A palynological study of the Ordovician to Devonian sediments of the Anti Atlas, Morocco

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PULLOUTS

Summary

Approximately 300 field and well samples from the Ordovician to Devonian interval of the Anti Atlas, Morocco have been prepared for palynological investigation. Of these, 118 were selected for detailed analysis based on the quality of the palynological recovery, an attempt to achieve the best stratigraphic coverage as possible from the material available and also based on the presence of macrofossil data.

A rapid palynological preparation technique for observation by light microscopy has been developed to analyse thermally mature, *brittle* assemblages, such as those encountered.

Reviews of the Acritarcha, the fossil Prasinophyta and the Chitinozoa are presented with discussion of their morphology, biological affinity and classification. Taxa from these groups are treated systematically with 389 described species recorded, assignable to 115 genera. A total of 71 unpublished forms are described in open nomenclature. Miospores have also been recorded to enhance biostratigraphic resolution and environmental interpretation of the assemblages studied. The miospore taxa recorded are illustrated with their authors cited in the plate captions.

Semi-quantitative analyses of the assemblages has enabled the recognition of 33 Palynological Associations from the Ordovician through Devonian based on the presence, absence and abundance of the taxa recorded. Cluster analysis of the samples has been undertaken to assist in the recognition and to quantify the similarity of the assemblages. The Ordovician field samples yielded poorly preserved assemblages from which 12 Associations are recognised. The Silurian to Lower Devonian field samples yielded moderate to well preserved assemblages despite the high thermal grade of the material. Twelve Associations are defined from this interval, the ages of which are all highly constrained by the generally rich graptolite assemblages. Nine Associations are recognised from the Devonian assemblages recovered from Well Oum Doul-1 core samples. These assemblages are well preserved with abundant and often diverse marine and terrestrial elements present. The age interpretations of the 33 Associations are based on both macrofaunal evidence, when present, and on comparison with previous palynological studies, primarily those from Northern Gondwana.

A general palaeoenvironmental interpretation of the formations studied is attempted from the semi quantitative analysis of the relative proportions of environmentally sensitive palynomorph groups and the relative proportions of morphotypes within palynomorph groups. The major bathymetric fluctuations in the environment of deposition which are evident from the palynological assemblages (e.g. the deep water event in the early Silurian) are believed to be eustatically controlled during the Ordovician to Devonian in the Anti Atlas.

The broad nature of the study, geographically and stratigraphically, has revealed much potential for future work, of both academic and commercial interest, in the North African and Middle East region.

Acknowledgements

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Chapter 1. Introduction.

The kingdom of Morocco occupies an area of approximately 731 000 square km situated at the north-west margin of the African continent. It houses a population of about 25,000 people and is ruled by a stable democratic monarchy. The economy of Morocco was initially developed on the basis of agriculture and fishing but in more recent years it has become significant in the international market place with industrial developments primarily in the form of engineering and computer technology.

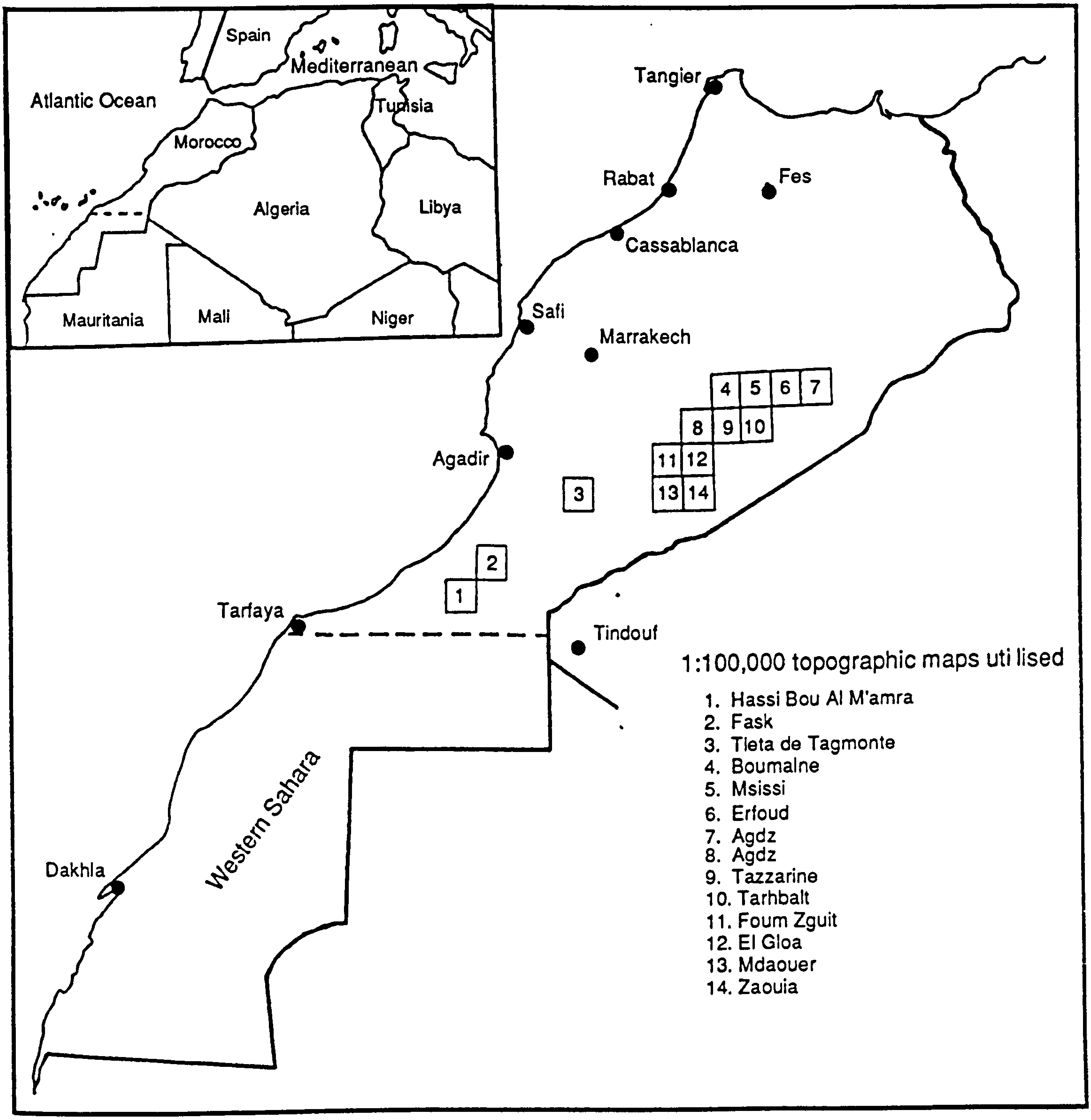
Despite the relatively low energy consumption per capita of its inhabitants, Morocco is still almost entirely dependant on imported energy resources. This problem was addressed by the government in 1981 with the establishment of the Office National de Recherches et d'Exploitations Petrolieres, commonly referred to by its acronym ONAREP. This organisation, based at its headquarters in Rabat, is the state government oil company which has total responsibility for all petroleum exploration activities and all exploitation of discovered hydrocarbons in Morocco.

