27.5	2	1	22.5
GOG3/119-A	33.21		6.15			6.3						174	39.5			38
GOG3/122-A	34.35		17.55	1		5.15				0.35		156.5	20	3.5		41.5
GOG3/124-A*	35.47		8			6.8						90	17	2.5		20.5
GOG3/127-A	36.415		6.15	1.15		13.85				0.25	0.25	108.5	35.5	14.5		61.5
GOG3/131-A	37.545		16.8			4.25						81	21	2.5		25.5
GOG3/135-A	38.67		18.25	0.9		3.65					0.15	134.5	27	1		41.5
TRENCH3/141-A**	39.71		5.65			4.95						195.5	41	5.5		37.5
TRENCH3/144-A	40.89		183.6			18.45						185	51.5			40.5
TRENCH3/147-A	42.04		16.05			12.05					0.5	163	38	4.5		46
TRENCH3/151-A	43.17		51.55			18.3						283	101.5	7.5		109.5
TRENCH3/154-A	44.37		56.85			8.7						247	85.5	4		72.5
TRENCH3/156-A	46.05		157.75			2.95						306.5	65			89
TRENCH3/160-A	47.23		99.7			2.2						323.5	38	2.5		46
TRENCH4/163-A	50.43		13.45			13.05						501	83	8.5		99.5
TRENCH4/165-A	51.03		70.35			3.75						741.5	186.5			181.5
TRENCH4/LE2-A	51.25		3.85			5						1511.5	194	36	16	308.5
TRENCH4/ LE1-A	51.465		108.9			26.3					2.1	3199	612.5	48		1093
TRENCH4/ ME1-A(a+b)	51.605		147.95			5.4						3988	1396	66.5		1392.5
TRENCH4/ME2-A(a+b)	51.805		38.4			16.65					0.85	1790	376	76		718.5
TRENCH4/167-A	52.27		124.7			9					1.4	1182	354.5	30.5		310
TRENCH4/170-A	53.35		76.7			6.2						3349	749	35.5		873
TRENCH4/174-A	54.8		8.45			7.7					0.75	1539.5	368	16		434.5
TRENCH4/176-A	55.92		34.1			21						2980	665.5	98		860
TRENCH4/180-A	57.37		19.8			37.8					2	1289.5	215	25		590
TRENCH4/183-A	58.37		36.4			49.8					1.55	4481	619.5	95.5		1525.5
TRENCH4/187-A	59.64		68.65			42.25						5843.5	1017	95	63	1605.5
TRENCH4/189-A	60.76		0.6			2.25						2652.5	419.5	35.5		714.5
TRENCH4/192-A	61.81		0.65			4.2						3326	332.5	26.5		851.5
TRENCH4/195-A	62.87		1.55			2.35						2313	381.5			613.5
TRENCH4/197-A	63.98					1.1						3702	793.5	127.5		1320
TRENCH4/200-A	65.18		0.5			0.5						3466.5	730	70		695

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Helosphaeridium. latispinosum	Helosphaeridium pseudodictyum	Helosphaeridium sp. A	Helosphaeridium sp. B	?Helosphaeridium sp. C	Hoegklintia spp.	Hoegklintia cf. corallina	Hoegklintia cf. digitata	Leiofusa estrecha	Leiofusa parvitatis	(<3µm)Leiosphere <46µm	(<3µm)Leiosphere 46-85µm	(<3µm)Leiosphere 85-132µm	(<3µm)Leiosphere 132µm+	(>3µm)Leiosphere <46µm
GOG4/204-A	66.31					0.35						2403.5	598.5	88.5	10.5	817.5
GOG4/207-A	67.465											2444	668	93	13	1189.5
GOG4/209-A	68.545						0.95					5818	1118	129	PRESENT	1088.5
GOG4/212-A	69.595		0.75									3012	582	98.5	PRESENT	1372.5
GOG4/214-A	70.715		22.5			7.9						1580	359.5	24		671.5
GOG4/216-A	71.835		14.4		5.1	22.5					6.3	4533.5	1179	141.5	46	1553
GOG4/218-A	72.955		7.7		6.4	15.3					6.35	4581.5	833	64		1739.5
GOG4/220-A	74.075		9.95		3.55	3.55					1.45	4121.5	994	89.5		2192.5
TRENCH5/222-A	75.195		24.65								32.05	5088	1415.5	133		3113.5
TRENCH5/225-A	76.315		12.5		6.4	18.7					4.7	4765.5	726	112	21	1713
TRENCH5/228-A	77.435		101.45		1.5	7.45					13.4	2145	437.5	15		978
GOG5/232-A	78.435		14.6			2.6					2.1	3535	1242	101	34.5	2184
GOG5/234-A	79.545		118.45		5.75	15.85						8322	601.5	133.5		3378.5
GOG5/236-A	80.665		112.05		7	11.7					3.5	11228.5	1490.5	99		3875
GOG5/238-A	81.785		26.5		0.75	0.75					3.35	1957.5	173	39		336.5
GOG5/241-A	83.465		271.35		3.05	13.85					9.55	6556	1139	142		2745.5
GOG5/243-A	84.585		45.6			2.15					2.5	4822	529	44	19	1660
GOG6/252-A	86.555		208.15			15.45					1.7	6627.5	836	28		3644.5
GOG6/254-A	87.675		60		16.75	1.45					2.95	3274.5	471	53		747.5
GOG6/256-A	88.81		286.05		62.6	12.35					33.1	8162.5	2358	163		3499
GOG6/259-A	89.835		131.9		2.2	2.25					3.45	3352.5	630	65.5	33	862
GOG6/263-A	90.95	3.05	84.75		6.1	2					14.05	5069.5	2159.5	95.5		2460
GOG6/266-A	92.09		134.45		15.4	26.6					32.5	19118	2610	130.5		9983
GOG6/269-A	93.49		177.8			16.95						8759.5	1163	36.5		3166
GOG6/271-A	94.61		119.2		37.15	19.65						22425.5	5266	602.5	78.5	7021
GOG6/273-A	95.73		122.1			7.2					37	10891.5	3132	126.5		2745.5
GOG6/275-A	96.85		89.3		12.3						6.85	11600.5	2399	186	72.5	3773
GOG6/277-A	97.97		84.4		12.3	19.1					1.7	8322	1068.5	129.5	75.5	2579.5
GOG7/282-A	104.19		54.6		3.1	9.2					3.6	4044	694.5	19.5		1594.5
GOG8/288-A	113.715		227.8		56.35	45.45					13.5	4814	522.5	56	52.5	2144
GOG9/292-A	116.505		93.75		3.75	14.95					1.45	2851	269	37.5	37.5	1035
GOG10/294-A	119.21		228		5.75	29.8					8.2	6807	716			2974.5
GOG11/298-A**	123.315		17.8			9.95						3939.5	523.5	32.5		1353.5
GOG11/300-A*	125.405		19.55		0.8	10.85						3900	623.5	148	21.5	1713.5
GOG12/302-A	128.58	29	331.9		102.3	970.35					30.05	3077	485.5		33.5	1599

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	(>3μm)Leiosphere 46-85μm	(>3μm)Leiosphere 85-132μm	(>3μm)Leiosphere >132μm	Leptobrachion spp.	Leptobrachion arbusculiferum	Leptobrachion digitatum	Leptobrachion sp. A	Leptobrachion sp. B	Lophosphaeridium spp	Lophosphaeridium sp. A	Micrhystridium spp.	Micrhystridium inflatum	Micrhystridium intonsurans	Micrhystridium stellatum	Micrhystridium sp. A
GOG1/2-C	-2.56	9				0.45	2.7				5.75	0.45	11.2	18.5	92	0.35
GOG1/5-C	-1.8	26			2.65	2.1	2.65	0.9		0.35	1.7	0.35	10.45	24.5	75	1.95
GOG1/7-C	-1.12	14.5				2.75	1.2	1.3			6.15		17.8	57	190	
TRENCH1/9-C	-0.39	27.5	5.5			3.65	2.35	0.55			6.75	0.85	16.35	26.5	151.5	
TRENCH1/10-A	-0.015	23				14.1	16.25	2.45					16.45	5	141.5	
TRENCH1/11-A	0.015	29.5	6			10.35	16.4	2.65			1.55	1.05	18.2	5.5	117	
TRENCH1/12-A	0.145	53.5	4.5			11.25	11.1	2.05		4.15		1.3	16.25	9.5	126	
TRENCH1/14-A	0.54	63.5				3.25	5.2	0.45					9.55	2.55	87	
TRENCH1/17-A	0.85	39			0.4	1.95	9.4	3.2		3.3	0.85	1.1	16.85	2	20.5	
TRENCH1/23-A	1.92	16	2.5		0.5	0.5	9.15			1.3	0.65		15.75	48.5	90	
TRENCH1/29-A	3.13	82				7.55	12.55						37.6	10.5	277	
GOG2/34-A	4.23	46.5				1.4	7.6	3.45					29.85	47	174	
GOG2/37-A	5.275	48				1.15	6.3	2.6				2.6	46.45	6	128	
GOG2/42-A	6.65	20.5			1.1		11.35	7.95					36		266	1.15
GOG2/47-A	7.73	34					13.1	5.05					26.3	21	482	
GOG2/50-A	8.825	16.5				1.45	8						26.95	19.5	110.5	
GOG2/55-A	9.99	42.5					2.75	0.95				0.5	10.1	17.5	77	
GOG2/62-A	11.15	12					7.75	3.05					39.35	21	350.5	
GOG2/65-A	12.15	4.5				0.95	3	1.9					30.25	32	129	
GOG2/69-A	13.37	27	4		0.65	1.2	1.9	0.55		1.35			58.45	2.5	74.5	
GOG2/72-A	14.49	5	3.5				0.8	1.15					23.25	3.5	52.5	
GOG2/75-A	15.56	20	7				6.15	0.75					31.3	3	155.5	
GOG2/77-A*	16.62	15.5	1.5				0.4						1		1	
GOG2/81-A	17.67	19					0.55						12.3	4.5	59.5	
TRENCH2/83-A	18.55	30	2				1.05	0.7					15	4.5	91.5	0.4
TRENCH2/88-A	19.85	36	3.5			1.95	1.05	0.55		0.45			33.7	3.5	100.5	
TRENCH2/90-A	20.985	8					0.4	0.5					18.25		95	
TRENCH2/94-A	22.2	18					0.8	0.75		0.7			7	2	49	
TRENCH2/96-A	23.315	32				0.85	0.5	0.95					17.25	13	90.5	
GOG3/98-A	24.44	22.5					0.2	0.2		PRESENT			3.95	PRESENT	16.5	
GOG3/100-A	25.63	31.5	4			0.2		0.75		2.05			6.1	3	29	
GOG3/103-A	26.68	25.5	2.5			0.4	0.7						2.15	2.5	31.5	
GOG3/106-A	27.83	28	1.5				0.45	PRESENT					1.6	2.5	24.5	
GOG3/108-A	28.76	28	2					0.75		0.25			2.25	4	20	
GOG3/111-A	29.95	21.5					0.45	0.2					1.25	1	32.5	
GOG3/113-A	31.01	40	4.5	1.5									2.2		26.5	
GOG3/116-A*	32.095	10					0.2			0.35		0.2	0.95	3	6.5	
GOG3/119-A	33.21	24.5	1.5				0.45	0.45				0.2	7.4	7	41.5	
GOG3/122-A	34.35	20					1.4	0.35		1.7			10.65	3.5	41.5	
GOG3/124-A*	35.47	16.5	0.5				0.65			0.2			1.65	0.5	8.5	
GOG3/127-A	36.415	52.5	1.5			0.25	0.85	1.7		0.6		0.6	11.35	2	12	
GOG3/131-A	37.545	13.5				0.45	0.25	0.25		0.25			2.5	2.5	25	
GOG3/135-A	38.67	33.5	1.5							1.15			1.4	1.5	6.5	
TRENCH3/141-A**	39.71	26	5							0.5					9	
TRENCH3/144-A	40.89	48					4.05					PRESENT	10.25	11	133	
TRENCH3/147-A	42.04	44.5	2			1.75	1.4			1.8		0.9	7.4		46.5	
TRENCH3/151-A	43.17	75	8.5				0.7			1.45		0.7	3.55		84	
TRENCH3/154-A	44.37	47											5.3		17.5	
TRENCH3/156-A	46.05	28.5					0.9						2.95		16.5	
TRENCH3/160-A	47.23	38.5										1.4	2.05		32.5	
TRENCH4/163-A	50.43	33.5	3									0.4	1.25		22	
TRENCH4/165-A	51.03	57								1.35			25.7	PRESENT	61	
TRENCH4/LE2-A	51.25	65	17.5										0.35		25	
TRENCH4/ LE1-A	51.465	255.5	26.5							2.1		1.35	20.9		52.5	
TRENCH4/ ME1-A(a+b)	51.605	246.5	23							2.05		4.15	5.85	PRESENT	46	
TRENCH4/ME2-A(a+b)	51.805	283	52.5				0.85						5.15			
TRENCH4/167-A	52.27	94	9.5							1.4			20.75		72.5	
TRENCH4/170-A	53.35	323.5								1.95			34.9		48.5	
TRENCH4/174-A	54.8	292.5	32							0.75			0.75		46	
TRENCH4/176-A	55.92	448.5	102										2.65		PRESENT	
TRENCH4/180-A	57.37	218.5	26.5										3		37	
TRENCH4/183-A	58.37	738.5	167	24						3		1.55	1.55		71.5	
TRENCH4/187-A	59.64	361.5	68							10.35					114.5	
TRENCH4/189-A	60.76	209.5	37							2.25			2.3	PRESENT	PRESENT	
TRENCH4/192-A	61.81	216	53							8.5			4.5		53.5	
TRENCH4/195-A	62.87	168.5	34.5							4.2					59	
TRENCH4/197-A	63.98	540	112.5	22						6.35					22	
TRENCH4/200-A	65.18	156	13.5	13.5						1.1		1.05	1.1		59	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m).	(>3µm)Leiosphere	(>3µm)Leiosphere	(>3µm)Leiosphere	Leptobrachion	Leptobrachion	Leptobrachion	Leptobrachion	Leptobrachion	Lophosphaeridium	Lophosphaeridium	Micrhystridium	Micrhystridium	Micrhystridium	Micrhystridium	Micrhystridium
	(above/below Wenlock-	46-85µm	85-132µm	>132µm	spp.	arbusculiferum	digitatum	sp. A	sp. B	spp	sp. A	spp.	inflatum	intonsurans	stellatum	sp. A
	Ludlow boundary)															
GOG4/204-A	66.31	374	44.5	13						1.05		2.05		10.5	13	
GOG4/207-A	67.465	457.5	78.5	13						3					54	
GOG4/209-A	68.545	415								0.4		3	0.45		PRESENT	
GOG4/212-A	69.595	421	27.5												PRESENT	
GOG4/214-A	70.715	184	32											8	55.5	
GOG4/216-A	71.835	355	67.5					2.1	4.5			1.5	5.7	PRESENT	111	
GOG4/218-A	72.955	409			2.6			2.55				1.25	10.2	PRESENT	92	
GOG4/220-A	74.075	523.5	116										4.3	PRESENT	53	1.45
TRENCH5/222-A	75.195	419.5	137.5		2.95			6.4	9.4	3.45			16.6	66.5	66.5	
TRENCH5/225-A	76.315	722	50	25						4.55			11.15	PRESENT	41.5	1.5
TRENCH5/228-A	77.435	205.5								1.5		3	32.75	14	160	
GOG5/232-A	78.435	531	66.5	85					5.45				31.35	PRESENT	32	
GOG5/234-A	79.545	1130.5	133.5		1.25				2.25	2.5			4.25		130	1.25
GOG5/236-A	80.665	745	248.5		1.15					1.15		1.15	4.65		99.5	
GOG5/238-A	81.785	75	8		0.5					1.55			2.05		44.5	
GOG5/241-A	83.465	617	81.5	40.5						3.05			42.05	149.5	264	
GOG5/243-A	84.585	353	44							0.75			1.05	19	60	
GOG6/252-A	86.555	861	28	44						1.75				PRESENT	200	
GOG6/254-A	87.675	91						0.75		1.55			2.3	34	212.5	
GOG6/256-A	88.81	512			4.6			9.15				2.55	51.95	41	41	
GOG6/259-A	89.835	113		51	1.15					1.15		5.7	5.7	18	202.5	
GOG6/263-A	90.95	628.5	41		6.1							2	4	41	205	
GOG6/266-A	92.09	1827	326.5		3.4	1.75		3.55		4.9			18.7	PRESENT	457	
GOG6/269-A	93.49	424	36.5						2.5	2.35		2.5	9.8	44.5	206	
GOG6/271-A	94.61	1074	78.5	78.5						14		2.1	9.8	PRESENT	367	
GOG6/273-A	95.73	458.5	84.5							3.3		3.3	3.9	42.5	271.5	
GOG6/275-A	96.85	679	81						3.4	5.3		1.7	3.4	PRESENT	153.5	
GOG6/277-A	97.97	572	32.5	43					1.7				5.05		75.5	
GOG7/282-A	104.19	243	19.5										25.65		103	
GOG8/288-A	113.715	242	24.5				3		2.1			2.1	3	PRESENT	129.5	
GOG9/292-A	116.505	86.5		22			0.75						1.45	PRESENT	53	
GOG10/294-A	119.21	742.5											2.1		196	
GOG11/298-A**	123.315	143.5												PRESENT	18.5	
GOG11/300-A*	125.405	231.5	37	21.5						13.75			0.8	PRESENT	15.5	
GOG12/302-A	128.58	207								26.6			49.85	240	1104.5	