The present study is based on samples from the Anti Atlas region which were collected by The Robertson Group (now Simon Petroleum Technology) for a study commissioned by ONAREP in 1985. The samples utilised are from the Ordovician to Devonian stratigraphic interval and are predominantly from outcrop and shallow water wells. These samples are supplemented by core from a single exploration well from the south of the region, Oum Doul-1. A full list of the samples analysed is given in Appendix I, with the geographic and stratigraphic position given for each. In the course of the South Atlas Study, The Robertson Group sub-contracted macropalaeontological work to experts in their respective fields, namely Dr. Mike Romano (University of Sheffield) and Dr. Tim Young (University of Cardiff) who looked at the Ordovician shelly faunas and Dr. Barry Rickards (University of Cambridge) who looked at the Silurian-Lower Devonian graptolitic assemblages. The data relevant to the present study generated by these workers is integrated with the palynological investigations undertaken. The results of their analysis can also be found in Appendix I.

The geographic setting.

The study area is situated in the Anti Atlas region of Morocco (figs. 1 and 2). This region is bounded to the north by the South Atlas Fault Zone which extends from the coastal resort of Agadir in an ENE direction. This boundary separates the High Atlas mountainous region to the north from the more varied topography of the Anti Atlas to the south (fig. 2). The Anti Atlas is dominated by the high topographic relief of the Anti Atlas mountains which are composed primarily of Precambrian and Lower Palaeozoic rocks. However, in some areas, tectonic influences have resulted in large scale depressions within the Palaeozoic aged landscape which are commonly infilled with Mesozoic sediments and Tertiary and Quaternary desert deposits. To the south of the Anti Atlas, the relatively

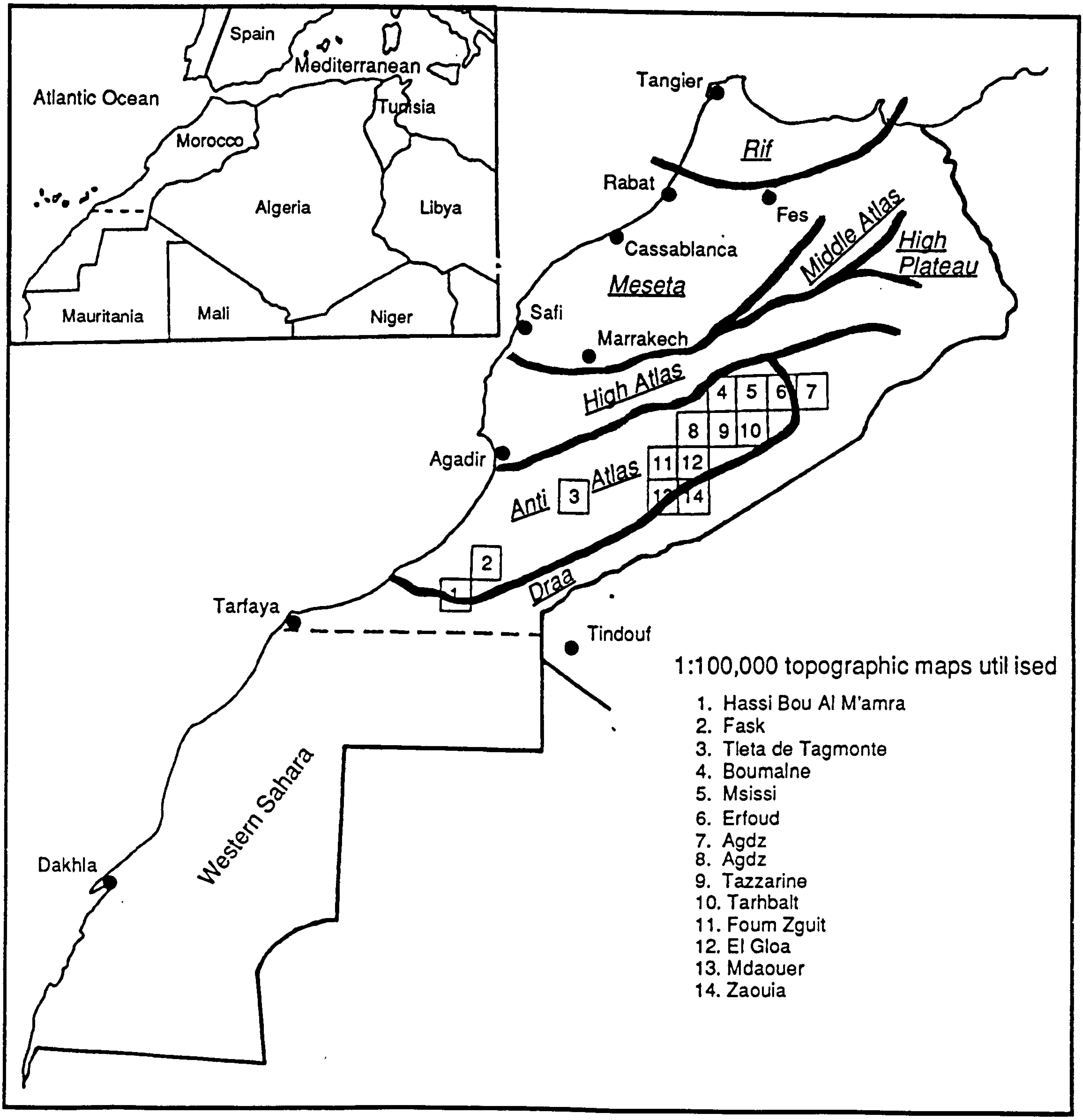
Figure 1. Geographic map of Morocco showing the positions of the topographic maps utilised.