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Micrhystridium ? sp. B	Multiplicisphaeridium spp.	Multiplicisphaeridium arbusculum	Multiplicisphaeridium arbusculum var. A	Multiplicisphaeridium eltonense	Multiplicisphaeridium variabile	Multiplicisphaeridium sp. A	Multiplicisphaeridium sp. B	Multiplicisphaeridium sp. C	Neoveryhachium mayhillensis	Onondagella deunffii	Oppilatala spp.	Oppilatala ramusculosa	Oppilatala septispinosum
GOG1/2-C	-2.56		5.05	4.55		32.2	8.8	0.45	1.15		0.45	0.45			2.45
GOG1/5-C	-1.8		9.1	6.95		41.7	17.8	1.05			1.05			PRESENT	8.55
GOG1/7-C	-1.12		13.5	10.5		38.6	11.45	3.9			PRESENT	0.7			9.3
TRENCH1/9-C	-0.39		16.45	5.45		41.85	16	1.2				PRESENT		PRESENT	10.75
TRENCH1/10-A	-0.015		12.3	21.3		42.45	27.9	2.5	PRESENT		2.45				23.65
TRENCH1/11-A	0.015		9.55	8.05		26.6	12.5	0.8			1.55				17.7
TRENCH1/12-A	0.145		3.9	14.55		35.1	7.25	0.7			1.25		0.6		15
TRENCH1/14-A	0.54		3.05	7.1		19.25	1.8		0.45	2.5	2.15				12.75
TRENCH1/17-A	0.85		1.65	6.4		42.1	3.15				2.35	1.8			7.55
TRENCH1/23-A	1.92		6.95	12.8		71.55	12.4	0.65			1.8	3.2	0.65		14.2
TRENCH1/29-A	3.13		20	75.15		216	70.25	17.6			5				117.65
GOG2/34-A	4.23		12.75	26.45		50.25	30.35	6.2	3.45		PRESENT	1.4			52.3
GOG2/37-A	5.275		9.9	36.95		37	8.6	4.8	1.3		1.3	1.15			27.2
GOG2/42-A	6.65		3.4	6.8		74.4	15.7	14.6	1.15	PRESENT		7.9			7.9
GOG2/47-A	7.73		21.2	36.4	PRESENT	33.2	36.2	8.25	PRESENT		1.6	3.3			19.65
GOG2/50-A	8.825		17.7	21.05		23.85	14.25	6.15	3.45		0.65				5.7
GOG2/55-A	9.99		11.35	4.05		3.7	6	3	0.4			1.65			16.15
GOG2/62-A	11.15		28.2	53.3	5.4	61.05	39.6	7.55							30.85
GOG2/65-A	12.15		4.75	21.1	PRESENT	80.1	30.85	11.15				0.95			19.8
GOG2/69-A	13.37		6.35	8.95		4.2	3.15	4.9				3.6			12.3
GOG2/72-A	14.49		2.35	0.8		9.9	4.35	1.55				0.8			8.25
GOG2/75-A	15.56		8.4	4.6		9.15	3.05	7.65	1.5			0.75			28.25
GOG2/77-A*	16.62		1.25			0.25		0.25	0.15			0.95			
GOG2/81-A	17.67		0.8	0.55		12.35		0.25	0.25			0.75			6.1
TRENCH2/83-A	18.55		0.75	4.85		12.85		1.85				1.45			8.85
TRENCH2/88-A	19.85		0.45	4.95	3.7	18.1		1.05				0.55			13.2
TRENCH2/90-A	20.985		2.2	2.25	10.65	10.2		0.9	0.4			3.25			13.65
TRENCH2/94-A	22.2		2.6	2	1.1	5.5		0.8	0.4	1.45		3.15			10.65
TRENCH2/96-A	23.315		3.4		2.95	20.7		1.8	0.45			8.6			13.75
GOG3/98-A	24.44		0.4			0.85		0.2				3			4.4
GOG3/100-A	25.63		1.55	0.25		6.9		0.45				2.1			4.9
GOG3/103-A	26.68		2.05	0.3		6.6	0.4	2.9	0.4			5.1	2.5	41.55	7.75
GOG3/106-A	27.83		0.45	0.25		0.55		1.9				2.65		0.9	5.1
GOG3/108-A	28.76		1.5		1.5	5.1		1.25	0.25			6.6	1	25.6	4.85
GOG3/111-A	29.95		0.45			7.15		0.25				2.45		0.45	1.75
GOG3/113-A	31.01		1.6	0.75	0.85	0.75		0.35	0.35			6.3			4.4
GOG3/116-A*	32.095		0.4		0.95	1.7		0.35		0.95		5.85			1.5
GOG3/119-A	33.21		0.85		1.6	2.15		1.05				3.15			3.5
GOG3/122-A	34.35		1		2.75	25.35	0.7	1.05		0.7		0.7			2.1
GOG3/124-A*	35.47		0.4		0.4	0.2	0.2	0.2		0.4		1.55			2.8
GOG3/127-A	36.415		1.7	0.25	3.45	10.45		2.25				1.6	0.3	0.25	11.35
GOG3/131-A	37.545		6.25		1.8	5.65		0.25				0.2			5.35
GOG3/135-A	38.67		0.3		0.9	0.65		0.5	0.15			0.9			0.8
TRENCH3/141-A**	39.71					0.5	0.7	0.5				3.05	1.15		1.4
TRENCH3/144-A	40.89		2.65		PRESENT	9.75					0.65	3.15			29.6
TRENCH3/147-A	42.04		5.3		0.5	2.65	1	2.25				5.7		3.45	35.7
TRENCH3/151-A	43.17		3.6		1.45	0.7	0.7	5.95	1.35			4.25			28.65
TRENCH3/154-A	44.37				0.4	0.4		1.15				1.55			2.3
TRENCH3/156-A	46.05		2.7			3.85		2.8							12.65
TRENCH3/160-A	47.23		0.85			1.25						0.9			27.7
TRENCH4/163-A	50.43		1.6			1.65		0.4				2.8			23.9
TRENCH4/165-A	51.03		2.55									6.15			45.1
TRENCH4/LE2-A	51.25		1					0.75				9			0.3
TRENCH4/ LE1-A	51.465		6.2									34			22.25
TRENCH4/ ME1-A(a+b)	51.605					2.05		10.9				5.85			12
TRENCH4/ME2-A(a+b)	51.805		0.85			0.85		1.05				9.4		1.05	5
TRENCH4/167-A	52.27		2.9			1.4		1.5				10.2		1.4	40.55
TRENCH4/170-A	53.35		18.9			8.1		1.95	1.95			3.85			50.7
TRENCH4/174-A	54.8		1.55			0.75		1.5				2.3			10
TRENCH4/176-A	55.92		3.9					1.4		1.25		9.5			20.25
TRENCH4/180-A	57.37		1			0.75		1.45				17.9			14.7
TRENCH4/183-A	58.37		12.1			5.95		4.55				10.55			27.25
TRENCH4/187-A	59.64		23.1			2.15		70.2				4.15			42
TRENCH4/189-A	60.76		2.2			0.55		6.8				2.3			1.15
TRENCH4/192-A	61.81		3.55					12.55							0.65
TRENCH4/195-A	62.87		2.8					15.7				10.65			
TRENCH4/197-A	63.98		5.15					16.65				19.35			
TRENCH4/200-A	65.18		0.6					11				56.95			

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Micrhystridium ? sp. B	Multiplicisphaeridium spp.	Multiplicisphaeridium arbusculum	Multiplicisphaeridium arbusculum var. A	Multiplicisphaeridium eltonense	Multiplicisphaeridium variabile	Multiplicisphaeridium sp. A	Multiplicisphaeridium sp. B	Multiplicisphaeridium sp. C	Neoveryhachium mayhillensis	Onondagella deunffii	Oppilatala spp.	Oppilatala ramusculosa	Oppilatala septispinosum
GOG4/204-A	66.31		0.35			0.35		1				10.2			
GOG4/207-A	67.465		3.2					12.9				12.3			
GOG4/209-A	68.545		6.6			0.95		7.05				5.65			
GOG4/212-A	69.595		4.35			0.7		5.85				10.25			
GOG4/214-A	70.715		5.5					9.75				4.3		4.3	6.1
GOG4/216-A	71.835		9.9			50.7		24.9	5.1						35.7
GOG4/218-A	72.955		28.05			11.45	1.3	28.1				8.9	1.25		21.75
GOG4/220-A	74.075		8.5			14.3	2.1	19				5.65		1.45	21.35
TRENCH5/222-A	75.195		48.25			63.4		18.7				PRESENT	3.45	6.85	9.4
TRENCH5/225-A	76.315		9.25			29.65	1.7	3.2	1.5			3.2	1.7		20.4
TRENCH5/228-A	77.435		14.9			53.65		11.9				25.4		3	70.05
GOG5/232-A	78.435		6.8			42.25		5.45	2.6			9.9		22.45	88.9
GOG5/234-A	79.545		5.75			7.2		4.5				5.95		2.25	12.4
GOG5/236-A	80.665	1.15	6.95			2.3		2.3				5.85		2.35	3.45
GOG5/238-A	81.785	0.5	5.7			4.65		5.7				7.45		1.25	14.4
GOG5/241-A	83.465		27.75			9.1		7.4	3.05			31.65		11.25	35.1
GOG5/243-A	84.585		5.1			2.85		1.8				9.4			2.9
GOG6/252-A	86.555	1.75	8.55					8.5				10.25			17
GOG6/254-A	87.675	0.8	10.6			20.6		4.65	1.55			6.1			26.6
GOG6/256-A	88.81		81.45			65.65		29.05	2.55			19.9		14.8	71.75
GOG6/259-A	89.835		28			10.2	1.15	5.6	2.3			40.55			65.2
GOG6/263-A	90.95		50.45			43.3	2	5.95				26.3		4	88
GOG6/266-A	92.09		63.4			9.95		13.75				8.6		6.95	43.2
GOG6/269-A	93.49		57.85			19.3		9.95	2.35			45.55			110.6
GOG6/271-A	94.61		44.9			19.6	2.1	2.1	7.7			21.75		4.2	82.05
GOG6/273-A	95.73		38.2			10.2		9.75		5.55		33.45			66.4
GOG6/275-A	96.85	PRESENT	45.5			10.35	1.7	6.9	1.7			12.25		3.5	119.5
GOG6/277-A	97.97	1.8	29.4			1.7		1.8	1.7			29.55			73.8
GOG7/282-A	104.19		12.35			7.2		2.05				7.15			30.85
GOG8/288-A	113.715		46.1			92.2		43.1				20.5			78.45
GOG9/292-A	116.505					9.65		3.05	0.75			5.25			27.1
GOG10/294-A	119.21		28.35			38.15		9.6				36.25			66.4
GOG11/298-A**	123.315		6.6			2.6		12.55				17.7			8.55
GOG11/300-A*	125.405		4.3			1.05		17.5				8.65			12.1
GOG12/302-A	128.58		44			44		17.4			PRESENT	27.4			86.5

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Ozotobrachion cf. dicros	Percultisphaera spp.	Percultisphaera stiphrospinata	Psenotopus chondrocheus	Pulvinosphaeridium dorningii	Pulvinosphaeridium oligoprojetum	Salopidium spp.	Salopidium granuliferum	Salopidium sp. A	Schismatosphaeridium spp.	Schismatosphaeridium rugulosum	Schismatosphaeridium sp. A	Stellechinatum ? sp. A	Tunisphaeridium tentaculaferum	Veryhachium spp.
GOG1/2-C	-2.56	0.45					0.8		46.15	0.35					0.45	
GOG1/5-C	-1.8	PRESENT					1.25		14.95				0.55	PRESENT	PRESENT	
GOG1/7-C	-1.12						1.3		26.15				PRESENT			
TRENCH1/9-C	-0.39						1.2		24.75						0.55	
TRENCH1/10-A	-0.015		1.7		PRESENT		1.7		16.45					4.15		
TRENCH1/11-A	0.015				0.8		2.9		19.55					PRESENT		
TRENCH1/12-A	0.145				0.7		2.65		14.3					PRESENT		
TRENCH1/14-A	0.54								22.85							
TRENCH1/17-A	0.85				PRESENT		0.95		14.45							
TRENCH1/23-A	1.92		1.95		0.5		0.65		50			PRESENT		0.65		
TRENCH1/29-A	3.13						5		366.45							
GOG2/34-A	4.23	1.4			1		4.8		37.9					3.05		
GOG2/37-A	5.275	1.3			2.45				10.95			1.15	1.15	1.3	1.3	
GOG2/42-A	6.65	1.1			1.1		1.15		129.7			PRESENT		5.65		
GOG2/47-A	7.73	6.65			3.3		1.7		234.95							
GOG2/50-A	8.825	0.7			2	3.45	2.75		13.7						0.7	
GOG2/55-A	9.99				3	PRESENT	0.4		69.65							
GOG2/62-A	11.15					2.1	1.15		98.3							
GOG2/65-A	12.15				3	2.05			61.75		1.05					
GOG2/69-A	13.37				1.15	2.9	0.65		31.3					0.65		
GOG2/72-A	14.49				0.8	1.15			30.35						0.4	
GOG2/75-A	15.56				0.75	0.75			16.8			PRESENT				
GOG2/77-A*	16.62				0.1	0.45			1		0.75					
GOG2/81-A	17.67				0.25				18.7				0.25			
TRENCH2/83-A	18.55				1.45				14.3					0.75		
TRENCH2/88-A	19.85				1.05	PRESENT			45.1							
TRENCH2/90-A	20.985		0.4		1.35	0.45			60.2							
TRENCH2/94-A	22.2		0.35			2.3			37.45							
TRENCH2/96-A	23.315					0.4			32.35							
GOG3/98-A	24.44				0.75				7.7							
GOG3/100-A	25.63		0.2		0.45	0.2			7.05							
GOG3/103-A	26.68				1.35				29.7		0.4					
GOG3/106-A	27.83				0.35				14.45			0.25				
GOG3/108-A	28.76	0.25	0.25		0.75				2.25			0.25				
GOG3/111-A	29.95				0.65				12.9							
GOG3/113-A	31.01				0.35				32.8							
GOG3/116-A*	32.095				0.55				4.7							
GOG3/119-A	33.21				0.45				27.35							
GOG3/122-A	34.35		0.35			0.6			36.35					0.35		0.35
GOG3/124-A*	35.47				0.2	PRESENT			14.35					0.4		
GOG3/127-A	36.415	0.3			0.3	0.2			2.15				0.75	1.9		
GOG3/131-A	37.545		0.2		0.7				1.8		0.65		1.15	0.65	0.45	
GOG3/135-A	38.67				0.15				11.55		0.15	0.15	1	0.15		
TRENCH3/141-A**	39.71								12.3				0.7			
TRENCH3/144-A	40.89				0.65				104.05					4.25		
TRENCH3/147-A	42.04				PRESENT				9.2				0.4	2.55		
TRENCH3/151-A	43.17	0.75			0.7				24.25	0.7						
TRENCH3/154-A	44.37	0.4			1.55				39.45		0.75			0.4		
TRENCH3/156-A	46.05				2.8				142.55			1		0.9	1	
TRENCH3/160-A	47.23								46.65			0.4				
TRENCH4/163-A	50.43	1.65			0.4				64.2							
TRENCH4/165-A	51.03	15.2			1.2				253.75				1.35		PRESENT	
TRENCH4/LE2-A	51.25	0.95							41.75			0.3	3.2			
TRENCH4/ LE1-A	51.465	3.45							182.25				4.2	97.05		
TRENCH4/ ME1-A(a+b)	51.605	3.35							237.4				5.05	69.75		
TRENCH4/ME2-A(a+b)	51.805	0.85							64.25					76.05		
TRENCH4/167-A	52.27				1.4				85.35				2.9	604.9		
TRENCH4/170-A	53.35	2.1							105.25					454.7		
TRENCH4/174-A	54.8				0.75				123.25				1.55	10		
TRENCH4/176-A	55.92	PRESENT							104.1				2.5	81.65	2.65	
TRENCH4/180-A	57.37								50.25				7.5	2.75		
TRENCH4/183-A	58.37								66.4		1.55		6.05	PRESENT	PRESENT	
TRENCH4/187-A	59.64				2.15				123.3				4.15			
TRENCH4/189-A	60.76								6.2				3.9			
TRENCH4/192-A	61.81								6.8				10.35	0.65		
TRENCH4/195-A	62.87								1.45				4.75			
TRENCH4/197-A	63.98								2.05		1.05		1.05	2.05		
TRENCH4/200-A	65.18								1.05				3.6			

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Ozotobrachion cf. dicros	Percultisphaera spp.	Percultisphaera stiphrospinata	Psenotopus chondrocheus	Pulvinosphaeridium dorningii	Pulvinosphaeridium oligoprojetum	Salopidium spp.	Salopidium granuliferum	Salopidium sp. A	Schismatosphaeridium spp.	Schismatosphaeridium rugulosum	Schismatosphaeridium sp. A	Stellechinatum ? sp. A	Tunisphaeridium tentaculaferum	Veryhachium spp.
GOG4/204-A	66.31								0.35				0.7			
GOG4/207-A	67.465	0.6									0.6		1.25			
GOG4/209-A	68.545								0.45							
GOG4/212-A	69.595	0.7							0.7				1.45			
GOG4/214-A	70.715								10.35				1.8			
GOG4/216-A	71.835								31.5	1.5	2.1			24.9		
GOG4/218-A	72.955								34.45		1.3		8.95	79.2	6.4	
GOG4/220-A	74.075							2.1	30.55				1.45	458.8		
TRENCH5/222-A	75.195							3.45	32.95					798.55		
TRENCH5/225-A	76.315								45.95	1.7			12.5	43.1	1.5	
TRENCH5/228-A	77.435								13.4	1.5			20.85	143.2	7.45	
GOG5/232-A	78.435	16.2							12				70.1	67.35	4.7	
GOG5/234-A	79.545	8.45							48.15				4.95			
GOG5/236-A	80.665	17.55							26.85				4.65		2.35	
GOG5/238-A	81.785								43.2				3.1			
GOG5/241-A	83.465			10.8					48.55				44.6	91	3.05	
GOG5/243-A	84.585				PRESENT				29.25		1.05		9.4		1.05	
GOG6/252-A	86.555								97.05				8.6			
GOG6/254-A	87.675				0.8				24.35				3		2.3	
GOG6/256-A	88.81			159.35					7.65				12.25		53.45	
GOG6/259-A	89.835			12.35					30.3				6.7		10.15	
GOG6/263-A	90.95			18.2					43.3		3.05		10.1		27.25	
GOG6/266-A	92.09			90.3					1.65						20.7	
GOG6/269-A	93.49			41.05					14.45	2.35			7.3		14.6	
GOG6/271-A	94.61			109.4					18.9				11.9		2.1	
GOG6/273-A	95.73			64.75									3.9		12.75	
GOG6/275-A	96.85			19.45					1.7						12.3	
GOG6/277-A	97.97			31.55					24.5						5.4	
GOG7/282-A	104.19			11.85					6.75					394.05	1.55	
GOG8/288-A	113.715			230.15					8.15				6.05		5.1	
GOG9/292-A	116.505			82.7					2.2							
GOG10/294-A	119.21			199.45					3.85				14		4.2	
GOG11/298-A**	123.315			10.65					1.35				0.65			
GOG11/300-A*	125.405			8.2							0.8					
GOG12/302-A	128.58			243.65					10				5.8	30.05		