1:100,000 topographic maps uti lised

1. Hassi Bou Al M'amra
2. Fask
3. Tleta de Tagmonte
4. Boumalne
5. Msissi
6. Erfoud
7. Agdz
8. Agdz
9. Tazzarine
10. Tarhbalt
11. Foum Zguit
12. El Gloa
13. Mdaouer
14. Zaouia

Figure 2. The physiographic regions of Morocco.



subdued topography of the Draa plain is composed primarily of the relatively soft Silurian shales and post Alpine superficial deposits.

The main centres of commerce and trade in the Anti Atlas include the towns of Agadir, Tiznit, Taroudannt and Ouarzazate in the central and western parts of the region, together with Zagora and Erfoud further to the east. There is a good network of tarred roads between these centres which are supplemented by many well used dirt tracks for communication with the more rural towns and villages.

Several sets of topographic maps at various scales exist for Morocco which are published by the government. The series utilised in the present study, the 1:100,000 series, is that used by Robertsons' geologists in the field. The relevant sheets are those on which the samples analysed here are located which are listed in figure 1.

Previous work on the Lower Palaeozoic and Devonian rocks of the Anti Atlas.

The Anti Atlas is essentially the type area for the Lower Palaeozoic and Devonian interval of Morocco (Destombes, Hollard & Willefert 1985). Geological research in the region was initiated in the early part of this century with discoveries of Cambrian (Bourcart 1927, Bondon & Neltner 1933), Ordovician (Roch 1933) and Silurian (Savornin 1921) faunas. Work in the latter half of the century in Morocco has become focused on the Anti Atlas with the realisation of the near complete succession of Lower Palaeozoic rocks in that area.

From 1959 onward, Destombes became the most prolific worker in the anti Atlas with over 30 publications to his name. His work in the region culminated in 1985 with a summary of the Lower Palaeozoic rocks of Morocco (Destombes, Hollard & Willefert 1985) in which a comprehensive review of the Lower Palaeozoic stratigraphy is made upto that date. In addition, a wealth of unpublished data generated by him, e.g. field guides, have benefited geologists working in the area (T.P. Young pers. comm. 1992).

From 1942 and upto 1947, Choubert established the first type section for the Ordovician in the Anti Atlas, but it was not until 1954 that the first Tremadoc (earliest Ordovician) sediments were recognised from the Agdz region (Choubert, Hindermeyer & Hupe 1955). Several palynological investigations of the Ordovician succession of Morocco are evident in the literature, the earliest of these was made by Cramer *et al.* (1974) from subsurface material from the Tadla basin. More recently, several publications by Elaouad-Debbaj (1984, 1986, 1988a & 1988b) focused on the palynology of the Ordovician succession in the Anti Atlas which address both the acritarch and chitinozoan assemblages.

The names associated with early faunal discoveries of Silurian age in the Anti Atlas include Bondon, Clariond & Neltner (1934). Hollard and Willefert in conjunction with Destombes have been largely responsible for establishing the Silurian stratigraphic nomenclature of the area (e.g. Destombes, Hollard & Willefert 1959 & 1985). It is interesting to note that the prolific Silurian aged graptolitic faunas in the region are largely undescribed (Destombes, Hollard & Willefert 1985) and that several new lineages are evident from the Silurian to early Devonian material analysed here (R.B Rickards pers. comm. 1990).

Hollard (e.g. 1965) has also been instrumental in establishing the Devonian stratigraphy of the Anti Atlas. The Devonian palynology of Oum Doul-1, a well utilised in the present study, has been previously analysed by Grignani & Mantovani (1964), however the authors only accounted for the chitinozoan components of the palynological assemblages in their contribution. No further publications on this stratigraphic interval in Morocco are apparent in the literature, however, in-house palynological investigations have been undertaken in recent years by organisations with commercial interests in the region (R. Rozza, Agip Ltd., pers. comm. 1991).

A brief summary of the tectonic and palaeogeographic evolution of the Anti Atlas region.

The tectonic evolution of the Anti Atlas is rather unique in that the region has experienced the effects of the Pan-African Event and each of the Caledonian, Hercynian and Alpine orogenies.

Morocco is positioned on the northern margin of the West African Craton which was cratonised in the early Proterozoic. The craton occupies most of West Africa and has acted as a core through the late Proterozoic and Phanerozoic interval.

The Pan-African Event occurred during the late Proterozoic and early Palaeozoic in the Anti Atlas and can be recognised as an east-west trending set of thrusts and faults effecting the Precambrian basement and overlying early Palaeozoic sediments. This event is largely masked by younger sedimentary cover, however it is believed that the Anti Atlas region is entirely underlain by the rocks of the Pan-African basement complex.

The palaeogeographic position of Morocco during the Ordovician was at the northern margin of Gondwana which, through that system, migrated towards the southern magnetic pole (figs. 3 & 4). By the culmination of the Ordovician (Ashgill), Morocco was situated at or near to the pole which is evident from the glacio-marine sediments recorded in the Anti Atlas of that age (Destombes, Hollard & Willefert 1985).

The Caledonian Orogeny can be regarded generally as the result of the collision between Laurentia and Eurasia during the Silurian and early Devonian (figs. 4 & 5). Morocco is believed to have been effected by the collision of one or more microplates with the northern margin of the West African Craton (e.g. the 'Avalon-Florida microplate [Matte 1986] forming a northeast-southwest trending folds

Figure 3. An early Ordovician palaeogeographic reconstruction of Northern Gondwana, from Paris 1990.