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Veryhachium trisphaeridium	Visbysphaera microspinosa Group	Visbysphaera pirifera	Visbysphaera sp. A	TOTAL ACRITARCHS	TOTAL PRASINOPHYTA	SPORES	NUMBER OF SPECIES	ALPHA DIVERSITY
GOG1/2-C	-2.56	7.05	0.45	1.4		632.1	35.4	2.35	64	17.4346
GOG1/5-C	-1.8	6.95	0.9	PRESENT		627.65	66.15	1.75	61	16.1144
GOG1/7-C	-1.12	15.55	0.7	1.3		1023.3	70.05	3.05	59	13.3572
TRENCH1/9-C	-0.39	11.4	PRESENT	0.55	PRESENT	977.55	76.2	6	60	13.7974
TRENCH1/10-A	-0.015	4.9	PRESENT	3.25		1083.6	75.2	4.8	55	12.0093
TRENCH1/11-A	0.015	7.2	1.3	4.7		1113.4	75.5	8.9	53	11.3764
TRENCH1/12-A	0.145	10.4	1.3	3.9		1002.9	61.8	7.2	56	12.5852
TRENCH1/14-A	0.54	2.5		4.95		1092.35	86.45	8.9	54	11.677
TRENCH1/17-A	0.85	1.1	1.65	3.35		722	100.75	8.35	52	12.3371
TRENCH1/23-A	1.92	2.75		0.65		902.9	48.5	5.05	55	12.7042
TRENCH1/29-A	3.13	20	PRESENT	5.05		3870.3	185.5	50.3	43	6.713
GOG2/34-A	4.23	18.95	3.75	3.75		1812.65	98.15	19.25	55	10.5716
GOG2/37-A	5.275	9.45	4.8	1.3		1694.2	193.4	18.45	57	11.0817
GOG2/42-A	6.65	14.7	6.75	2.25	1.1	1898.5	92.55	23.65	53	10.0027
GOG2/47-A	7.73	14.85	5	1.7		3240.55	105.2	40.85	53	8.9415
GOG2/50-A	8.825	6.25	2.15	0.65		1335.8	85.15	12.45	50	10.092
GOG2/55-A	9.99	2.5	1.3	0.8		1058.45	51.3	23.9	49	10.4907
GOG2/62-A	11.15	5.9	1.15	1.15		2458.25	86.8	27.55	46	7.9733
GOG2/65-A	12.15	10.75	4.95	2		2194.4	97.3	45.5	49	8.804
GOG2/69-A	13.37	2.35	2.95	2.25		1099.8	84.6	28.2	55	11.9375
GOG2/72-A	14.49	3.55	3.15	1.55		625.35	84.45	28.15	48	11.6286
GOG2/75-A	15.56	9.95	3.05	4.6		1267.05	67.15	26	51	10.5125
GOG2/77-A*	16.62		0.15	0.3		285.25	50.25	3.65	43	13.1064
GOG2/81-A	17.67	0.25	1.75	3.6		552.25	55.15	16.3	47	11.8901
TRENCH2/83-A	18.55	4	4.4	3.25		849.3	48.65	12.45	49	11.2191
TRENCH2/88-A	19.85	8.35	1.95	2.9		1013.9	45.7	24.65	51	11.1791
TRENCH2/90-A	20.985	0.5	0.5	PRESENT		721	110.85	21.65	43	9.616
TRENCH2/94-A	22.2		0.35	1.15		594.6	98.25	9.9	46	11.0803
TRENCH2/96-A	23.315	4.15	2.4	3.3		936.3	69.45	18.75	52	11.6293
GOG3/98-A	24.44	0.4	PRESENT	2.2		322.45	81.3	6.55	45	12.9688
GOG3/100-A	25.63	4		1.4		471.6	46.7	25.4	52	14.4021
GOG3/103-A	26.68	1.65	0.4			593.5	59.9	15.1	55	14.3129
GOG3/106-A	27.83	1.7	0.2	0.6		422.2	57.5	12.3	48	13.2812
GOG3/108-A	28.76	3	0.5	3		533.8	49	8.85	52	13.8076
GOG3/111-A	29.95	0.9	0.25	0.85		427.75	42.6	13.3	47	12.998
GOG3/113-A	31.01	1.5	0.35			533.8	45.55	22.2	47	12.0789
GOG3/116-A*	32.095	0.2				291.95	26.5	8.7	42	12.9558
GOG3/119-A	33.21	0.25	1.9			596.3	54.95	10	47	11.6234
GOG3/122-A	34.35	1.05		4.15		664	40.55	12.35	47	11.338
GOG3/124-A*	35.47			1.25		259.5	40.15	5.95	48	16.1416
GOG3/127-A	36.415	0.25		1		582.35	66	9.2	57	15.0574
GOG3/131-A	37.545	0.9				420.95	20.05	14.55	49	14.1047
GOG3/135-A	38.67	0.15	0.3			404.55	22.9	6.15	51	15.0977
TRENCH3/141-A**	39.71		0.25			425.05	53.15	11.8	39	10.0408
TRENCH3/144-A	40.89	0.65		5.6		1408.7	71.15	16.7	44	8.5227
TRENCH3/147-A	42.04	1.8		0.8		811.1	60.3	26.2	48	10.9317
TRENCH3/151-A	43.17	2.1	0.7			1359.05	57.25	36.6	46	9.1023
TRENCH3/154-A	44.37		3.45			784.75	44.85	20.85	42	9.3372
TRENCH3/156-A	46.05	1.8		1		1403.15	62.45	59.75	38	7.1284
TRENCH3/160-A	47.23		0.85	0.85		824.3	29.7	23.65	34	7.0825
TRENCH4/163-A	50.43	2.85		0.4		1061.3	42.65	15.9	43	8.9066
TRENCH4/165-A	51.03			4.05		2334.2	77.3	66.75	34	5.6043
TRENCH4/LE2-A	51.25	2.7				2348.6	83.8	30.2	40	6.7998
TRENCH4/ LE1-A	51.465	1.35	2.1			6752.1	161.65	190.65	37	5.1346
TRENCH4/ ME1-A(a+b)	51.605					8294.95	337.95	221.95	41	5.5825
TRENCH4/ME2-A(a+b)	51.805	2.75				3866.6	229.2	116.85	42	6.5167
TRENCH4/167-A	52.27		1.4	2.9		3448.25	79.25	61.85	42	6.7007
TRENCH4/170-A	53.35		4.25			6721.35	176.95	323.7	41	5.7876
TRENCH4/174-A	54.8	0.75	6.9			3125.1	147.05	135.55	41	6.605
TRENCH4/176-A	55.92		3.25			5650.55	465.2	134.45	39	5.5697
TRENCH4/180-A	57.37		6.45			2737.45	286.05	188.25	42	6.9028
TRENCH4/183-A	58.37		5.95			8245	576.4	169.05	44	6.0376
TRENCH4/187-A	59.64	2.15	10.6			10112.25	591.5	221.1	46	6.1664
TRENCH4/189-A	60.76	1.15	2			4178.6	262.3	25.95	40	6.0626
TRENCH4/192-A	61.81	3.25				5041.15	333.45	63	39	5.6923
TRENCH4/195-A	62.87	0.8				3698.15	343.05	24.2	34	5.0913
TRENCH4/197-A	63.98	2.25				6823.6	498.1	35.9	37	5.0877
TRENCH4/200-A	65.18	0.6				5378.45	213.45	85.85	41	5.9948

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

Sample.	Height (m). (above/below Wenlock-Ludlow boundary)	Veryhachium trisphaeridium	Visbysphaera microspinosa Group	Visbysphaera pirifera	Visbysphaera sp. A	TOTAL ACRITARCHS	TOTAL PRASINOPHYTA	SPORES	NUMBER OF SPECIES	ALPHA DIVERSITY
GOG4/204-A	66.31		0.35			4437.15	120.85	30.05	40	6.0346
GOG4/207-A	67.465					5111.45	217.35	27	33	4.6899
GOG4/209-A	68.545					8653.55	210.1	138.8	32	4.1773
GOG4/212-A	69.595	0.7				5604.9	326.8	102.8	39	5.5982
GOG4/214-A	70.715		3.05			3112.2	224.7	133.95	47	7.7456
GOG4/216-A	71.835	4.5	28.5			8689.5	505.05	662.6	53	7.4441
GOG4/218-A	72.955	3.85	23.05			8723.4	324.55	552.1	53	7.4637
GOG4/220-A	74.075	1.45	14.8			9117	197.7	342.1	53	7.4283
TRENCH5/222-A	75.195	19.2	25.15			12593.1	273.4	519.15	44	5.6974
TRENCH5/225-A	76.315	23.1	38			8997.65	255.2	859.65	56	7.9286
TRENCH5/228-A	77.435	13.4	8.95			5092.5	132.75	220.65	50	7.661
GOG5/232-A	78.435	253.7	4.7			9455.35	276.3	1086.65	51	7.0536
GOG5/234-A	79.545	1.25	7.7			14559.8	234.6	805.75	53	6.9106
GOG5/236-A	80.665	24.45	PRESENT			18642.3	234.5	809.15	53	6.6677
GOG5/238-A	81.785		3.1			3264.45	54.2	139.65	41	6.5872
GOG5/241-A	83.465	5.2	19			13938.35	236.1	1147.75	54	7.1065
GOG5/243-A	84.585	1.45	3.05			8016.9	198	198.8	52	7.4171
GOG6/252-A	86.555		5.1			13304.5	341.65	411.8	47	6.0923
GOG6/254-A	87.675	3.9	7.65			5873.05	82.45	281.4	56	8.5533
GOG6/256-A	88.81	40.25	23.95			17425.65	516.15	2059.25	52	6.5719
GOG6/259-A	89.835	5.6	6.75			6241.75	132.35	356.35	54	8.0961
GOG6/263-A	90.95	30.3				12789.4	196.75	2191.1	53	7.0484
GOG6/266-A	92.09	29	3.3			36936.95	195.45	1044.05	48	5.4365
GOG6/269-A	93.49	9.65	16.8			15587.8	358.5	2303.05	52	6.6861
GOG6/271-A	94.61	9.1	2.1			39133.25	436.75	1324.55	57	6.5464
GOG6/273-A	95.73	18		1.65		19386.2	255.75	626.45	52	6.4871
GOG6/275-A	96.85	36.85	3.4			21281.2	327.6	964.45	54	6.6817
GOG6/277-A	97.97	6.85	7.1			14384.8	222	537.1	54	7.0743
GOG7/282-A	104.19		16.9			7791.5	331.85	574.55	46	6.4422
GOG8/288-A	113.715	17.45	9.05			10133.6	400.9	772.4	51	6.9652
GOG9/292-A	116.505	3.75	1.5			5126.65	91.2	202.2	48	7.3026
GOG10/294-A	119.21	10.15				13421.4	342.8	694.05	45	5.7882
GOG11/298-A**	123.315		0.65			6267.7	164.25	149.3	37	5.1981
GOG11/300-A*	125.405	1.85				7232.1	269.9	155.5	44	6.1975
GOG12/302-A	128.58	185.4	PRESENT		5	11818.75	490.95	270.05	51	6.7981

* = one slide <500 count; ** = two slides <500 count.

APPENDIX 3: Acritarchs and prasinophyte algae - Abundance per gram at Goggin Road.

APPENDIX 4

ACRITARCHS AND PRASINOPHYTE ALGAE - ABUNDANCE PER GRAM AT PITCH COPPICE QUARRY.

Sample.	Height (m) above below Wenlock-Ludlow boundary	Lycopodium spores	Cymatiosphaera spp.	Cymatiosphaera aff. cornifera	Cymatiosphaera ? cf. imperfecta	Cymatiosphaera lawsonii	Cymatiosphaera aff. ledburica	Cymatiosphaera mariae	Cymatiosphaera multicrista	Cymatiosphaera aff. multisepta	Cymatiosphaera octoplana	Cymatiosphaera pavimenta	Cymatiosphaera triangula	Dictyotidium spp.	Dictyotidium faviforme	Dictyotidium stenodictyum	Duvernaysphaera aranides
PC/1-C (1-a)	-2.89	250.5	1.4	6	1.4		1.4		1.4		4.75	2	6.75		8.15		2
PC/3-C (1-a)	-1.87	360.5	3.45	6.9	2.3		1.15		5.8			2.3	4.6	1.15	23.1	12.7	10.25
PC/5-C (1-b)	-1.31	349	3.8	14.6	1		2.05	PRESENT	1		7.2	7.65	4.45		17.6	4.1	5.2
PC/7-C (1-a)	-0.55	429.5		6.55	1.1	1.75	1.1		1.1		1.1	0.9	4.15		4.4	3.05	2
PC/9-C (1-a)	-0.23	341.5	1.2						1.2		2.45	4.9	8.5		3.65	1.25	4.9
PC/10a-A (1-a)	-0.135	217.5	12.7								2.05	4.05	4.35		4.55		2.05
PC/10e-A (1-a+b)*	-0.015	792.5	2.7	4.4	0.5					0.55		4.75	3.15		2.1		1.55
PC/12-A (1-a)	0.03	192	2.6	2.6	1.85						2.6	7.75	14		7		9.6
PC/13-A(1-a)	0.095	303	2.6	6.75		1.45	1.15		1.15	3.7		4.05	1.45		7.8		5.85
PC/14-A(1-a)	0.175	165	19.2	5			10.9		4.6		PRESENT	10.45	7.3				2.7
PC/16-A(1-a)	0.655	232.5	17.6	6.95			19.45		5.5	1.9	3.4	7.2	3.8		11.9		1.7
PC/18-A(1-a)	1.515	143.5	18.95	5.1	2.95		8.8					2.55	5.85		19.3		10.9
PC/20-A(1-a)	2.165	182.5	6.9				2.3		2.3		2.3	2.3	2.3		6.9		9.15

Sample.	Height (m) above below Wenlock-Ludlow boundary	Melikeriopalla amydra	Polyedrixium wenlockium	Pterospermella spp.	Pterospermella foveolata	Pterospermella sp. A	Pterospermella sp. B	Quadratitum fantasticum	Tasminites spp.	Ammonidium waldronense	Baltisphaeridium spp.	Baltisphaeridium muldiensis	Baltisphaeridium sp. A	Buedingiisphaeridium pyramidale	Buedingiisphaeridium reticulaum	Comasphaeridium brevispinosum	Comasphaeridium williereae
PC/1-C (1-a)	-2.89		PRESENT		1.4	PRESENT		3.4	46.15	8.25	9.5	8.15		2	7.4	8.75	5.4
PC/3-C (1-a)	-1.87				1.15	1.15	6.95	6.95	18.45	26.6	1.15	4.6		3.45	3.45	4.65	5.8
PC/5-C (1-b)	-1.31	1			2.4	4.85	1.4	10.45	52.5	25.65		12.75		2.4	2.8	25.4	19.35
PC/7-C (1-a)	-0.55	PRESENT	7	1.75	5			6.55	45.5	17.85		11.6		6.75		11.35	5.9
PC/9-C (1-a)	-0.23		8.4		1.25	3.7	2.4	1.2	25.5	13.45		9.85		3.75	1.2	3.65	7.4
PC/10a-A (1-a)	-0.135		67.1		6.35	6.1	12.95	4.35	46	21.75	2.05	28.6		17.2	2.3	8.6	6.35
PC/10e-A (1-a+b)*	-0.015		13.1		2.2	0.55	0.5	0.5	11.5	4.25	0.55	8.5		1.6		0.55	2.2
PC/12-A (1-a)	0.03		8.1		9.9	7	2.6	2.6	45.5	35.6		4.45		16.45		2.6	2.6
PC/13-A(1-a)	0.095		16.3		2.25	1.15	1.45	1.45	25.25	8.9		13.9		6.6	1.15	2.6	3.7
PC/14-A(1-a)	0.175		25.45		17.7	2.3		2.3	38.35	25.45		40	7.3	27.7		13.15	9.15
PC/16-A(1-a)	0.655		16.05		3.6	1.9	1.9	1.7	59	11.35		43.3	1.9	21.4	11	7.4	
PC/18-A(1-a)	1.515		18.9		5.85	8.8	2.95	27.3	32.35	92.35		24.35		13.45	2.55	2.55	
PC/20-A(1-a)	2.165		25.15		6.9	4.55	2.3	9.2	34.25	31.95		45.75		43.45	4.6	4.6	

Sample.	Height (m) above below Wenlock-Ludlow boundary	Dateriocradus spp.	Dateriocradus cf. monterrosae	Dateriocradus sp. A	Dorsennidium spp.	Dorsennidium europaeum	Dorsennidium formosum	Dorsennidium pentagonale	Dorsennidium rhomboidium	Dorsennidium wenlockianum	Dorsennidium sp. A	Eisenackidium wenlockense	Eisenackidium sp. A	Estiastra granulata	Eupoikilofusa filifera	Evittia remota Group	Glyptosphaera speciosa
PC/1-C (1-a)	-2.89		2	40.1	29.2	165.95	23.05	13.5	39.35	198.35		12.15		PRESENT	20.3	340.5	2.75
PC/3-C (1-a)	-1.87			34.65	19.6	72.8	12.7	12.7	19.65	58	2.3	9.25		1.15	10.4	129.5	1.15
PC/5-C (1-b)	-1.31			7.9	12.75	41.95	6.9	11.1	23.8	122.05	4.45	5.85			8	136	1.4
PC/7-C (1-a)	-0.55		1.1	16.6	16.8	58.8	12	4.35	26.75	120.75		1.75	0.9		3.05	109	
PC/9-C (1-a)	-0.23	1.2	5	13.4	32.8	68.3	13.7	4.8	28.15	181.05	2.5	1.25			1.2	220	1.25
PC/10a-A (1-a)	-0.135		8.9	30.15	36.25	210.5	8.6	8.6	30.45	261.45		2.05			4.55	432.5	
PC/10e-A (1-a+b)*	-0.015	0.5	1.55	6.8	10.5	36.35	2.1	4.2	7.75	56.65		0.55			4.15	92	
PC/12-A (1-a)	0.03			42.4	27.85	264.25	18.75	8.8	33.85	306					6.25	462	
PC/13-A(1-a)	0.095			18.9	32.2	134.45	18.15	7.1	29.6	172.65	1.45				7	313.5	
PC/14-A(1-a)	0.175		2.3	61.3	47.35	250.05	35.05	6.85	58.6	311.55	2.3				22.7	633	2.7
PC/16-A(1-a)	0.655			56.5	38.2	147.15	16.45	18.15	59.05	143.55	1.9				59	719	1.7
PC/18-A(1-a)	1.515			50.15	53.2	305.45	27.3	15.95	26.95	240.15		2.95			11.55	464.5	
PC/20-A(1-a)	2.165		2.3	20.55	22.85	288.05	9.15	11.45	52.6	311	2.3				4.6	487.5	

* = one sample with <500 count.

APPENDIX 4: Acritarchs and prasinophyte algae - Absolute abundance per gram at Pitch Coppic Quarry.

Sample.	Height (m) above below Wenlock-Ludlow boundary	Gorgonisphaeridium spp.	Gorgonisphaeridium citrinum	Gorgonisphaeridium ramosum	Gorgonisphaeridium succinum	Hapsidopalla jeandeunffi	Helosphaeridium pseudodictyum	Hoegklintia spp.	Hoegklintia cf. corallina	Hoegklintia cf. digitata	Leiofusa parvitatis	(<3µm)Leiosphere <46µm	(<3µm)Leiosphere 46-85µm	(<3µm)Leiosphere 85-132µm	(<3µm)Leiosphere 132µm+	(>3µm)Leiosphere <46µm	(>3µm)Leiosphere 46-85µm
PC/1-C (1-a)	-2.89	8	25.15		35.2	17.55	18.95	3.4			8.75	283.5	102	6.5		73	26
PC/3-C (1-a)	-1.87	2.3	20.75	1.15	13.85	19.65	8.55	2.3	2.3	3.45	6.95	252.5	74.5			103	46
PC/5-C (1-b)	-1.31		13.5		32.75	10.8	9.9	3.8	2.4	1.4	4.85	270.5	62			78.5	22
PC/7-C (1-a)	-0.55		3.8	0.9	12.4	2.85	37.5			0.9	6.1	141	58	3.5		35.5	14.5
PC/9-C (1-a)	-0.23		1.2	1.25	12.25		26.95	1.25			8.6	365.5	143.5	15.5	7.5	69	23
PC/10a-A (1-a)	-0.135	2.3	4.05	6.6	53.2		62.35				21.55	818	360.5			255.5	36
PC/10e-A (1-a+b)*	-0.015		1.6	1.05	5.7		11.35		1.05	1.1	1.6	171	93			50	13
PC/12-A (1-a)	0.03		1.85		44.7		62.95	2.6	1.85	2.6	30.9	513	134	8		132	103
PC/13-A(1-a)	0.095		7.9		12.6		60	1.15	2.6	13.65	9.95	332.5	123	13.5		106	47
PC/14-A(1-a)	0.175		7.75	2.7	27.75		67.35		PRESENT	4.6	2.3	514	436.5	42		30	59.5
PC/16-A(1-a)	0.655		1.9	1.7	13.05		52.4	1.9	PRESENT	5.5		466	147.5			77.5	27
PC/18-A(1-a)	1.515		5.85	2.95	2.95	2.95	115.9	2.95		2.55	42.45	612	107.5	14		138	51.5
PC/20-A(1-a)	2.165				16	20.55	66.35			6.85	6.9	481	222			131	79.5

Sample.	Height (m) above below Wenlock-Ludlow boundary	(>3µm)Leiosphere 85-132µm	Leptobrachion spp.	Leptobrachion arbusculiferum	Leptobrachion digitatum	Leptobrachion sp. A	Lophosphaeridium spp.	Lophosphaeridium sp. A	Micrhystridium spp.	Micrhystridium inflatum	Micrhystridium intonsurans	Micrhystridium stellatum	Micrhystridium sp. A	Multiplicisphaeridium spp.	Multiplicisphaeridium arbusculum	Multiplicisphaeridium arbusculum var. A	Multiplicisphaeridium eltonense
PC/1-C (1-a)	-2.89			6.75	14.9					30.45	46.1	471.5	2	39.65	32.85	2	127.95
PC/3-C (1-a)	-1.87	5.5	1.15	2.3	4.6	2.3	1.15	9.25		11.5	68.2	374.5	4.65	16.15	10.4		95.8
PC/5-C (1-b)	-1.31			2.4	5.5	4.8		13.5		25.15	160	420.5	2.8	33.2	17.1	2	100
PC/7-C (1-a)	-0.55			1.1	1.1	2.15		3.75		20.9	106	472.5		34	20.05		82.15
PC/9-C (1-a)	-0.23			9.75	11.05	1.2	1.2	3.6		29.3	358.5	953.5		29.3	9.8		53.85
PC/10a-A (1-a)	-0.135			30.65	13.15		10.4	2.05		47.9	118	1321.5		47.65	32.2		96.5
PC/10e-A (1-a+b)*	-0.015			2.2	6.8	1.55				7.6	88.5	209.5		12.25	3.5		27.3
PC/12-A (1-a)	0.03			19.15	18.7	2.6				32.25	179	886.5	2.6	36.85	30.1		114.2
PC/13-A(1-a)	0.095			26.55	8.9	2.9	2.25		2.9	12.15	168.5	562.5		22.6	6.3		64.5
PC/14-A(1-a)	0.175		2.7	55.05	26.9	2.3				29.55	292.5	1191		43.6	32.35		154.75
PC/16-A(1-a)	0.655			5.3	12.65	3.6		1.9		21.95	141	860.5		21.75	7		83.45
PC/18-A(1-a)	1.515	14		11.7	22.6	5.5	2.95			33.6	429	723.5		29.4	14.25		148.1
PC/20-A(1-a)	2.165			6.9	11.45	16		2.3		45.75	100.5	510	2.3	50.3	43.45		134.85

Sample.	Height (m) above below Wenlock-Ludlow boundary	Multiplicisphaeridium variabile	Multiplicisphaeridium sp. A	Multiplicisphaeridium sp. B	Neoveryhachium mayhillensis	Onondagella deunffii	Oppilatala spp.	Oppilatala septispinosum	Ozotobrachion cf. dicros	Percultisphaera spp.	Psenotopus chondrocheus	Pulvinosphaeridium oligoprojetum	Salopidium granuliferum	Schismatosphaeridium sp. A	Stellechinatum ? sp. A	Tunisphaeridium tentaculaferum	Veryhachium spp.
PC/1-C (1-a)	-2.89	34.45	2.75	1.4	1.4		2	16.25		1.4		8.75	32.1				1.4
PC/3-C (1-a)	-1.87	6.9	3.45	2.3	1.15			12.7				8.05	55.45			1.15	
PC/5-C (1-b)	-1.31	17.3		1.4	2.4			20.4				15.65	21.4	1		1	
PC/7-C (1-a)	-0.55	17.4	5.65		0.9	PRESENT	1.1	21	0.9	1.1			28.55		1.1	0.9	
PC/9-C (1-a)	-0.23	18.3	1.25	1.25	6.2			16				2.5	40.5				
PC/10a-A (1-a)	-0.135	27.85	9.1		4.35			76.2	2.05			2.3	62.35		4.35	2.05	
PC/10e-A (1-a+b)*	-0.015	2.5	2.25	0.55				13.25		0.55	0.5	1.05	5.15		1		
PC/12-A (1-a)	0.03	29.8	33.45		8.1	1.85		89.7		1.85		2.6	72.85		9.6		
PC/13-A(1-a)	0.095	12.95	19.8		1.45			45.45	2.25	1.15	1.45		30.4				
PC/14-A(1-a)	0.175	43.2	113.1		2.7			90.95		2.7		2.3	11.45		10.45	5.45	
PC/16-A(1-a)	0.655	27.45	28.4	3.8		1.9		68.25					30.65		10.8		
PC/18-A(1-a)	1.515	14.25	98.05	2.55	5.5	5.5		65.05			PRESENT	PRESENT	119.5	2.55	2.95		
PC/20-A(1-a)	2.165	96.05	68.55		4.6	PRESENT		153.25	2.3		PRESENT	PRESENT	45.75			2.3	

* = one sample with <500 count.

APPENDIX 4: Acritarchs and prasinophyte algae - Absolute abundance per gram at Pitch Coppic Quarry.

Sample.	Height (m) above below Wenlock-Ludlow boundary	Veryhachium trisphaeridium	Visbysphaera microspinosa Group	Visbysphaera pirifera	ACRITARCH UNIDENT	TOTAL ACRITARCHS	TOTAL PRASINOPHYTA	SPORES
PC/1-C (1-a)	-2.89	71.8	PRESENT	8.9	36.7	2538.1	86.2	9.6
PC/3-C (1-a)	-1.87	64.6	PRESENT	1.15	46.2	1801.35	108.35	12.6
PC/5-C (1-b)	-1.31	78.65	3.45	1.4	22.05	1955.95	141.25	10.25
PC/7-C (1-a)	-0.55	46.4	2.85	1.75	16.8	1632.35	93	10.35
PC/9-C (1-a)	-0.23	88.25		2.45	31.85	2959	70.5	12.25
PC/10a-A (1-a)	-0.135	100.85		10.9	54.75	4818	172.6	29.55
PC/10e-A (1-a+b)*	-0.015	19.75	1.05	1	11.65	1010.65	48.05	7.3
PC/12-A (1-a)	0.03	108.1		1.85	58.15	4009.15	123.7	33.1
PC/13-A(1-a)	0.095	42.9	PRESENT	2.9	32.75	2575.2	83.8	14.65
PC/14-A(1-a)	0.175	91.55	2.3	4.6	95.95	5058.35	146.25	15.85
PC/16-A(1-a)	0.655	23.25	3.8	5.5	77.35	3591.7	163.55	39.75
PC/18-A(1-a)	1.515	89.95		8	108.3	4391.7	170.55	95.35
PC/20-A(1-a)	2.165	34.25		2.3	43.5	3749.5	116.8	32.45

* = one sample with <500 count.

APPENDIX 4: Acritarchs and prasinophyte algae - Absolute abundance per gram at Pitch Coppic Quarry.

APPENDIX 5

PALYNOFACIES ANALYSIS OF GOGGIN ROAD -
ABSOLUTE ABUNDANCE PER GRAM.

Sample	Height (above/below Wenlock-Ludlow series boundary)	Sporomorphs	Prasinophyte Alage	Acritarchs	Chitinozoans	Scolecodonts	Graptolites	Land Plants	AOM	Indeterminate Organic Matter	Zoomorph Fragments	Tubes	Lycopodium Spores	Total POM	Marine index
GOG1/2-C	-2.56	0	8.5	676.5	23	8	0	24	21.5	193	640	5.5	190.5	1600	0.968
GOG1/5-C	-1.8	2.5	18.5	639	10.5	19	0	40	11	241.5	604.5	5.5	246	1592	0.942
GOG1/7-C	-1.12	7	26	1076.5	7	26	0	113	11	207	712.5	18	142	2204	0.904
TRENCH1/9-C	-0.39	16	20	1149.5	61.5	10.5	0	138	35.5	224.5	1421.5	26.5	106.5	3103.5	0.890
TRENCH1/10-A	-0.015	10	10	1591	83	81	0	132.5	41.5	347	3473.5	37.5	38	5807	0.925
TRENCH1/11-A	0.015	0	13	1236.5	191	90.5	0	111	44.5	62	4420	13	42	6181.5	0.932
TRENCH1/12-A	0.145	0	57.5	1075	37	37	0	208.5	53.5	225.5	2660	42	56	4396	0.853
TRENCH1/14-A	0.54	0	22	908	32	63	0	158.5	41	214.5	5096.5	66	37.5	6601.5	0.866
TRENCH1/17-A	0.85	20.5	36	709.5	55	26	0	41.5	8	62.5	2934	13	65.5	3906	0.930
TRENCH1/23-A	1.92	8.5	14	864	8.5	34	0	39.5	14.5	88.5	633.5	6	155	1711	0.950
TRENCH1/29-A	3.13	0	44.5	3331.5	33.5	45	11	90.5	80	362.5	2728.5	33	37	6760	0.975
GOG2/34-A	4.23	14.5	22	1825	28.5	29	0	72.5	102	231.5	2006	14.5	56.5	4345.5	0.956
GOG2/42-A	6.65	6.5	27	2263	15.5	22	0	123.5	7.5	186	1667	0	56.5	4318	0.947
GOG2/50-A	8.825	0	47.5	1784.5	5.5	14	0	147.5	16.5	150	2005	0	62	4170.5	0.926
GOG2/62-A	11.15	0	24.5	1716	26	21.5	0	82	27.5	69	1710.5	11	66	3688	0.956
GOG2/69-A	13.37	21.5	69	1286	12	28	0	66	118	318.5	1615.5	5	70.5	3539.5	0.941
GOG2/75-A	15.56	4.5	21.5	1175.5	4	13	0	28.5	4	120.5	1253.5	0	90	2625	0.974
GOG2/81-A	17.67	8.5	18	533.5	3	13.5	0	13	37	63.5	893	2.5	157	1585.5	0.964
TRENCH2/90-A	20.985	2.5	21.5	924	2.5	2.5	0	14.5	16.5	50	394.5	0	175	1428.5	0.982
TRENCH2/96-A	23.315	4	22.5	972.5	4.5	6.5	0	13	18	18.5	291.5	0	184	1351	0.983
GOG3/100-A	25.63	19.5	25	664.5	8	5.5	0	45.5	17	19.5	859.5	2.5	146	1666.5	0.915
GOG3/103-A	26.68	4.5	37.5	649.5	2	4	0	4.5	10	5.5	493	8	211	1218.5	0.987
GOG3/106-A	27.83	2	22	462	0	0	0	20.5	7	25.5	555	0	205.5	1094	0.956
GOG3/111-A	29.95	4	13	537	7.5	4	0	12	5.5	13	528	2	230	1126	0.972
GOG3/116-A	32.095	1.5	3	415	0	0	0	4.5	9.5	34	341.5	1.5	312	810.5	0.986
GOG3/122-A	34.35	4.5	8	698	0	1.5	0	3.5	1.5	25	200.5	3.5	240.5	946	0.989
GOG3/127-A	36.415	0	15.5	760	15.5	5	0	31.5	2.5	21	738	13	154	1602	0.962
GOG3/135-A	38.67	0	10	450.5	4.5	1.5	0	11	19.5	20.5	462	3.5	257	983	0.977
TRENCH3/144-A	40.89	15.5	40.5	942	11	0	0	19	92	20	1085.5	3.5	109.5	2229	0.966
TRENCH3/151-A	43.17	19.5	46	1162	83.5	10.5	0	45.5	77.5	71	1465	10	79	2990.5	0.952
TRENCH3-155b	46.095	11	51	2092	5.5	0	0	14.5	82	143	1421	0	65	3820	0.988
TRENCH3/160-A	47.23	0	16.5	989.5	0	0	0	88	292.5	69.5	1664	5	80.5	3125	0.920
TRENCH3/163-A	50.43	0	16.5	1200	16.5	0	0	98	238	65.5	1102.5	36	91	2773	0.926
TRENCH4/165-A	51.03	0	39.5	2371.5	9.5	16.5	0	49	814	178.5	1360.5	26	52.5	4865	0.980
TRENCH4/LE2-A	51.25	21	47	2333	0	0	0	5	36.5	137.5	567	0	78.5	3147	0.989
TRENCH4/LE1-A	51.465	62	123.5	7001.5	33	0	0	51	493	43.5	2051.5	0	26	9859	0.984
TRENCH4/ME1-A	51.605	36.5	111.5	7433	125.5	13	26	0	3255	533.5	3356.5	0	33.5	14890.5	0.995
TRENCH4/ME2-A	51.805	34.5	12	5699.5	53	0	0	36	1800	319	5492	42.5	34	13488.5	0.988
TRENCH4/167-A	52.27	22.5	9	3070.5	41.5	9	0	46	989.5	64	1298	0	90	5550	0.979
TRENCH4/170-A	53.35	97	57	4974.5	649.5	10.5	20.5	184.5	2305.5	199	2901.5	29	42.5	11428.5	0.953
TRENCH4/174-A	54.8	76	23.5	4033.5	94	16	0	27.5	615	209.5	4604	0	50	9699	0.976
TRENCH4/176-A	55.92	31	186.5	7329	410	0	0	205	2702	503	7267.5	0	27.5	18634	0.971
TRENCH4/180-A	57.37	55	143	4124	670.5	0	0	89	1137	307.5	6781.5	11.5	37	13319	0.972
TRENCH4/183-A	58.37	23	415.5	7253	118.5	0	0	59.5	1485.5	367	4249	23	35	13994	0.990
TRENCH4/187-A	59.64	88.5	392.5	8634.5	493.5	0	19.5	376	3705.5	415	7399	69	23	21593	0.954
TRENCH4/189-A	60.76	0	124.5	3442	35.5	0	0	34.5	217	242.5	1830	9.5	84	5935.5	0.991
TRENCH4/192-A	61.81	0	207.5	5945	40	0	0	103	218.5	288	2452.5	16	53.5	9270.5	0.984
TRENCH4/195-A	62.87	9.5	257.5	3656	15.5	0	0	129	60	267	1663	25.5	81.5	6083	0.966
TRENCH4/197-A	63.98	12.5	513	7237.5	36.5	0	0	158.5	319.5	255.5	1906	45	52	10484	0.979
TRENCH4/200-A	65.18	0	177	4060	31	0	39	2569	165	190.5	5006.5	592.5	37.5	12830.5	0.626
GOG4/204-A	66.31	0	244.5	4825.5	64	0	42	636.5	547.5	268.5	5341	96.5	41	12066	0.890
GOG4/207-A	67.465	0	216.5	4259.5	22.5	6	0	147.5	183	204	3042.5	40.5	61.5	8122	0.968
GOG4/209-A	68.545	14.5	322.5	7132	122	0	54	427	5674	267.5	3116.5	50.5	23.5	17180.5	0.945
GOG4/212-A	69.595	7.5	312	4422	0	0	6.5	229	159.5	55	3062.5	93	57	8347	0.952
GOG4/214-A	70.715	19.5	181	3480	29	0	21	234	942	92.5	3676	52	55	8727	0.936
GOG4/216-A	71.835	119.5	179	8943.5	1645.5	0	120	1286	16481.5	359	6640.5	120	16	35894.5	0.886
GOG4/218-A	72.955	101.5	502	12932.5	1578	34.5	688.5	945	15816	307	7043	98.5	12.5	40046.5	0.938
TRENCH5/220-A	74.075	110.5	280	9417.5	1110	21	396	556	11386.5	302.5	4820	158	17	28558	0.944
TRENCH5/222-A	75.195	385	728.5	24344	3794	0	2433	2983	42764	385	12083	825	7	90724.5	0.903
TRENCH5/225-A	76.315	493.5	973	27916	5492.5	0	1453	1426.5	33622	813	15078	720	5.5	87987.5	0.949
TRENCH5/228-A	77.435	49.5	172	6657	489	13.5	235.5	444	9396.5	276	3794.5	208	24	21735.5	0.939
TRENCH5/232-A	78.435	41.5	221	13911	938.5	0	6803.5	428	31686.5	276	11151	786.5	8	66243.5	0.979
GOG5/234-A	79.545	61.5	300.5	9372	952	0	1719.5	196	7085.5	64	5973.5	239	19	25963.5	0.980

APPENDIX 5: Palynofacies analysis of Goggin Road - Absolute abundance per gram.

Sample	Height (above Wenlock-Ludlow series boundary)	Sporomorphs	Prasinophyte Alage	Acritarchs	Chitinozoans	Scolecodonts	Graptolites	Land Plants	AOM	Indeterminate Organic Matter	Zoomorph Fragments	Tubes	Lycopodium Spores	Total POM	Marine index
GOG5/236-A	80.665	134.5	303	12550.5	1126	0	1342	132.5	11367.5	221.5	5564	191	14.5	32932.5	0.983
GOG5/238-A	81.785	24	40	3349.5	64	17.5	40	111	1235.5	157.5	1791	91.5	67.5	6921.5	0.963
GOG5/239-A	82.345	28.5	191	12659	1176	0	333	237.5	11847.5	240.5	4601	563	15	31877	0.982
GOG5/241-A	83.465	406.5	203	28625.5	1881.5	0	2440.5	254.5	43980.5	813.5	12609.5	305	6	91520	0.980
GOG5/243-A	84.585	60.5	248	11274	648	0	408.5	221	5014.5	215.5	4896.5	254.5	22	23241	0.978
GOG5/245-A	85.445	36	179.5	9096.5	508.5	0	451	72	2246.5	191	8638	129.5	25	21548.5	0.990
GOG6/252-A	86.555	113	197	15355.5	1014.5	0	1239.5	169	4085.5	704.5	10594	338	14	33810.5	0.984
GOG6/254-A	87.675	65.5	34	5231.5	205.5	22.5	68.5	65.5	4023	144	3412	165	34	13437	0.977
GOG6/256-A	88.81	220	194	15622.5	886.5	0	1125.5	647	37973	556.5	4625	252.5	8	62102.5	0.954
GOG6/259-A	89.835	59	197.5	8919.5	1188.5	16.5	625	161	5537.5	214	4689.5	214	23	21822	0.980
GOG6/263-A	90.95	307.5	205	38057	3280	0	2255	751.5	87764	376	10385.5	205	3.5	143586.5	0.976
GOG6/266-A	92.09	348	652.5	29492.5	4437	0	1914	1044	56592	304.5	8526	1087.5	6	104398	0.963
GOG6/269-A	93.49	639.5	213	29714	3224.5	0	1559	320	45370.5	160	6529	213	5.5	87942.5	0.973
GOG6/271-A	94.61	112.5	561.5	33739	3565	0	2470	533.5	98803	449	11367.5	309	4.5	151910	0.984
GOG6/273-A	95.73	0	422	25872	3907	0	1584	739.5	84912.5	422	8236.5	634	4	126729.5	0.977
GOG6/275-A	96.85	61	272	12347	798	33	615	1082.5	17691	178	3073.5	455	12	36606	0.925
GOG6/277-A	97.97	103	235.5	16523	671	0	503.5	609.5	16832	100.5	4648.5	397.5	11.5	40624	0.962
GOG6/278-A	98.53	0	288	13032	221.5	0	91.5	271.5	708	205.5	5762.5	275	24	20855.5	0.980
GOG7/279-A	103.07	49.5	302	14907	1675	0	642.5	277.5	10423.5	241	6363.5	284.5	13	35166	0.982
GOG7/282-A	104.19	48.5	203	8549	2286.5	23	48.5	23	2690.5	96.5	7253	119.5	23	21341	0.994
GOG7/283-A	104.75	0	367	8061.5	699.5	0	48	128.5	1229.5	128	8449	79.5	23.5	19190.5	0.986
GOG7/285-A	105.38	36	143.5	6270	179.5	0	12.5	70.5	1165.5	187.5	6275	71	33	14411	0.984
GOG8/286-A	112.94	131.5	335.5	19060.5	426.5	0	2187	345	21365.5	254	7100.5	517	9.5	51723	0.979
GOG8/289-A	114.775	22.5	393	15595	589.5	27	0	170	3891	1675	6946.5	147.5	16.5	29457	0.989
GOG9/292-A	116.505	24	79	5186.5	63.5	0	0	24	1364	190.5	2561.5	24	49	9517	0.991
GOG9/293-A	117.555	0	241.5	5242	35.5	0	39	5.5	41	171.5	1766.5	11.5	63	7554	0.999
GOG10/294-A	119.21	27.5	200	13987	775	0	83	55.5	11256.5	283.5	7448	88	18.5	34204	0.995
GOG10/296-A	120.695	20.5	211.5	4632	62	7	7	20.5	452.5	90	2642	14	58	8159	0.992
GOG11/297-A	122.27	25.5	346.5	12393	264	0	146.5	95	6101	446	6195.5	130.5	19.5	26143.5	0.991
GOG11/299-A	124.365	16	69	5068.5	38	0	23.5	23.5	382	175	3394.5	31.5	50.5	9221.5	0.992
GOG11/301-A	126.44	52.5	145	10589	49.5	0	10.5	0	1273	102	2572	10.5	30	14804	0.995
GOG12/302-A	128.58	21	232	11361.5	590	42	105	0	6450.5	189.5	6281.5	21	19	25294	0.998
GOG12/304-A	129.84	0	28.5	1331	0	0	0	16.5	20	19	1595	10	88	3020	0.988

APPENDIX 5: Palynofacies analysis of Goggin Road - Absolute abundance per gram.