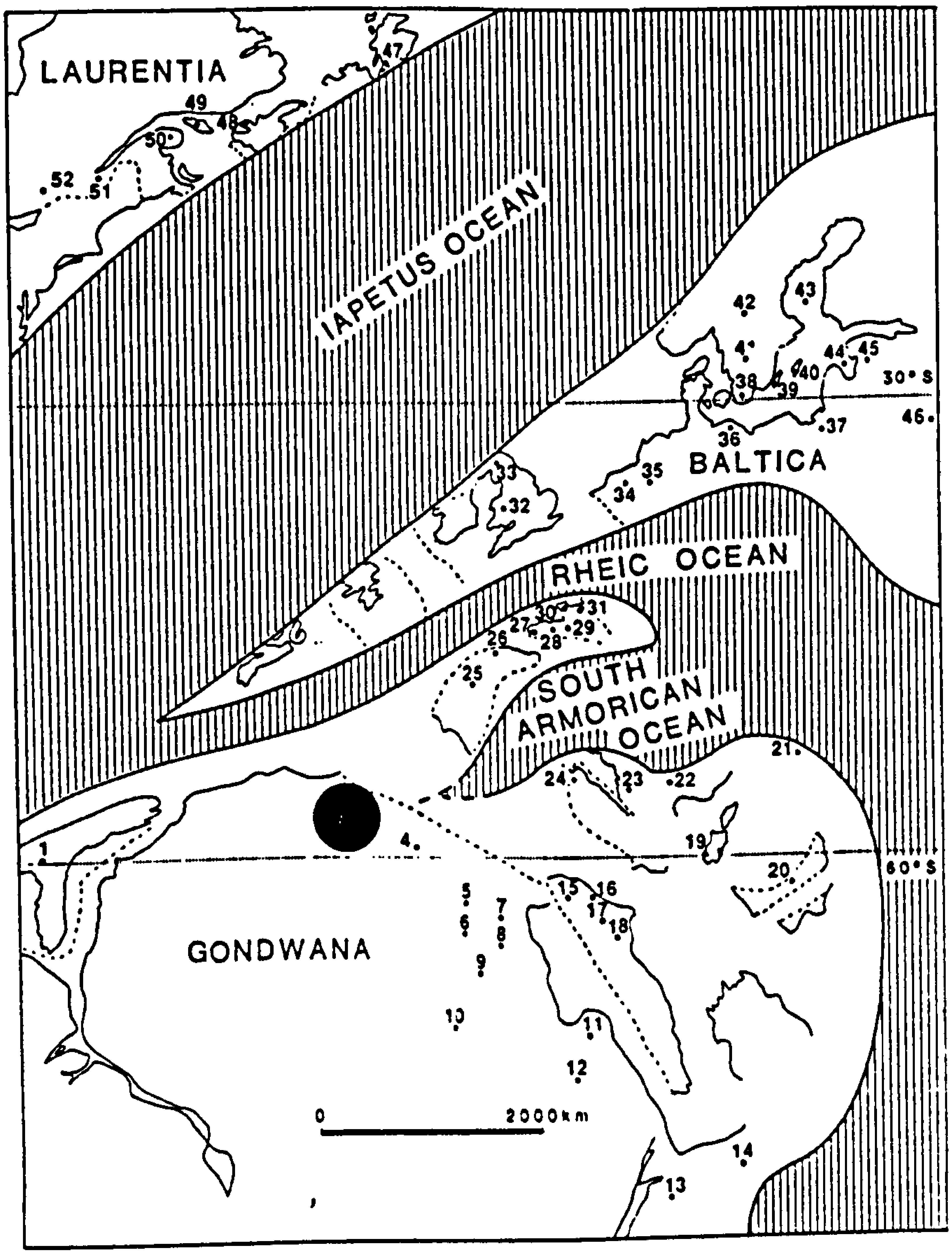
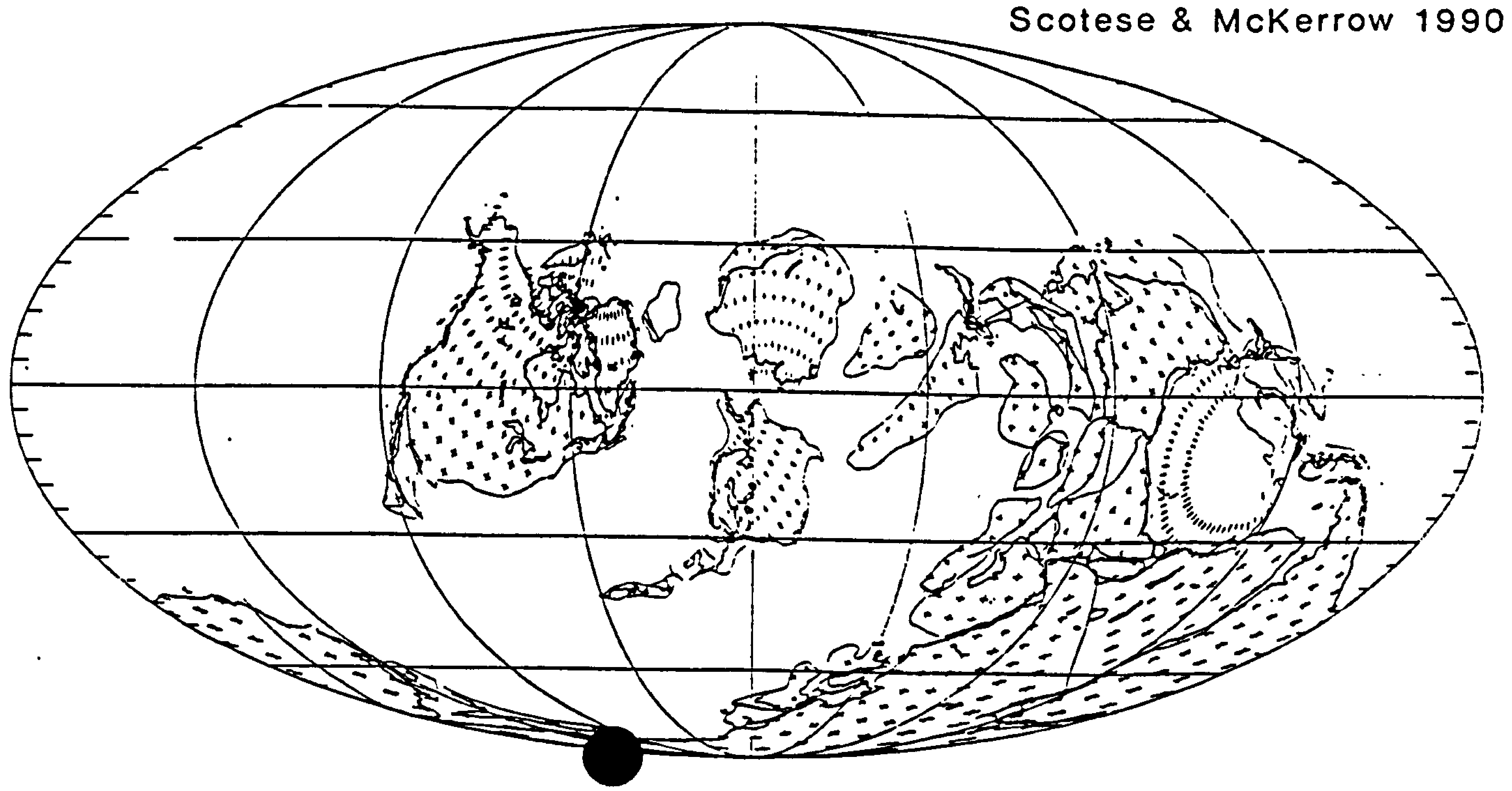
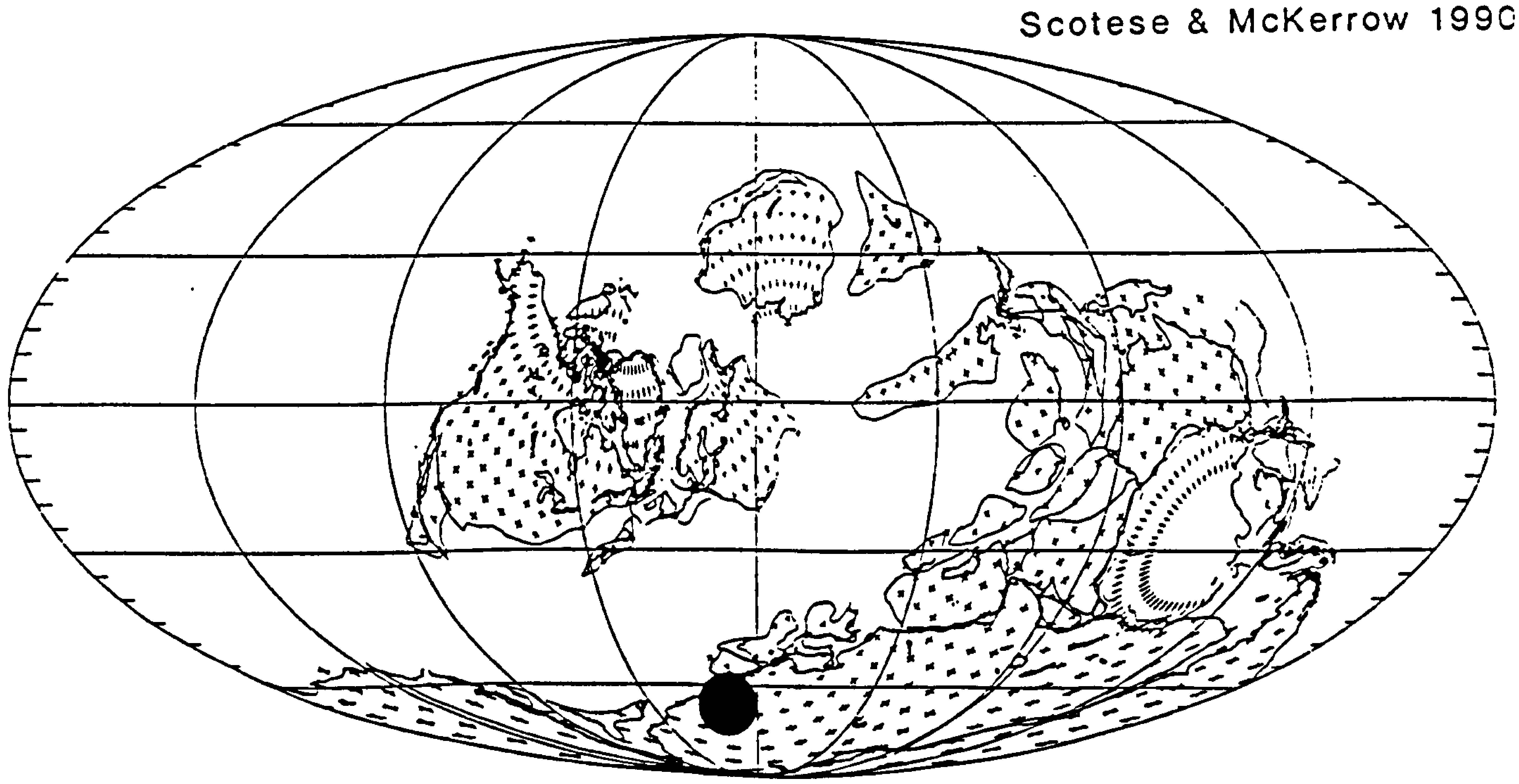