APPENDIX 6

PALYNOFACIES ANALYSIS OF PITCH COPPICE QUARRY - ABSOLUTE ABUNDANCE PER GRAM.

Sample	Height (m) above/below Wenlock-Ludlow boundary	Spores	Prasinophyte Algae	Acritarchs	Chitinozoans	Scolecodonts	Land Plants	AOM	Indeterminate Organic Matter	Zoomorph fragments	Tubes	Lycopodium spores	Total POM	Marine Index
PC/1-C	-2.89		27.5	5052.5	341	183.5	513.5	202	1321.5	6112.5	18.5	18.5	13772.5	0.916
PC/3-C	-1.87		15	2145.5	34	7.5	134.5	106	702.5	1967.5		49	5112.5	0.942
PC/5-C	-1.31		28.5	3030	51.5	43	172	212	1028.5	1440.5	8.5	42	6014.5	0.948
PC/7-C	-0.55		13.5	3105.5	128	107.5	291.5	156	1087.5	1971.5	9.5	37.5	6870.5	0.920
PC/9-C	-0.23		9	3109.5	93.5	102.5	442.5	26	708.5	2160	22	39	6673.5	0.882
PC/10a-A	-0.135	26	52	4953.5	181.5	155.5	960	648.5	1089.5	7469	26	18	15561.5	0.844
PC/10e-A	-0.015			1723.5	123.5	23	232.5	303.5	829	1601		53	4836	0.889
PC/12-A	0.03	89.5	24	5991	285.5	126.5	743	48.5	484.5	5573		18.5	13389.5	0.886
PC/13-A	0.095	32	53.5	2458	169.5	11.5	316.5	53.5	429.5	2772		37	6296	0.885
PC/14-A	0.175		30.5	4123	46.5	15	155	62.5	431.5	4421		26.5	9285	0.965
PC/16-A	0.655	41	93	5726.5	211.5	122.5	122.5	107.5	654.5	5150.5	41	22	12270.5	0.974
PC/18-A	1.515	52.5	104	6300.5	51	51	87	87	395.5	3241.5	17.5	22.5	10387.5	0.979
PC/20-A	2.165	15.5	139	4513.5	46.5	108.5	77.5	31		3879.5	62	27	9275	0.981

APPENDIX 6: Palynofacies analysis of Pitch Coppice Quarry - Absolute abundance per gram.

Cymatiosphaera octoplana Downie 1959 emend. 13

11 Specimen with striae membrane bases, x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - L10/1).

12 As fig. 11, showing reticulate vesicle ornament, x 1000(DIC).

13 Sub triangular example, x 1000 (DIC), Lower Elton Formation (GOG2/69-A (1) - R39).

Cymatiosphaera paucimembrana sp. nov. 14

18 Specimen showing large nature of fields, x 1000 (DIC), Middle Elton Formation (GOG6/275-A (1) - O35/1). Holotype.

19 x1000, Middle Elton Formation (GOG4/204-A (1) - O29/2).

Cymatiosphaera aff. *pavimenta* (Deflandre 1945) Deflandre 1954. 15

14 x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - S32/2).

15 Specimen almost split into two equal halves by unornamented rupture, x 1000 (DIC), Lower Elton Formation (GOG2/37-A (1) - R10).

Cymatiosphaera triangula sp. nov. 16

16 x 1000, Lower Elton Formation (TRENCH1/11-A (1) - L47/1). Holotype.

17 x 1000, Much Wenlock Limestone Formation (GOG1/2-C (2) - P38/1).

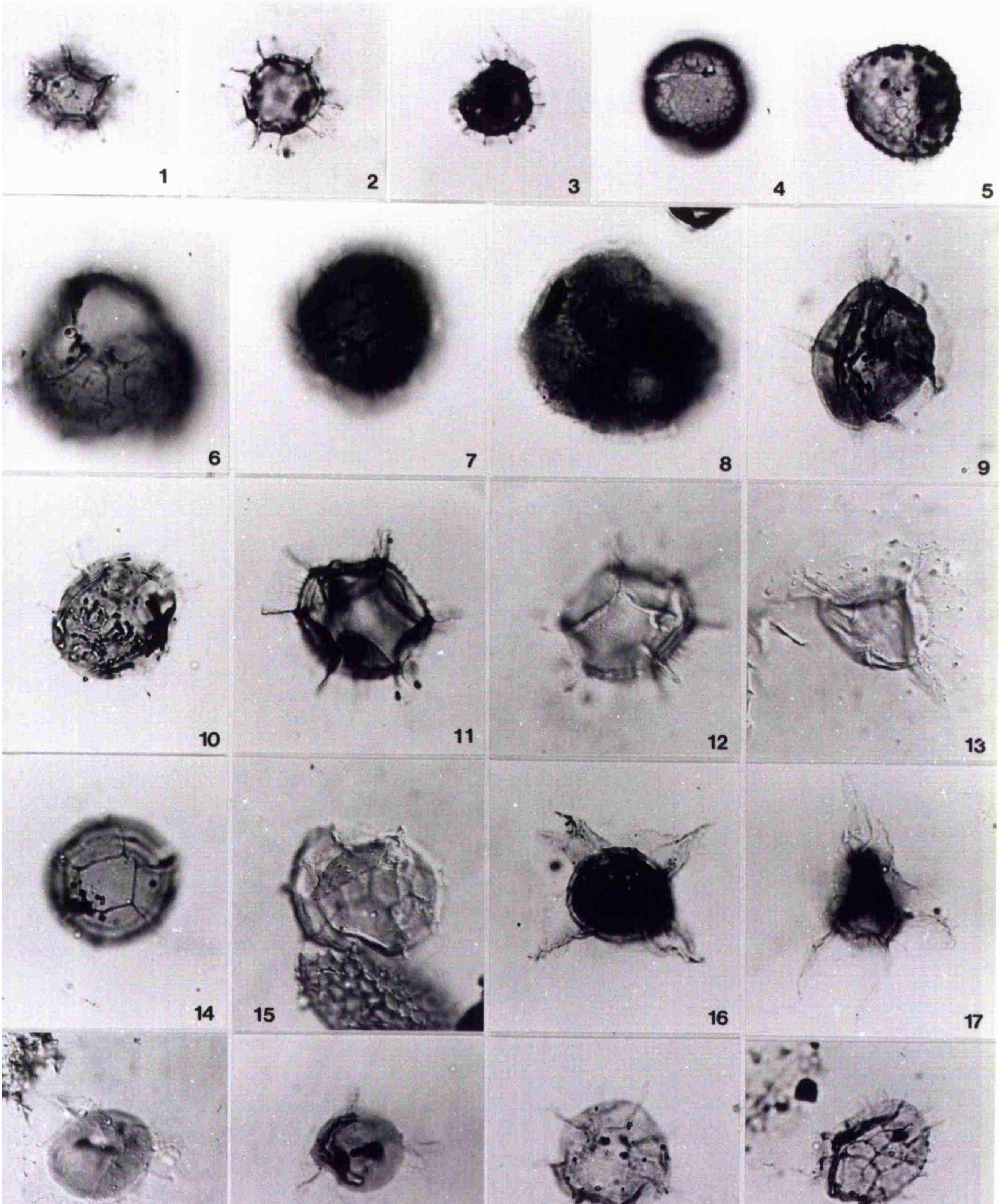
Cymatiosphaera sp. A. 16

20 x 1000, Middle Elton Formation (GOG12/302-A (1) - K31/1).

21 x 1000, Middle Elton Formation (GOG9/292-A (2) - S39/1).

PLATE 1

Fig.		Page
	Cymatiosphaera aff. *cornifera* Deunff 1955.	8
1	Specimen showing central projections, x 1000, Much Wenlock Limestone Formation (GOG1/2-C (2) - R46/2).	
2	As fig. 1, x 1000.	
	Cymatiosphaera ? cf. *imperfecta* Le Hérissé 1989.	9
6	Specimen with isolated fields, x 1000, Much Wenlock Limestone Formation (PC3-C (1) - T50).	
7	Specimen with irregular fields, x 1000, Much Wenlock Limestone Formation (GOG1/2-C (2) - R36/1).	
8	x 1000, Middle Elton Formation (TRENCH5/222-A (1) - Q34/4).	
	Cymatiosphaera aff. *ledburica* Dorning 1981a.	10
9	x 1000, Lower Elton Formation (TRENCH1/11-A (1) - Q46/2	
	Cymatiosphaera mariae Cramer, Diez, Rodriguez & Fombella 1976 emend Le Hérissé 1989.	11
10	x 1000, Middle Elton Formation (TRENCH4/187-A (1) - L48).	
	Cymatiosphaera multicrista sp. nov.	12
4	Specimen with unornamented rupture, x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - K42/4). Holotype.	
5	Thin walled example, x 1000, Much Wenlock Limestone Formation (GOG1/7-C (2) - U38/3).	
	Cymatiosphaera aff. *multisepta* Deunff 1955.	12
3	x1000, Lower Elton Formation (GOG3/131-A (1) - H37).	


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

Ammonidium sp. A. 34

21 x 1000, Middle Elton Formation (TRENCH5/220-A (1) - M30/4).

Baltisphaeridium muldiensis Le Hérissé 1989. 35

22 Specimen with circular structures, simple and branched processes, x 750 (DIC), Much Wenlock Limestone Formation (PC3-C (1) - S44).

14 Example with central dark area and linear fold, x 1000, Much Wenlock Limestone Formation (GOG1/7-A (2) - R39/3).

Melikeriopalla amydra Tappan & Loeblich Jr. 1971. 23

11 Specimen with large and fine pores, x 500, Much Wenlock Limestone Formation (GOG1/7-C (1) - M34).

3 As for fig. 11, detail of wall structure, x 1000.

12 x 500, Lower Elton Formation (GOG3/127-A (1) - P38/3).

Polyedrixium wenlockium (Dorning 1981a) Le Hérissé 1989. 26

13 x 500 (DIC), Much Wenlock Limestone Formation (TRENCH1/9-C (1) W43).

Pterospermella foveolata Dorning 1981a. 27

19 Large specimen with unopened rupture, x 500 (DIC), Lower Elton Formation (PC18-O (1) - K53/3).

Pterospermella sp. A. 28

17 x 1000, Much Wenlock Limestone Formation (PC5-C (2) - U59/4).

Pterospermella sp. B. 28

15 Specimen with laevigate vesicle, x 1000, Much Wenlock Limestone Formation (PC8-C (2) - Q19).

16 Example with granulate vesicle, x 1000, Much Wenlock Limestone Formation (PC7-C (2) - L54/3).

Quadratitum fantasticum Cramer 1964b. 30

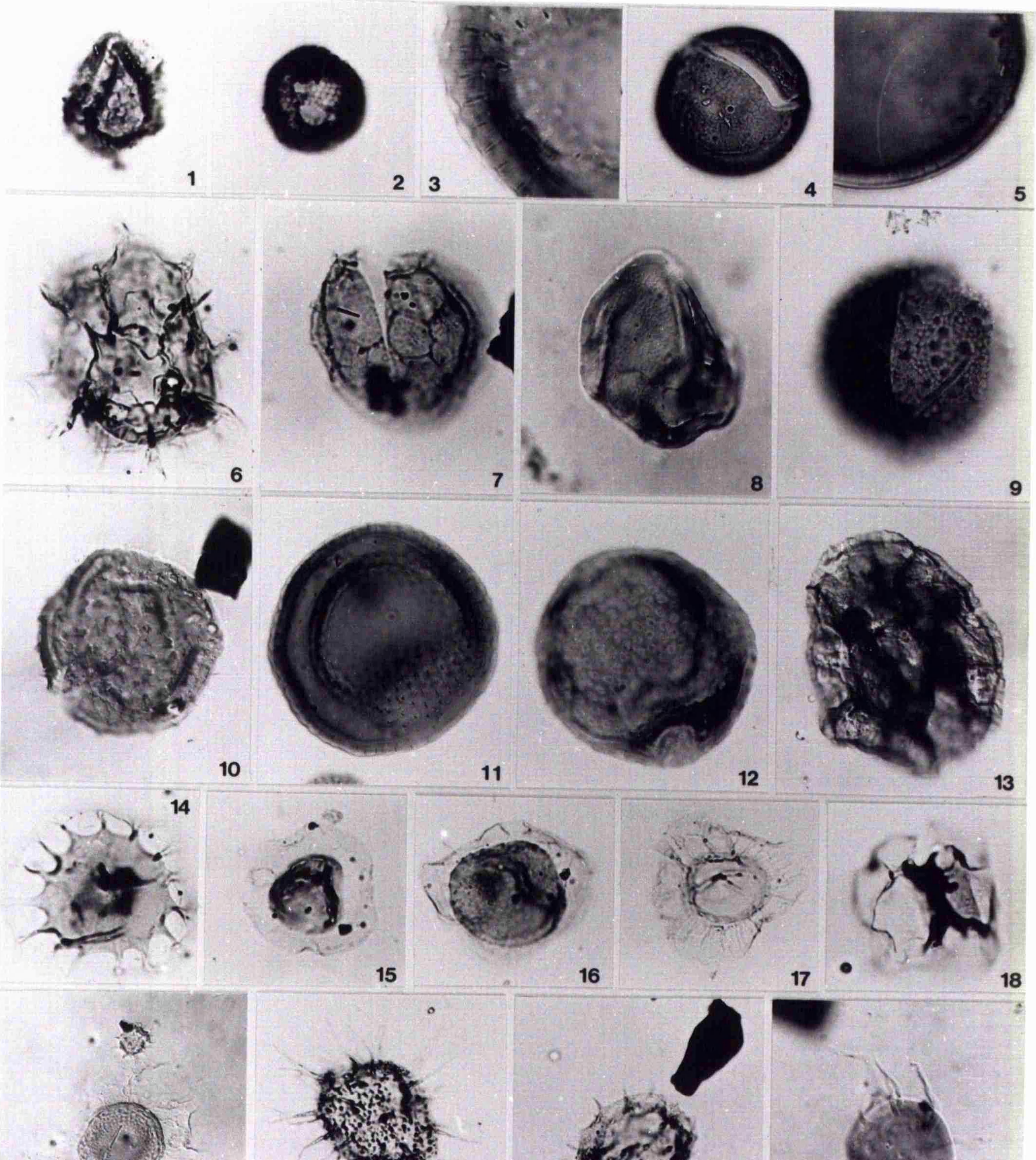
18 x 1000, Much Wenlock Limestone Formation (TRENCH1/9-C (1) - S38).

Ammonidium waldronense (Tappan & Loeblich Jr. 1971) Dorning 1981a. 33

20 x 1000, Middle Elton Formation (TRENCH5/216-A (2) - Q10).

PLATE 2

Fig.		Page
	Cymatiosphaera lawsonii sp. nov.	10
6	x 1000, Lower Elton Formation (TRENCH3/151-A (1) - Q36). Holotype	
	Cymatiosphaera sp. B.	17
1	x 1000, Middle Elton Formation (TRENCH4/192-A (2) - T51/2).	
	Dictyotidium biscutulatum Kiryanov 1978.	17
7	Example with unornamented rupture, x 1000, Middle Elton Formation (GOG6/259-A (1) - M40/1).	
	Dictyotidium faviforme Schultz 1967.	18
2	Small example, x 1000, Middle Elton Formation (TRENCH4/192-A (1) - T45).	
4	Specimen with a rigid wall, x 500, Much Wenlock Limestone Formation (GOG1/2-C (1) - J44).	
5	As for fig. 4, detail of porous wall (DIC).	
8	Large specimen, x 500 (DIC), Much Wenlock Limestone Formation (PC3-C (1) - Q44).	
	Dictyotidium stenodictyum Eisenack 1965a.	19
9	Specimen with dense reticulae, large projections and unopened rupture with thickened lips, x 500 (DIC), Much Wenlock Limestone Formation (GOG1/2-A (2) - U28/3).	
10	Example with large reticulae and small projections, x 500 (DIC), Middle Elton Formation (TRENCH4/167-A (2) - T38/3).	
	Duvernaysphaera aranides (Cramer 1964b) Le Hérissé 1989.	21


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Cymbosphaeridium pilar (Cramer 1964b) Lister 1970. 46

9 x 600 (DIC), Middle Elton Formation (TRENCH5/216-A (2) - P40).

10 Specimen showing vesicle ornament and rear side of the equatorial suture that almost divides the vesicle in two, x 600 (DIC), Middle Elton Formation (TRENCH5/216-A (2) - T14/2).

Cymbosphaeridium sp. A. 47

11 x 1000, Lower Elton Formation (GOG3/94-A (1) - M37/4).

Dateriocradus cf. *monterrosae* (Cramer 1969a) Pöthé de Baldis 1981. 47

12 x 1000, Much Wenlock Limestone Formation (TRENCH1/10-A (2) - T44/3).

Dateriocradus sp. A. 50

13 x 500 (DIC), Much Wenlock Limestone Formation (GOG1/7-C (1) - M12).

Dorsennidium europaeum (Stockmans & Willière 1960) Sarjeant & Stancliffe 1994 emend. 52

14 x 1000, Much Wenlock Limestone Formation (PC9-C (2) - S52).

Dorsennidium formosum (Stockmans & Willière 1960) Sarjeant & Stancliffe 1994. 53

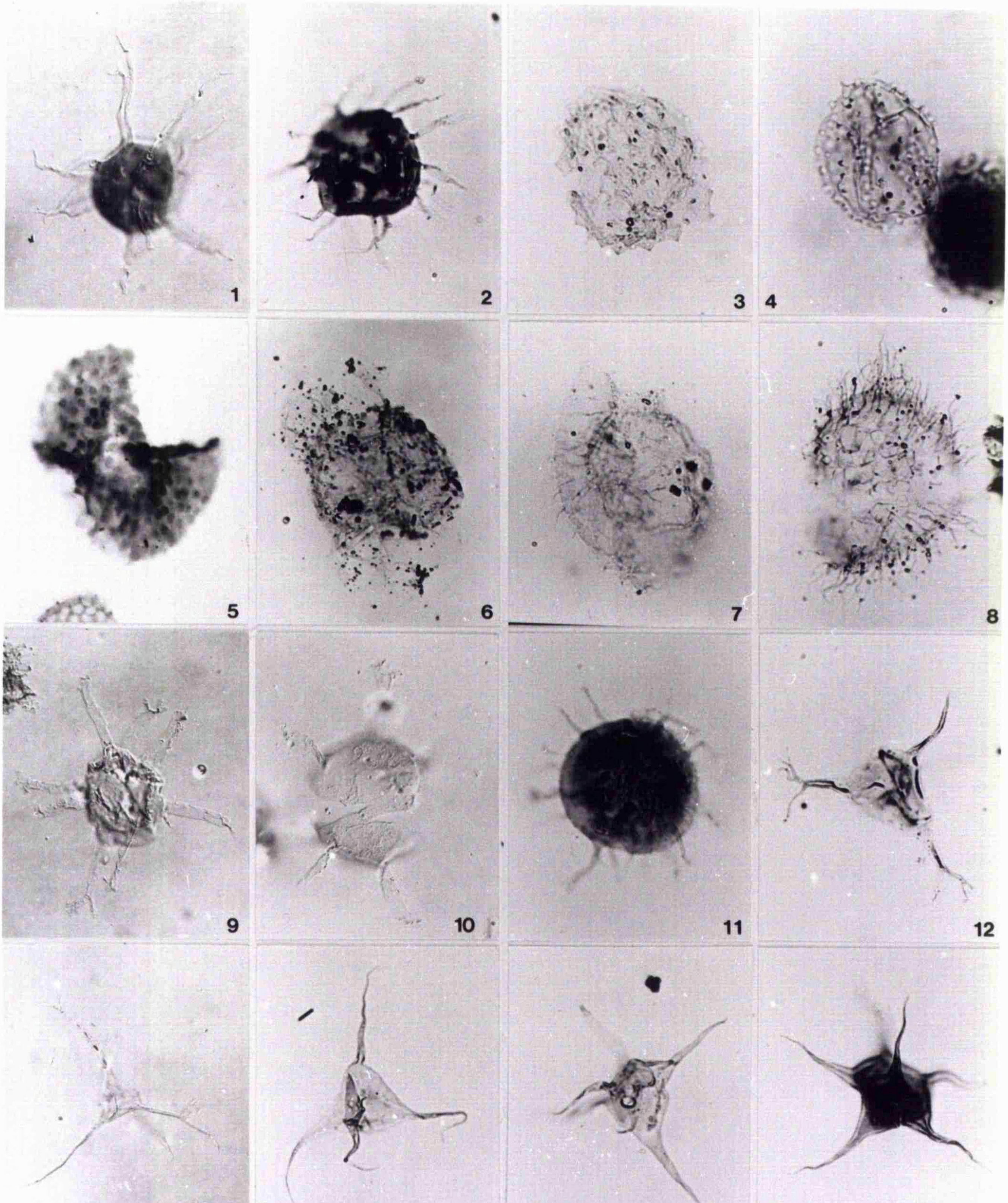
15 x 600, Lower Elton Formation (GOG3/127-A (1) - U29).