Figure 4. Global palaeogeographic reconstructions for the latest Ordovician (Ashgill) and middle Silurian (Wenlock), from Scotese & McKerrow 1990.

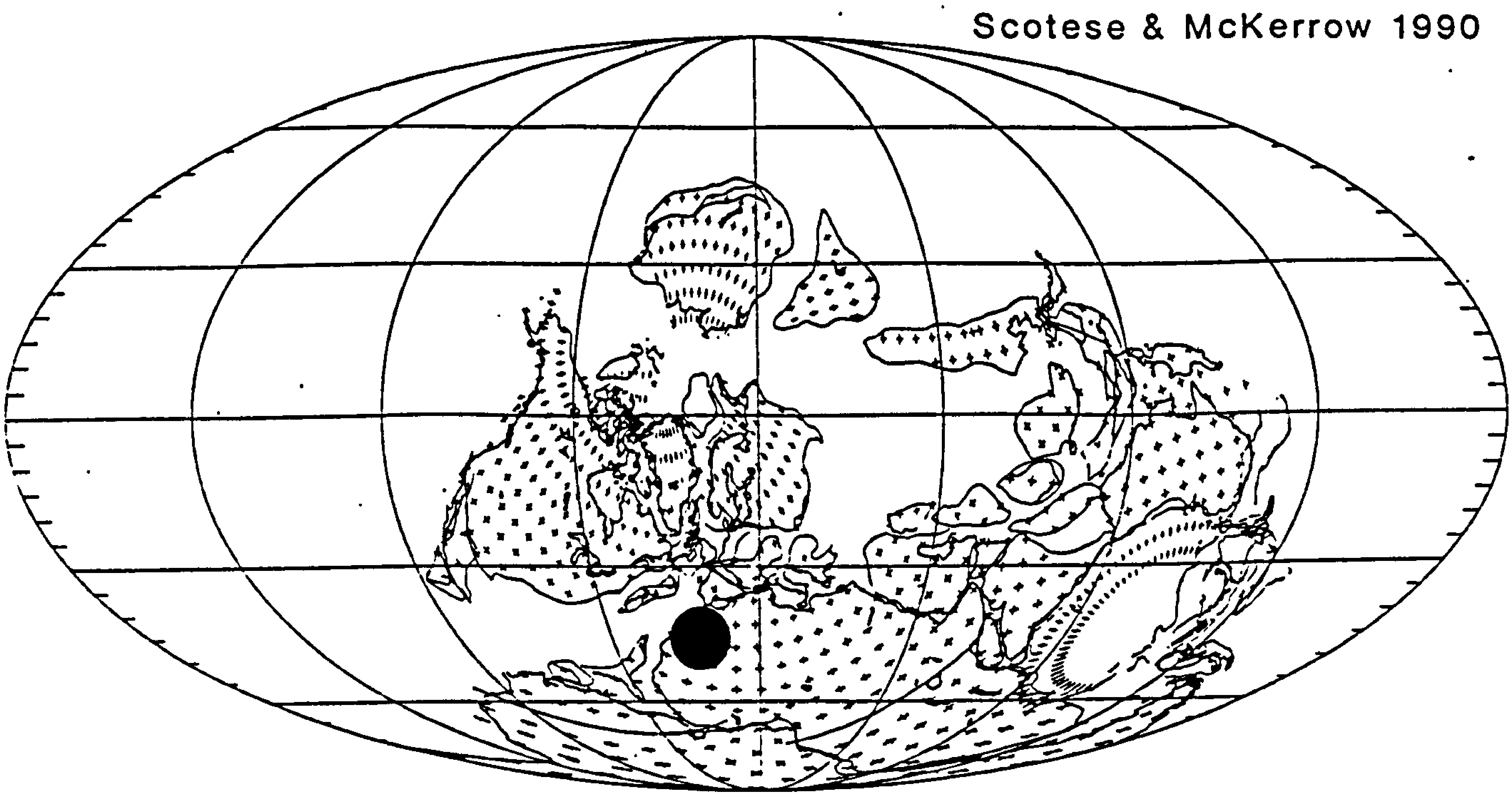


Latest Ordovician (Ashgill)

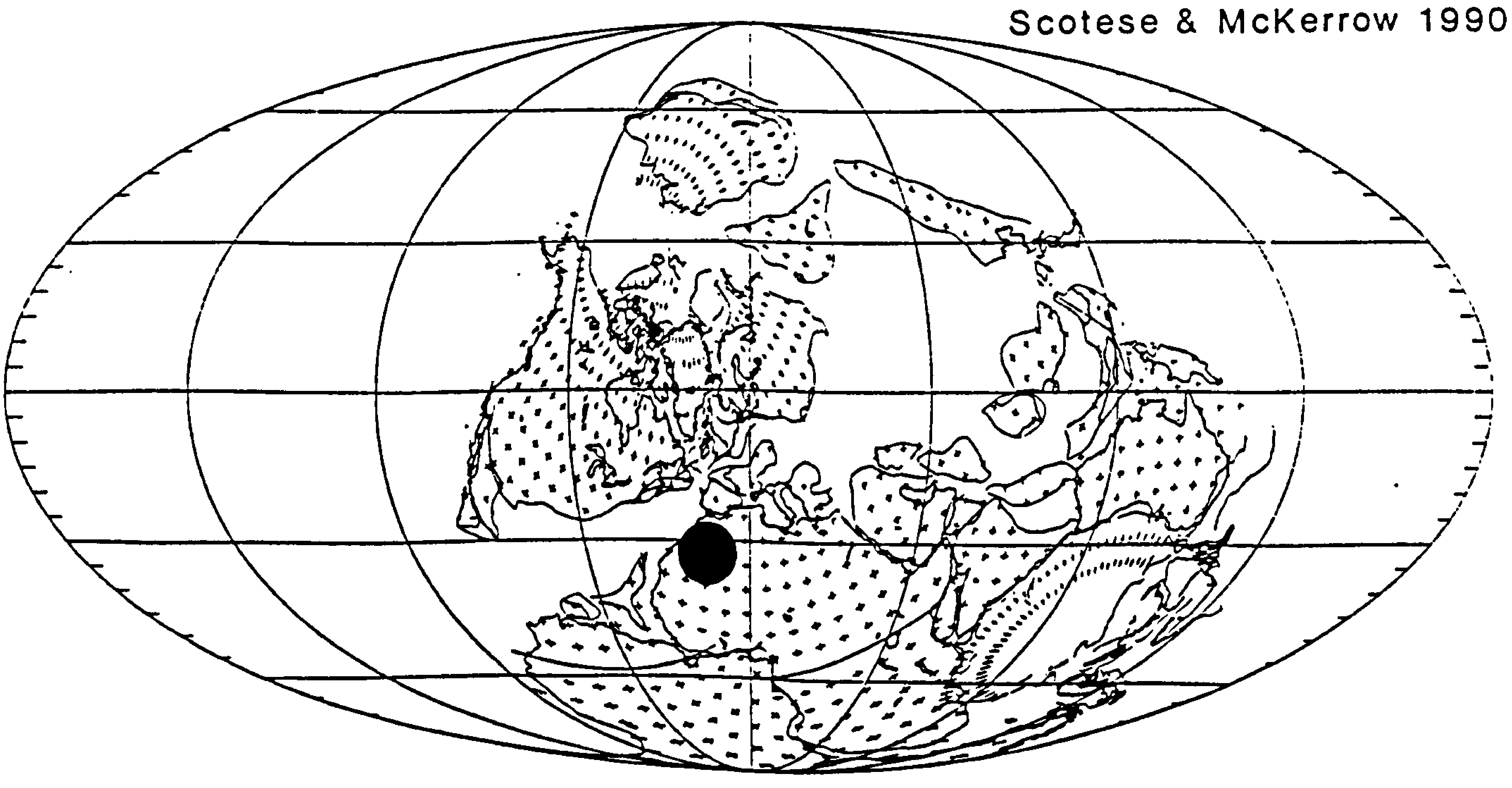


Middle Silurian (Wenlock)

Figure 5. Global palaeogeographic reconstructions for the early Devonian (Gedinnian) and late Devonian (Famennian), from Scotese & McKerrow 1990.



Early Devonian (Gedinnian)



Late Devonian (Famennian)

and thrusts. Accommodation of existing crustal material between these the colliding continental area is believed to have been achieved by northward dipping subduction at the northern margin of the West African Craton.

The effects of the Hercynian Orogeny, generally regarded to be the result of the collision of Gondwana and Laurasia, are more in evidence in the Anti Atlas. This is believed to be a near continuation of the Caledonian Orogeny with continued northerly directed subduction beneath the Laurasian continent.

Evidence for the early phase of this episode (late Devonian-early Carboniferous) is best exposed in the western part of the Anti Atlas. Continued subduction and subsequent collision of Laurasia and Gondwana gave rise to the Mauritanide mountain range and folded sediments in a similar southeast-northwest trend to that of the Caledonian phase. Later in the Hercynian orogeny (mid-late Carboniferous), continued collision of the continents gave rise to the Appalachians with associated large scale dextral movements which occurred mainly along the South Atlas and Elbe faults during the collision stage.

By the close of the Hercynian Orogeny, the super-continent of Pangea had formed. Relative continental movements resumed in the Middle Jurassic with the opening of the Atlantic and the Tethys Oceans. The Tethys Ocean is envisaged as being a relatively narrow seaway that extended between the continents of Africa and Eurasia. The spreading of these continents from each other was reversed in the Late Cretaceous and, as a consequence, collision of these two landmasses took place in the Neogene period and continues to the present day. This phase, known as the Alpine Orogeny, has had a major influence on shaping the Atlas Mountains of Morocco as we see them at the present day.

The lithostratigaphic framework.

By the mid 1960's, the lithostratigraphic framework for the Anti Atlas region was well established, since then minor alterations have been made. Chubert (1963) established the principal components of the Precambrian and Lower Palaeozoic framework, while Hollard (1963) was primarily responsible for formalising the stratigraphy of the Devonian part of the succession. Hollard in 1977 revised this part of the sequence himself. An overview and revision of the lithostratigraphy of the Ordovician and Silurian stratigraphy of the Anti Atlas region can be found in Destombes, Hollard & Willefert (1985).

Although well established, The Robertson Group (1985) in the course of their South Atlas study found that the published lithostratigraphic framework required modification "*in order to express more clearly the various aspects of the geology which are important to any consideration of the petroleum potential of southern Morocco*". In the report, considerable effort was made to preserve as much of the existing framework as was practically possible. However changes were considered necessary to produce a scheme that is rational but flexible, that is practicable for surface and subsurface analysis (i.e. field, well and seismic) and that has greater consideration for lateral facies variation. A direct comparison between the published and the proposed Robertson Group lithostratigraphic schemes is given in figs. 6, 7 & 8.

The present study utilises the more flexible Robertson Group scheme for the reasons of practicability. A brief description of the relevant formations to the study follows with the published equivalents of the formations indicated. The formations are described in stratigraphic order:

Fezouata Group

(Published equivalent: Outer Feijas Shales Group [part]).

This group is a coarsening upward sequence composed of shales of the Fezouata Formation and culminates in the western and central parts of the South Atlas region in the deposition of the Zini (sandstone) Formation.

Fezouata (shale) Formation.

(Published equivalents: Lower Fezouata Shales Formation, Upper Fezouata Shales Formation).

Age: Tremadoc-late Arenig.

Thickness: Upto 400m

Lithology: Greenish silty mudstones that were deposited on a shallow marine shelf. These sediments are generally poorly exposed.

Zini (sandstone) Formation.

(Published equivalent: Zini Sandstone Formation).

Age: Late Arenig.

Thickness: Upto 450m.

Lithology: Sandstones and quartzites interbedded with mudstones. This formation is laterally impersistant and is composed of a number of coarsening upward sequences. Deposition is thought to have taken place under shallow marine, storm dominated conditions.

Note: A non-sequence is apparent at the top of the Fezouata Group indicated by the absence of uppermost Arenig faunas in the Anti Atlas region.