Dorsennidium pentagonale (Stockmans & Willière 1963) comb. nov. 54

16 x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - K15/2).

PLATE 3

Fig.		Page
	Baltisphaeridium muldiensis var. A.	37
1	x 750 (DIC), Lower Elton Formation (GOG2/42-A (1) - K40/1).	
	Baltisphaeridium sp. A.	37
2	x 900, Much Wenlock Limestone Formation (PC6-O (1) - U48/1).	
	Buedingiisphaeridium pyramidale Lister 1970.	38
3	Example showing pyramidale processes with solid tips, x 1000, Lower Elton Formation (TRENCH4/163-A (1) - S47/2).	
4	Specimen with rounded processes, x 1000, Much Wenlock Limestone Formation (TRENCH1/9-C (1) - R44/4).	
	Buedingiisphaeridium reticulum sp. nov.	39
5	Specimen with unornamented rupture, x 750, Lower Elton Formation (GOG2/69-A (1) - G45/3). Holotype.	
	Carminella maplewoodensis Cramer 1968a.	40
6	x 750, Lower Elton Formation (TRENCH3/154-A (2) - O41/3).	
	Comasphaeridium brevispinosum (Lister 1970) comb. nov.	42
7	x 1000, Much Wenlock Limestone Formation (TRENCH1/9-C (1) - M48/4).	
	Comasphaeridium williereae (Deflandre & Deflandre-Rigaud 1965 ex Lister 1970) Sarjeant & Stancliffe 1994.	43
8	x 1000, Much Wenlock Limestone Formation (PC9-C (1) - O56/1).	


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

(

Glyptosphaera heltaskelta sp. nov. 69

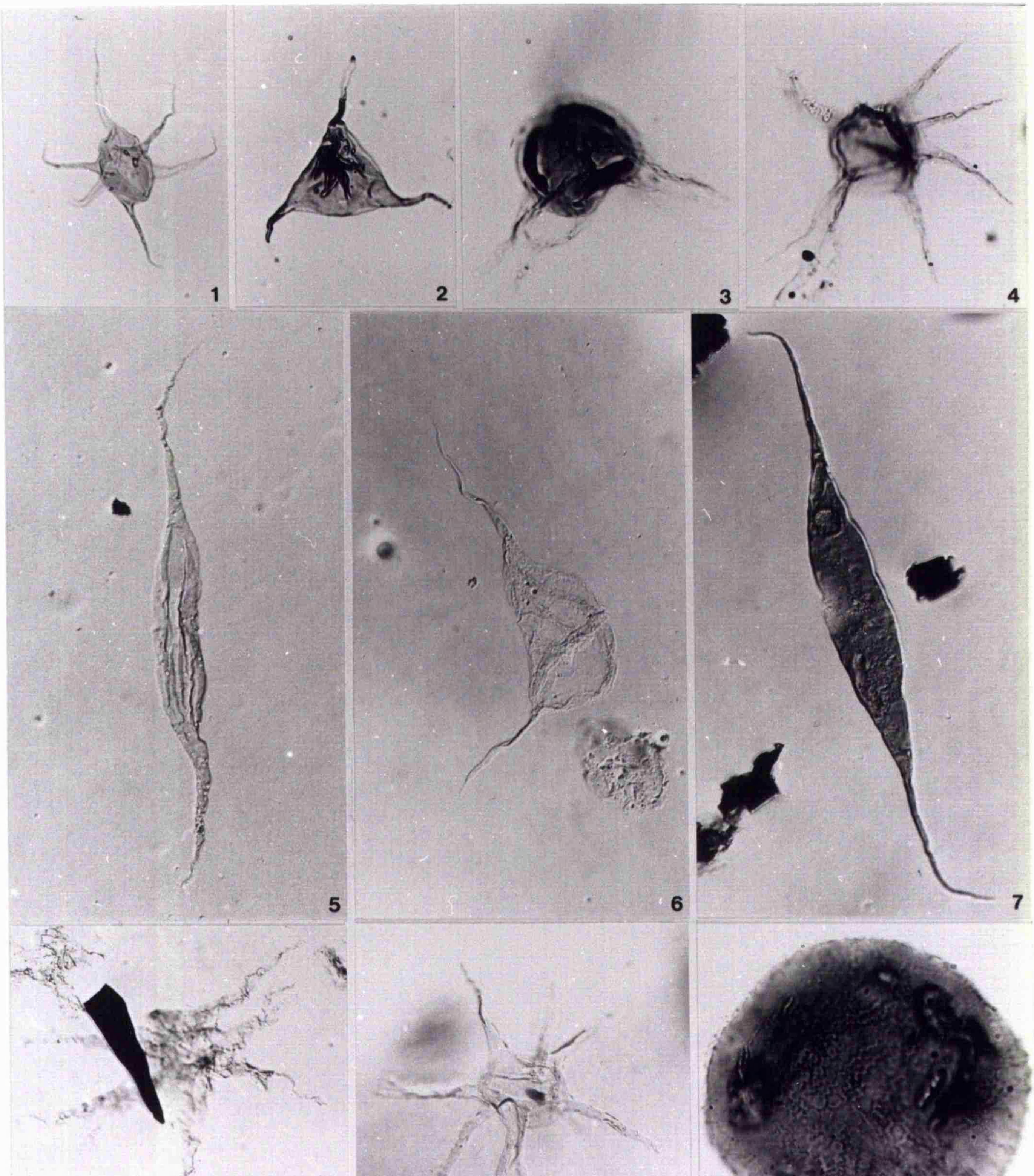
10 x 1000, Middle Elton Formation (TRENCH4/183-A (1) - L29/1).

Leiofusa estrecha Cramer 1964a 83

7 x 500 (DIC), Lower Elton Formation (GOG2/75-A (2) - X5).

PLATE 4

Fig.		Page
	Dorsennidium rhomboidium (Downie 1959) Sarjeant & Stancliffe 1994 emend.	55
1	x 600, Lower Elton Formation (GOG2/37-A (1) - N28/1).	
	Dorsennidium wenlockianum (Downie 1959 ex Wall & Downie 1963) comb. nov.	57
2	x 1000, Much Wenlock Limestone Formation (PC2-C (1) - S44/1).	
	Eisenackidium wenlockense Dorning 1981a.	59
3	x 1000, Much Wenlock Limestone Formation (GOG1/2-C (2) - O38).	
	Eisenackidium sp. A.	60
4	x 1000, Much Wenlock Limestone Formation (TRENCH1/7-C (2) - S48).	
	Estiastra granulata Downie 1963.	61
8	x 400 (DIC), Much Wenlock Limestone Formation (PC1-C (1) - G49/4).	
	Eupoikilofusa filifera (Downie 1959) Dorning 1981a emend.	63
5	x 500 (DIC), Lower Elton Formation (TRENCH1/17-A (1) - M40/3).	
	Eupoikilofusa tenuistriata (Pöthé de Baldis 1975) Pöthé de Baldis 1981.	64
6	x 750 (DIC), Middle Elton Formation (TRENCH5/214-A (1) - Q26).	
	Evittia remota (Deunff 1955) Lister 1970 Group	66
9	x 500 (DIC), Lower Elton Formation (GOG2/75-A (1) - O31).	


1
2
3
4
5
6
7
8
9
10

Helosphaeridium ? sp. C. 79

20 x 1000, Lower Elton Formation (GOG2/69-A (1) - O42/3).

8 x 1000 (DIC), Lower Elton Formation (GOG2/37-A (1) - J33).

Gorgonisphaeridium sp. A. 74

5 x1000, Much Wenlock Limestone Formation (PC2-C (1) - T45/1).

Gorgonisphaeridium sp. B. 75

9 Specimen with bifurcate and simple processes, x 1000, Lower Elton Formation (TRENCH1/11-A (1) - S40/4).

Hapsidopalla jeandeunffii Le Hérissé 1989. 76

14 Example showing an unornamented rupture, x 1000, Much Wenlock Limestone Formation (GOG1/7-C (2) - P45/3).

Helosphaeridium clavispinulosum Lister 1970. 77

15 x 1000, Lower Elton Formation (GOG2/62-A (1) - P41).

Helosphaeridium latispinosum Lister 1970. 77

16 x 1000, Middle Elton Formation (GOG12/302-A (1) - M40/3).

Helosphaeridium pseudodictyum Lister 1970. 78

18 Specimen with an unornamented rupture, x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - K17).

Helosphaeridium sp. A. 79

19 x 1000, Lower Elton Formation (GOG3/127-A (1) - R40/3).

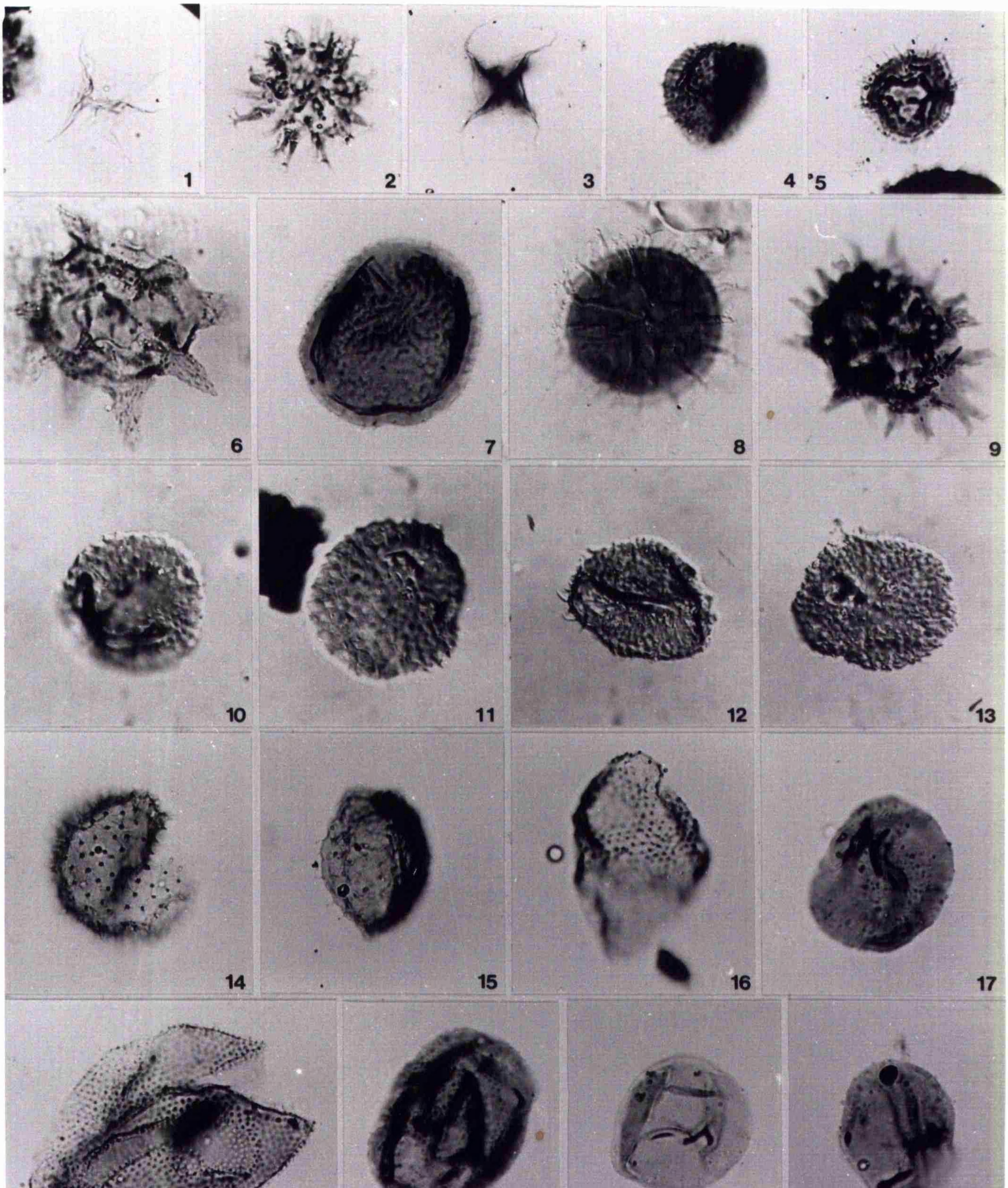
Helosphaeridium sp. B. 79

17 x 1000, Middle Elton Formation (GOG8/286-A (1) - P43).

21 x 1000, Middle Elton Formation (GOG7/279-A (1) - S32).

PLATE 5

Fig.		Page
	Dorsennidium sp. A.	58
1	x 1000, Much Wenlock Limestone Formation (PC5-C (1) - S23/4).	
3	x 1000, much Wenlock Limestone Formation ((PC7-C (1) - Q17/4).	
	Evittia robustispinosa (Downie 1959) Le Hérissé 1989 emend.	68
6	x 1000, Lower Elton Formation (GOG3/98-A (2) - T33).	
	Glyptosphaera speciosa Kiryanov 1978.	70
7	x 750, Lower Elton Formation (GOG3/100-A (1) - Q48).	
	Gorgonisphaeridium citrinum (Downie 1963) comb. nov.	71
4	x 1000, Much Wenlock Limestone Formation (PC1-C (1) - S42/3).	
	Gorgonisphaeridium ? *listeri* sp. nov.	72
10	Subtriangular specimen, x 1000, Middle Elton Formation (GOG6/269-A (1) - S45/4). Holotype.	
11	x 1000, Middle Elton Formation (GOG12/302-A (2) - Q29/3).	
	Gorgonisphaeridium ? *listeri* var. A	73
12	x 1000, Lower Elton Formation (TRENCH2/88-A (2) - P31/3).	
13	x 1000, Lower Elton Formation (TRENCH2/83-A (1) - O46/3).	
	Gorgonisphaeridium ramosum Pöthé de Baldis 1981	73
2	x 1000, Lower Elton Formation (TRENCH1/11-A (1) - Q40).	
	Gorgonisphaeridium succinum Lister 1970.	74


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

10 x 1000, Much Wenlock Limestone Formation (GOG1/2-C (2) - Q36).

Micrhystridium inflatum (Downie 1959) Lister 1970. 90

13 & 14 x 630, Lower Elton Formation (TRENCH1/23-A (2) - T51/4).

Micrhystridium intonsurans (Lister 1970) Dorning 1981a. 91

12 x 1000, Middle Elton Formation (GOG12/302-A (1) - Q47).

Micrhystridium stellatum Deflandre 1945a. 92

11 x 1000, Lower Elton Formation (GOG2/37-A (1) - G34/1).

Micrhystridium sp. A. 93

15 x 1000, Much Wenlock Limestone Formation (PC5-C (2) - U59/4).

Micrhystridium ? sp. B. 94

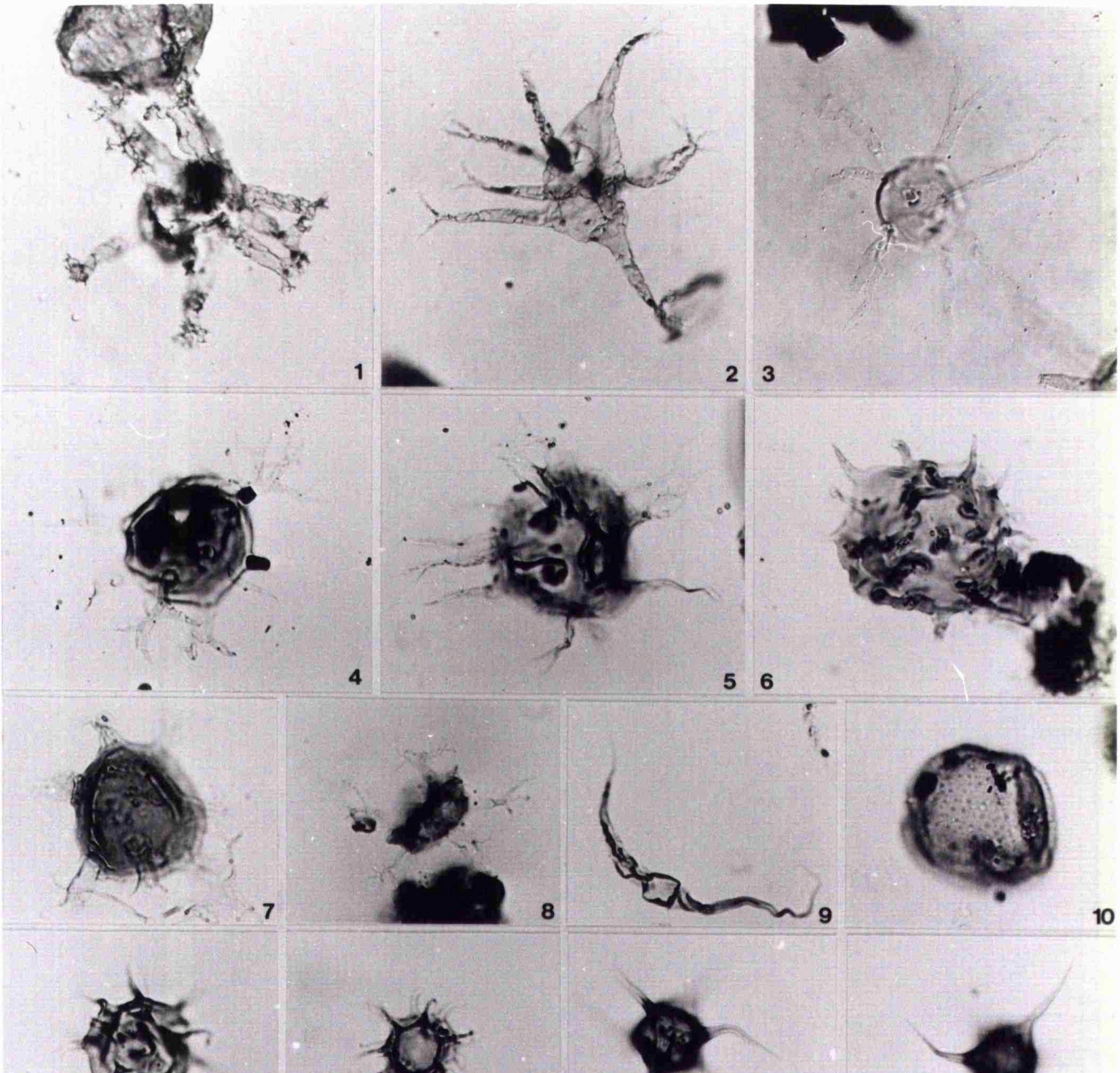
6 x 1000, Middle Elton Formation (GOG5/236-A (1) - Q41/3).
16 x 1000, Middle Elton Formation (GOG6/252-A (1) - O34).

Multiplicisphaeridium sp. A. 98

17 & 18 x 1000, Lower Elton Formation (GOG2/47-A (1) - L46/2).

PLATE 6

Fig.		Page
	Hoegklintia cf. *corallina* (Eisenack 1959) Le Hérissé 1989.	80
1	x 400 (DIC), Much Wenlock Limestone Formation (GOG1/5-C (1) - Q28/2).	
	Hoegklintia cf. *digitata* (Eisenack 1938) Dorning 1981a.	81
2	x 400 (DIC), Lower Elton Formation (TRENCH1/12-A (1) - R34/3).	
	Leiofusa parvitatis Loeblich Jr. 1970.	84
9	x 1000, Lower Elton Formation (GOG2/37-A (1) - N38).	
	Leptobrachion arbusculiferum (Downie 1963) Dorning 1981a.	86
4	x 1000, Much Wenlock Limestone Formation (PC2-O (1) - T46/2).	
	Leptobrachion digitatum sp. nov.	87
5	x 1000, Lower Elton Formation (TRENCH1/11-A (1) - N40/4). Holotype.	
	Leptobrachion sp. A.	87
3	x 750 (DIC), Lower Elton Formation (GOG2/37-A (1) - H46/3).	
	Leptobrachion sp. B.	88
8	x 1000, Middle Elton Formation (TRENCH5/222-A (2) - Q48/2).	
	Leptobrachion sp. C.	88
7	x 1000, Lower Elton Formation (PC18-A (1) - M63).	
	Lophosphaeridium sp. A.	89


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

9 x 1000, Lower Elton Formation (GOG3/103-A (1) - M35/4).

Oppilatala septispinosa (Lister 1970) Le Hérissé 1989. 104

8 Specimen with large rupture, x 1000, Lower Elton Formation (TRENCH4/165-A (1) - V46/1).

Ozotobrachion cf. *dicros* Loeblich Jr. & Drugg 1968. 105

7 x 500 (DIC), Lower Elton Formation (PC20-A (1) - Q42/2).

Percultisphaera stiphrospinata Lister 1970. 107

12 x 1000, Middle Elton Formation (GOG12/302-A (2) - Q3).
13 x 600 (DIC), Middle Elton Formation (GOG12/3020A (2) - O34).

Psenotopus chondrocheus Tappan & Loeblich Jr. 1971 emend. 108

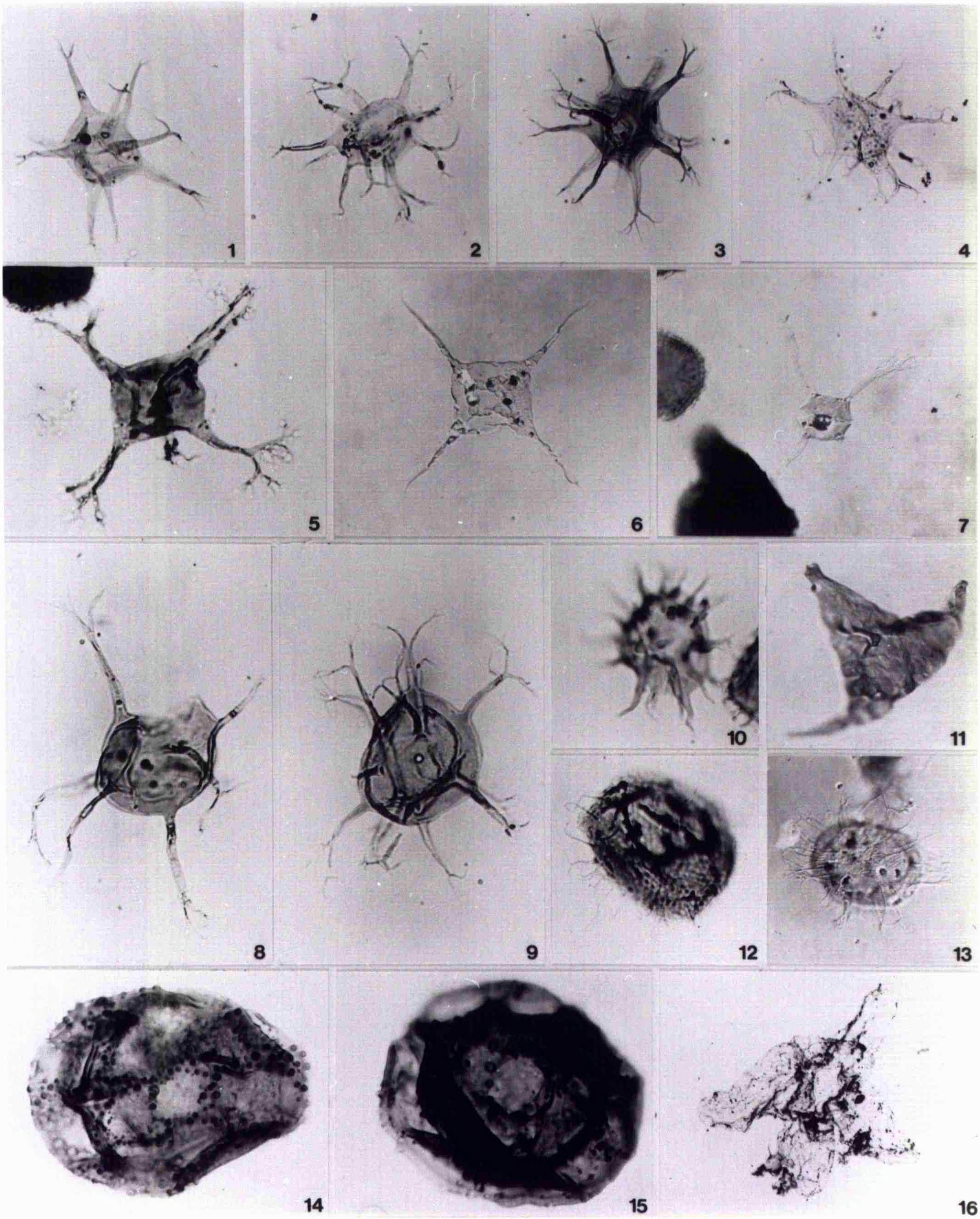
14 x 750, Lower Elton Formation (GOG2/75-A (1) - W35).
15 Specimen showing central, circular pylome ringed by ornament, x 750, Lower Elton Formation (TRENCH2/83-A (1) - S40/1).

Pulvinosphaeridium oligoprojectum Downie 1959 emend. 110

16 Thin walled specimen, x 250, Much Wenlock Limestone Formation (PC5-C (2) - V51).

PLATE 7

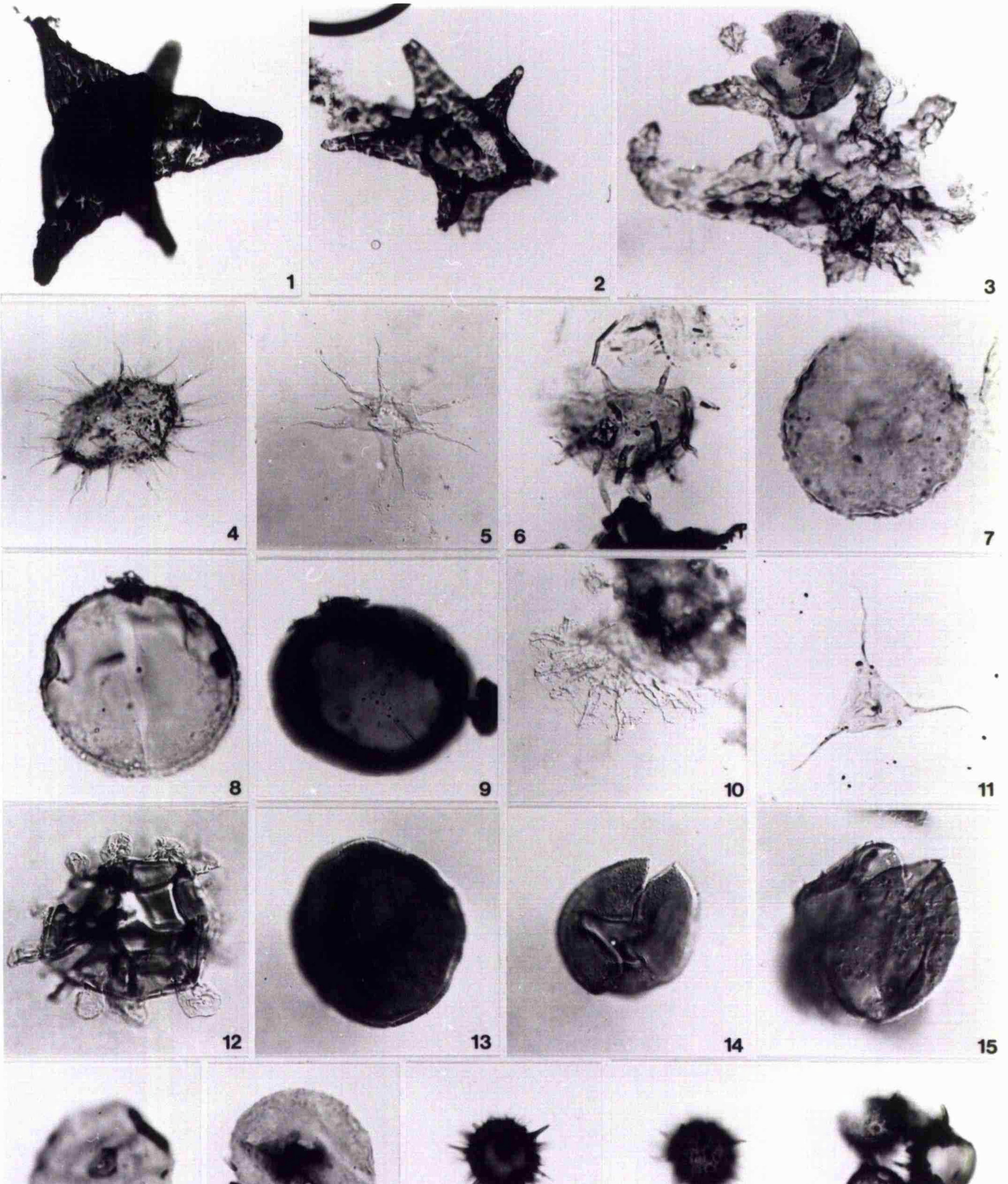
Fig.		Page
	Multiplicisphaeridium arbusculum Dorning 1981a.	95
1	x 750, Lower Elton Formation (TRENCH1/14-A (1) - U34/2).	
	Multiplicisphaeridium arbusculum var. A.	96
5	x750, Lower Elton Formation (TRENCH2/90-A (1) - O29/2).	
	Multiplicisphaeridium eltonense Dorning 1981a.	96
2	x 1000, Middle Elton Formation (GOG6/275-A (1) - U18/1).	
	Multiplicisphaeridium variabile (Lister 1970) Dorning 1981a.	97
3	x 750, Lower Elton Formation (GOG2/37-A (1) - M37/4).	
	Multiplicisphaeridium sp. B.	98
4	x 1000, Middle Elton Formation (GOG6/259-A (1) - Q39/4).	
	Multiplicisphaeridium sp. C.	99
10	x 1000, Lower Elton Formation (GOG2/62-A (1) - P43).	
	Neoveryhachium mayhillense Dorning 1981a.	100
6	x 500 (DIC), Much Wenlock Limestone Formation (PC9-C (1) - K55/3).	
	Onondagella deunffii Cramer 1966c emend. Le Hérissé 1989.	101
11	x 500 (DIC), Lower Elton Formation (GOG3/103-A (1) - Q34/3).	
	Oppilatala ramusculosa (Deflandre 1942 ex Deflandre 1945) Dorning 1981a.	102


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

5	x 500 (DIC), Lower Elton Formation (TRENCH1/11-A (1) - S36/1).	
	Tasmanites spp.	31
9	Specimen with unopened rupture, x 300, Middle Elton Formation (TRENCH4/197-A (2) - O41/4).	
	Tunisphaeridium tentaculaferum (Martin 1967) Cramer 1970a.	116
10	x 750 (DIC), Middle Elton Formation (GOG6/256-A (1) - G36/4).	
	Veryhachium trisphaeridium Downie 1963 emend.	118
11	x 1000, Much Wenlock Limestone Formation (PC8-O (2) - Q18).	
	Visbysphaera microspinosa (Eisenack 1954a) Lister 1970 Group.	120
13	x 500 (DIC), Lower Elton Formation (TRENCH1/11-A (1) - U38/4).	
14	Specimen with unornamented rupture, x 750 (DIC), Lower Elton Formation (TRENCH1/12-A (2) - T31/4).	
	Visbysphaera pirifera (Eisenack 1954a) Kiryanov 1978.	121
12	x 750 (DIC), Lower Elton Formation (GOG2/37-A (1) - R15).	
	Baltisphaeridium ? *spinatum* sp. nov.	37
18 & 19	x 1000, Middle Elton Formation (GOG5/245-A (1) - R44/2). Holotype.	
20	Group of 4 individuals, one with a circular pylome, x 1000, Lower Elton Formation (TRENCH4/LE2-A (1) - R42).	
	Visbysphaera sp. A.	123
15	x 1000 (DIC), Lower Elton Formation (GOG2/42-A (1) - L44/2).	

PLATE 8

Fig.		Page
	Pulvinosphaeridium dorningii sp. nov.	110
2	Thick walled specimen, x 250, Lower Elton Formation (GOG2/69-A (2) - N22).	
3	Thin walled specimen, x 400, Lower Elton Formation (GOG2/69-A (2) - R35). Holotype.	
	Pulvinosphaeridium oligoprojectum Downie 1959 emend.	110
1	Thick walled specimen, x 250, Much Wenlock Limestone Formation (PC5-C (2) - R52).	
	Salopidium granuliferum (Downie 1959) Dorning 1981a.	112
4	x 1000, Much Wenlock Limestone Formation (GOG1/7-C (1) - O9).	
	Salopidium sp. A.	113
6	x 1000, Middle Elton Formation (TRENCH5/216-A (1) - S45).	
	Schismatosphaeridium rugulosum Dorning 1981a emend.	114
7	Specimen showing thickened pseudopylome, x 1000, Lower Elton Formation (GOG2/37-A (1) - P35/4).	
8	Example displaying pseudopylome and unornamented rupture, x 1000, Lower Elton Formation (TRENCH1/23-A (2) - V36).	
	Schismatosphaeridium sp. A.	114
16	x 1000, Middle Elton Formation (GOG5/241-A (1) - O41/4).	
17	x 1000, Lower Elton Formation (GOG3/103-A (1) - L33/2).	
	Stellechinatum ? sp. A.	115


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Cymatiosphaera triangula sp. nov. 16

10 Specimen showing thicker walled inner body with projections from the fields, x 1000, Much Wenlock Limestone Formation (PC2-0).

11 As fig. 10, x 2000.

Dictyotidium biscutulatum Kiryanov 1978. 17

13 x1000, Middle Elton Formation (GOG4/212-A).

14 As fig. 13, detail showing reduced, or absent, ornamentation near the membranes, x 3000.

Dictyotidium faviforme Schultz 1967. 18

15 Small specimen, x 2000, Middle Elton Formation (GOG4/207-A).

16 Large specimen with unopened rupture, x 750, Much Wenlock Limestone Formation (PC1-C).

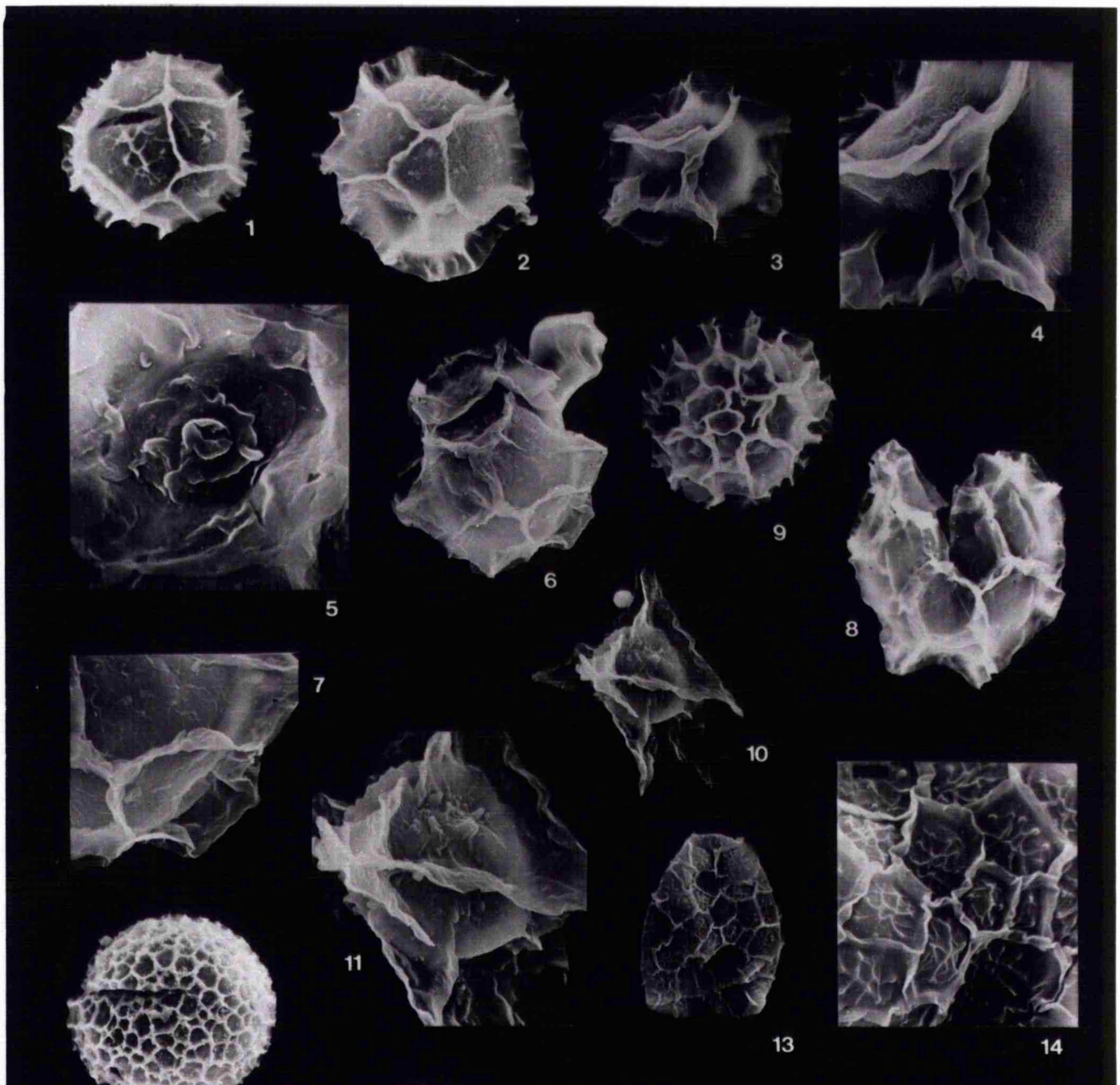
Dictyotidium stenodictyum Eisenack 1965a. 19

17 Specimen with unopened rupture, possessing thickened lips, dense reticulae and large projections, x 500, Lower Elton Formation (GOG2/42-A).

18 Specimen with larger reticulae and smaller projections, x 500, Middle Elton Formation (TRENCH5/220-A).

PLATE 9

Fig.		Page
	Cymatiosphaera aff. *cornifera* Deunff 1955.	8
1	Specimen with simple, unornamented, rupture and complex central projections, x 1000, Much Wenlock Limestone Formation (GOG1/2-C).	
2	Specimen possessing unopened rupture, with thickened lips, and sparse projections positioned randomly within fields, x 1000, Much Wenlock Limestone Formation, (GOG1/2-C).	
	Cymatiosphaera lawsonii sp. nov.	10
6	Specimen with simple rupture, x 1000, Lower Elton Formation (GOG2/42-A).	
7	As fig. 6, detail of reticulate vesicle ornament, x 2000.	
8	x 1000, Lower Elton Formation (GOG3/127-A).	
	Cymatiosphaera aff. ledburica Dorning 1981a.	10
3	x 1000, Middle Elton Formation (TRENCH6/251-A).	
4	As fig. 3, detail of fine reticulate vesicle ornament, x 2000.	
	Cymatiosphaera mariae Cramer, Diez & Fombella 1976 emend. Le Hérissé 1989.	11
5	Detail of a single field showing the central circular structure, x 3000, Middle Elton Formation (TRENCH5/216-A).	
	Cymatiosphaera multicrista sp. nov.	12
12	Specimen with unornamented rupture, x 1500, Much Wenlock Limestone Formation (GOG2-C).	
	Cymatiosphaera aff. *multisepta* Deunff 1955.	12
9	x 2000, Much Wenlock Limestone Formation (PC8-0).	


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

13 x 1000, Lower Elton Formation (TRENCH1/23-A).

Eupoikilofusa filifera (Downie 1959) Dorning 1981a emend. 63

14 Detail of folds in vesicle wall, x 2000, Lower Elton Formation (PC13-A).

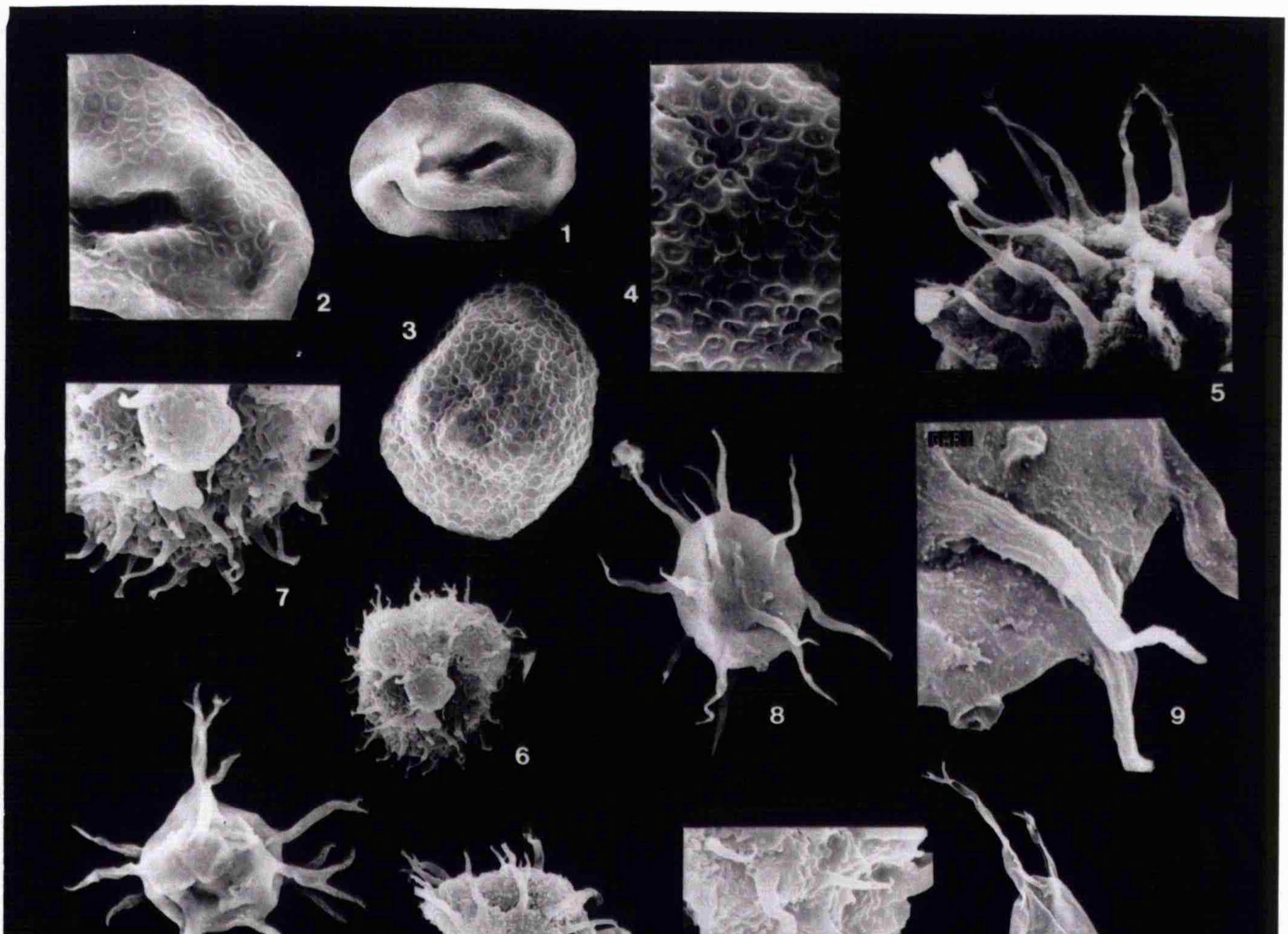
Evittia robustispinosa (Downie 1959) Le Hérissé 1989 emend. 68

15 x1000, Middle Elton Formation (TRENCH4/ME1-A).

16 As fig. 15, Detail of echinate processes and grano-reticulate vesicle ornament.

PLATE 10

Fig.		Page
	Melikeriopalla amydra Tappan & Loeblich Jr. 1971.	23
1	Specimen lacking large pores under transmitted light, x 1000, Middle Elton Formation (GOG4/207-A).	
2	As fig. 1, detail of central node strictures, x 2000.	
3	Specimen with large pores under transmitted light, x 500, Middle Elton Formation (GOG6/256-A).	
4	As fig. 3, detail of central node structures, x 1000	
	Ammonidium waldronense (Tappan & Loeblich Jr. 1971) Dorning 1981a.	33
5	Detail of vesicle ornament and process terminations, x 2000, Lower Elton Formation (TRENCH3/155b-A).	
	Ammonidium sp. A.	34
6	x 1000, Middle Elton Formation (TRENCH5/222-A).	
7	As fig. 6, x 2000.	
	Baltisphaeridium muldiensis Le Hérissé 1989.	35
8	Specimen with all simple processes, x 1000, Lower Elton Formation (TRENCH1/14-a).	
9	As fig. 8, detail of striate process and circular structures, x 4000.	
10	Specimen with simple and branched processes, x 1000, Lower Elton Formation (TRENCH1/11-A).	
	Cymbosphaeridium sp. A.	47
11	x 1000, Lower Elton Formation (GOG3/94-A).	
12	As fig. 11, detail of granulate vesicle and process branching, x 3000.	
	Dateriocradus cf. *monterrosae* (Cramer 1969a) Pöthé de Baldis 1981	47


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

12 As fig. 11, detail of processes, x 2000.

Gorgonisphaeridium ramosum Pöthé de Baldis 1981. 73

7 x 1000, Lower Elton Formation (PC12-O).

8 As fig. 8, detail of process branching, x 3000.

Gorgonisphaeridium succinum Lister 1970 emend. 74

9 Specimen with granulate vesicle, x 1000, Lower Elton Formation (GOG2/62-A).

10 Specimen with laevigate vesicle, x 1500, Lower Elton Formation (TRENCH1/23-A).

Hapsidopalla jeandeunffii Le Hérissé 1989. 76

17 x 1500, Lower Elton Formation (GOG2/62-A).

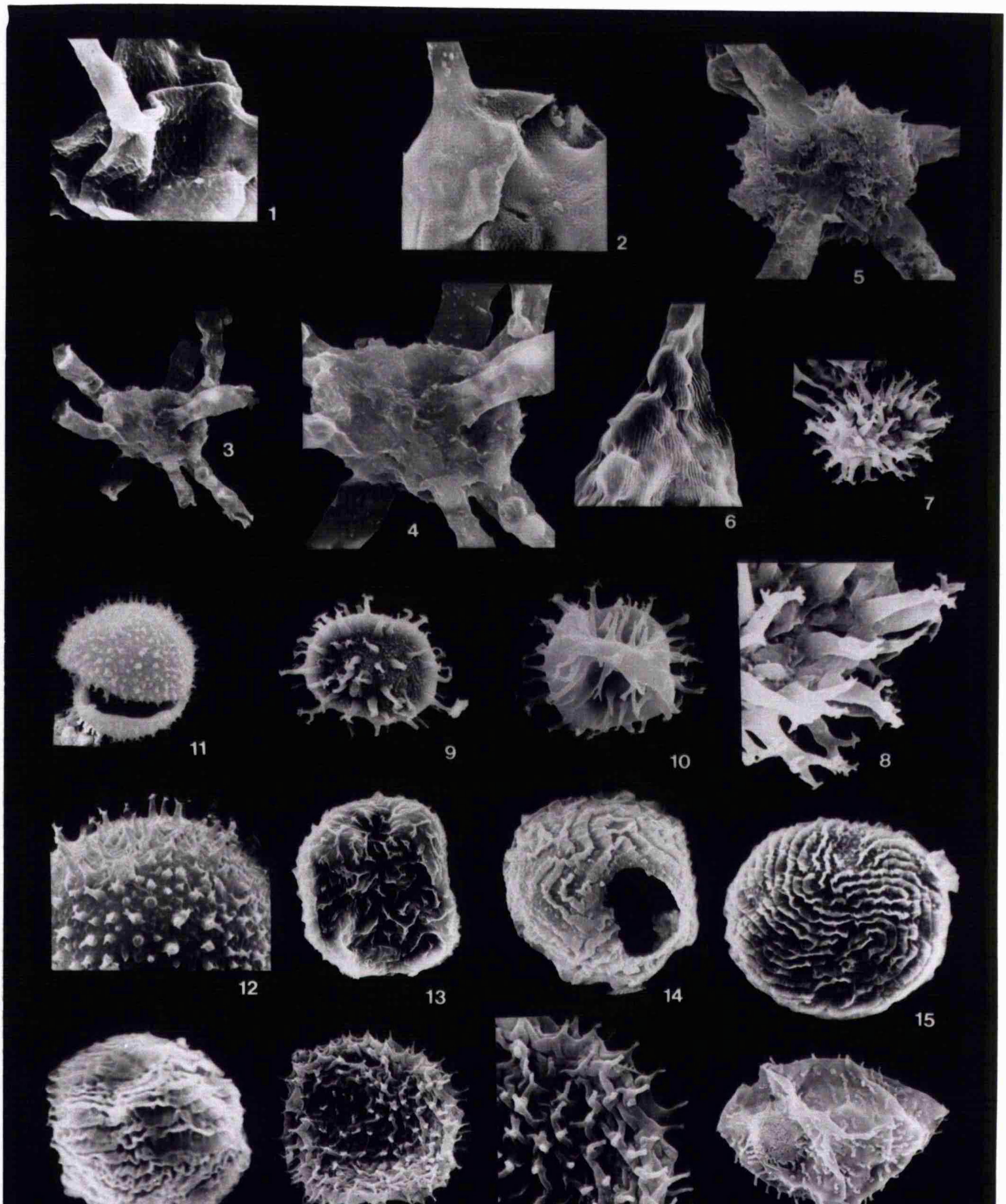
18 As fig. 17, detail of capitate processes and ridges joining processes, x 3000.

Helosphaeridium clavispinulosum Lister 1970. 77

19 x 1000, Lower Elton Formation (TRENCH1/23-A).

PLATE 11

Fig.		Page
	Dilatisphaera laevigata Lister 1970.	50
3	x 1000, Middle Elton Formation (GOG12/302-A).	
4	As fig. 3, detail of laevigate vesicle, x 2000.	
5	Specimen with a baculate vesicle, x 2000, Middle Elton Formation (GOG12/302-A).	
	Eupoikilofusa tenuistriata (Pöthé de Baldis 1975) Pöthé de Baldis 1981.	64
6	Detail of striate vesicle, x 2000, Middle Elton Formation (GOG5/234-A).	
	Evittia remota (Deunff 1955) Lister 1970 Group.	66
1	Specimen with grano-reticulate vesicle ornament, x 3000, Middle Elton Formation (TRENCH5/216-A).	
2	Specimen with punctate vesicle ornament and granulate excystment opening, x 2000, Lower Elton Formation (GOG2/42-A).	
	Glyptosphaera heltaskelta sp. nov.	69
15	Large specimen with tightly arranged cristae forming a swirl-like pattern, x 750, Middle Elton Formation (TRENCH4/176-A). Holotype.	
16	Small specimen, x 2000, Middle Elton Formation (TRENCH4/196-A)	
	Glyptosphaera speciosa Kiryanov 1978.	70
13	Large specimen with cristae forming a labyrinth-like pattern, x 1000, Much Wenlock Limestone Formation (PC2-0).	
14	Small specimen with a possible pylome, x 2000, Middle Elton Formation (TRENCH4/ME1-A).	
	Gorgonisphaeridium citrinum (Downie 1963) comb. nov.	71
11	x 1000, Much Wenlock Limestone Formation (GOG1/2-C).	


1
2
5
3
4
6
7
11
9
10
8
12
13
14
15
16
17
18
19

8 x 1000, Middle Elton Formation (GOG12/302-A).

11 As fir fig. 8, detail of vesicle ornament, x 3000.

Stellechinatum ? sp. A. 115

9 x 1000, Middle Elton Formation (TRENCH5/222-A).

10 As for fig. 9, detail of process ornament, x 2000.

Visbysphaera microspinosa (Eisenack 1954) Lister 1970 Group. 120

12 x1000, Lower Elton Formation (GOG2/62-A).

13 As for fig. 12, detail of spinose ornament, x 2000.

14 Detail of baculate ornament, x 1500, Lower Elton Formation (PC12-O).

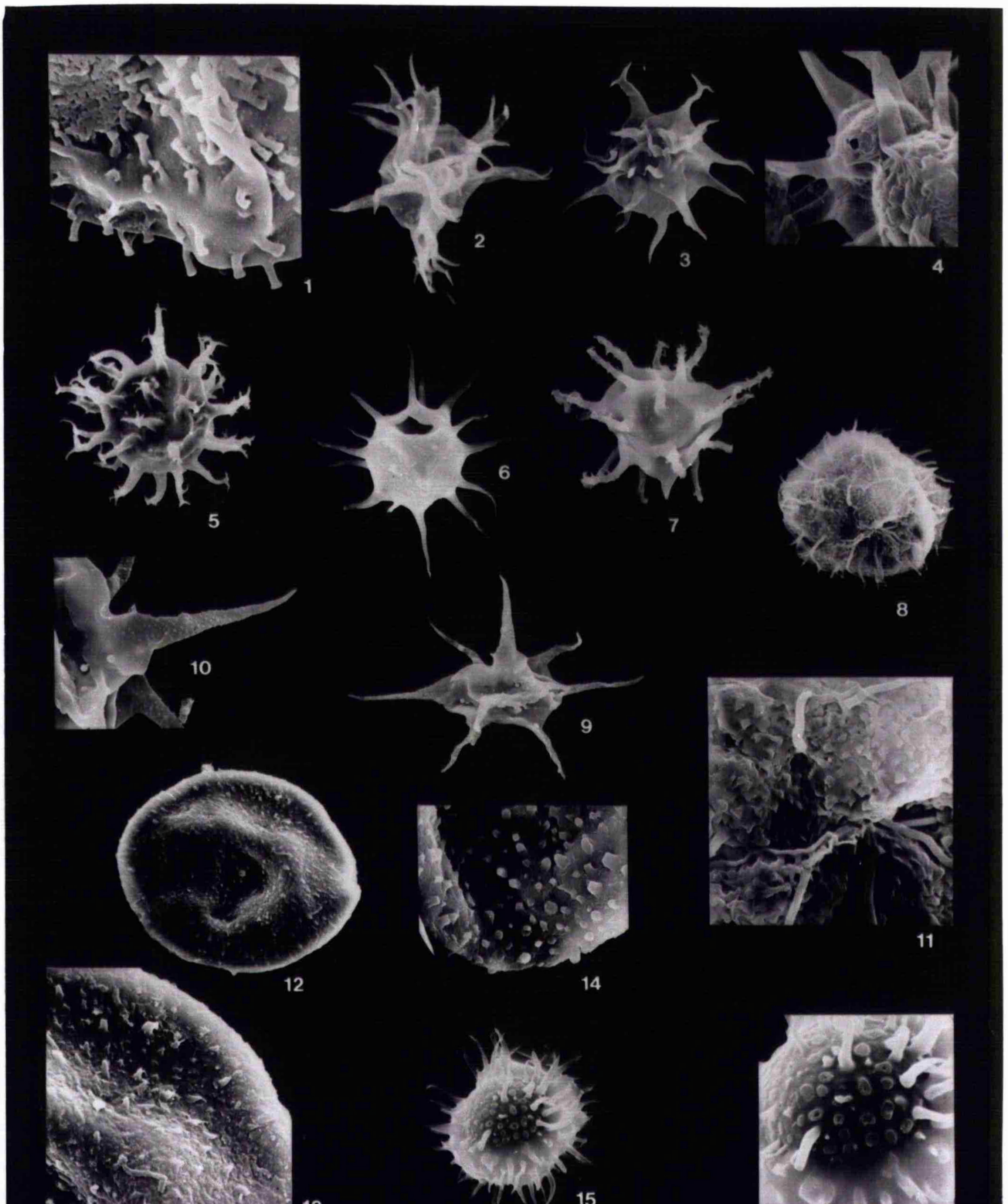
Baltisphaeridium ? *spinatum* sp. nov. 37

15 x 1500, Middle Elton Formation (GOG5/245-A).

16 As fig. 15, detail of broken off process bases, x 3000.

PLATE 12

Fig.		Page
	Helosphaeridium clavispinulosum Lister 1970.	77
1	As Plate 11, fig. 19, detail of capitate processes.	
	Leptobrachion digitatum sp. nov.	87
2	x 1000, Lower Elton Formation (TRENCH1/11-A).	
	Micrhystridium intonsurans (Lister 1970) Dorning 1981a.	91
7	Specimen showing simple, processes with rounded tips that have a dense arrangement of spines at their distal extremities, x 2000, Much Wenlock Limestone Formation (PC8-O).	
	Micrhystridium stellatum Deflandre 1945a.	92
6	Specimen showing unornamented rupture, x 1000, Much Wenlock Limestone Formation (PC10e-A).	
	Multiplicisphaeridium sp. A.	98
3	x 1500, Middle Elton Formation (TRENCH5/228-A).	
	Multiplicisphaeridium sp. B.	98
4	Detail of striae that extend from the vesicle onto the process bases, x 3000, Middle Elton Formation (GOG6/256-A).	
	Multiplicisphaeridium sp. C.	99
5	x1000, Lower Elton Formation (GOG3/122-A).	
	Percultisphaera stiphrospinata Lister 1970.	107


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16