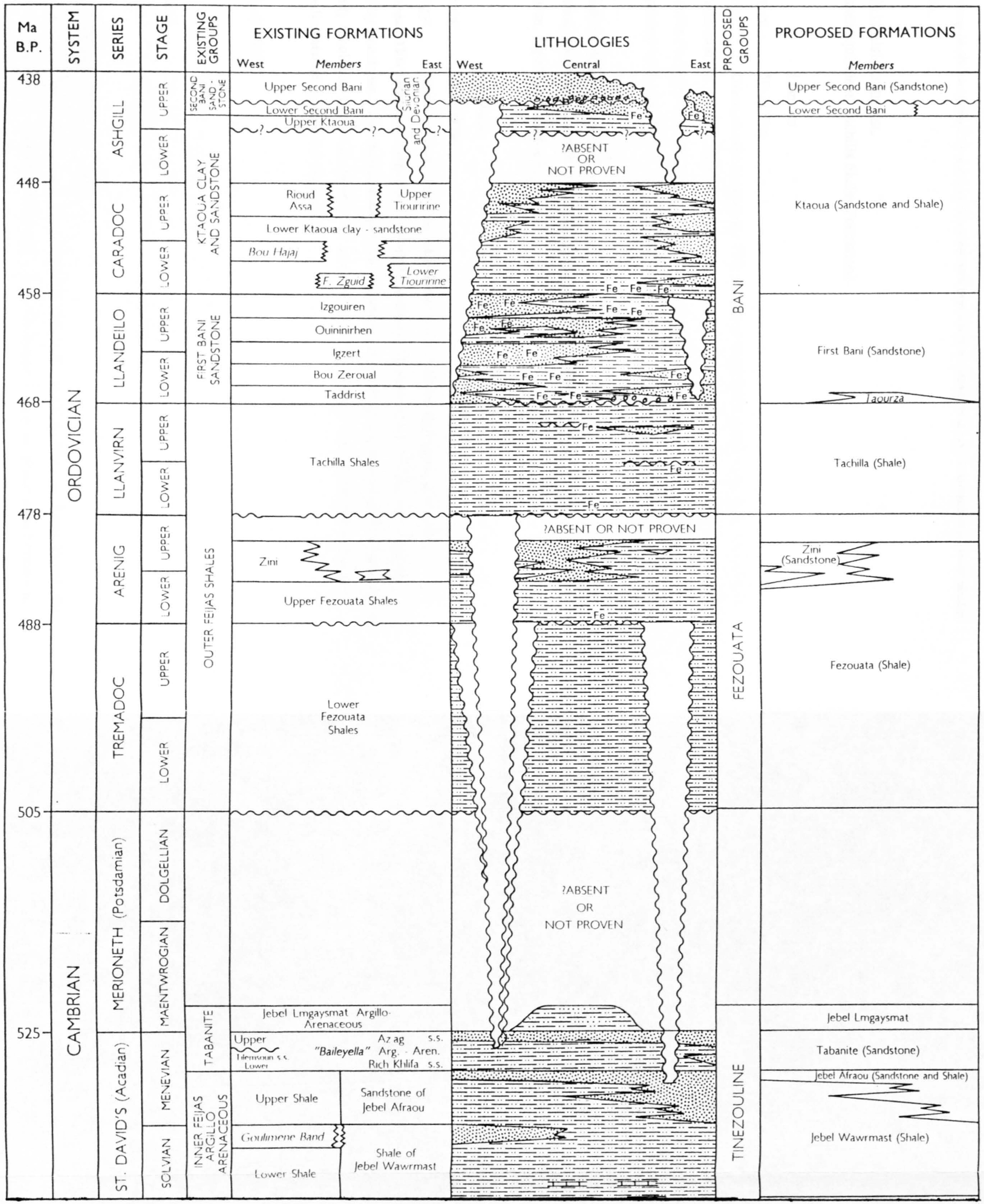


Figure 6. The lithostratigraphic framework for the Ordovician System showing the comparison between the published lithostratigraphy and that proposed by the Robertson Group (1985).

Bani Group.

(Published equivalents: Outer Feijas Shales Group [part], First Bani Sandstone Group, Ktaoua Clay and Sandstone Group, Second Bani Sandstone Group).

This group is characterised by numerous clean and argillaceous sandstone units intercalated with shales and silts.

Tachilla (shale) Formation.

(Published equivalent: Tachilla Shales Formation).

Age: Llanvirn.
Thickness: 50-1150m.
Lithology: Greenish silty mudstones. This formation is generally poorly exposed. Where the Zini Formation has not been deposited, distinction between the underlying Fezouata Formation from the Tachilla Formation on lithological grounds alone is a problem. However the later can be distinguished by the presence of Llanvirn aged macrofaunas.

First Bani (sandstone) Formation.

(Published equivalents: Taddrist Formation, Bou Zeroual Formation, Igzert Formation, Ounnrhen Formation, Izgouiren Formation).

Age: Llandeilo.
Thickness: Upto 550m.
Lithology: Sandstones and quartzites intercalated with greenish silty sandstones with frequent ironstones. This formation comprises a series of coarsening upwards sequences that are frequently capped by ironstones. The marine macrofaunas suggest a shallow shelf marine setting for deposition of the sandy lithologies and the frequent oolitic ironstone units are thought to represent periods of very slow sedimentation or omission surfaces.

Taourzo Member.

Age: Earliest Llandeilo.
Thickness: Upto 50m.
Lithology: Oolitic ironstones interbedded with mudstones.

Ktaoua (sandstone and shale) Formation.

(Published equivalents: Lower ktaoua Clay-Sandstone Formation which includes the Foum Zguid, the Lower Tiouririne and the Bou Hajaj Members, Upper Tiouririne Formation, Rioud Assa Formation, Upper Ktaoua Formation).

Age: Caradoc-Ashgill.

Thickness: 250-500m.

Lithology: Sandstones and quartzites interbedded with mudstones. The formation comprises coarsening upwards sequences of largely shallow marine sediments with occasional coquinas and bryozoan debris horizons. Laterally equivalent deep water mudstones accumulated to considerable thicknesses in more offshore settings.

Note: Lower Ashgill faunas have not, as yet, been recovered from the Anti Atlas region which suggests a possible non-sequence or hiatus at this level.

Lower Second Bani (sandstone) Formation.

(Published equivalent: Lower Second Bani Formation).

Age: Late Ashgill.

Thickness: Upto 160m.

Lithology: Sandstone. This coarsening upwards sequence has its upper surface truncated by an erosional surface.

Upper Second Bani (sandstone) Formation.

(Published equivalent: Upper second Bani Formation).

Age: Late Ashgill.

Thickness: Upto 100m.

Lithology: Coarse, locally pebbly sandstones. These fining upwards sandstones are believed to be glacio-marine in origin (Destombes, Hollard & Willefert, 1985) and are probably the time equivalent of glacial sediments which characterise the upper Ashgill elsewhere in North Africa.

Tizi Ambed Group.

(Published equivalent: Taskala Group [part]).

This group represents a marine transgression that occurred over the Anti Atlas region in the early Silurian. The sediments rest disconformably on the glaciated palaeotopography of the late Ashgill. The formations of the Tizi Ambed Group have restricted lateral distribution and are normally overlapped by the overlying Carbonaceous Shale Formation.

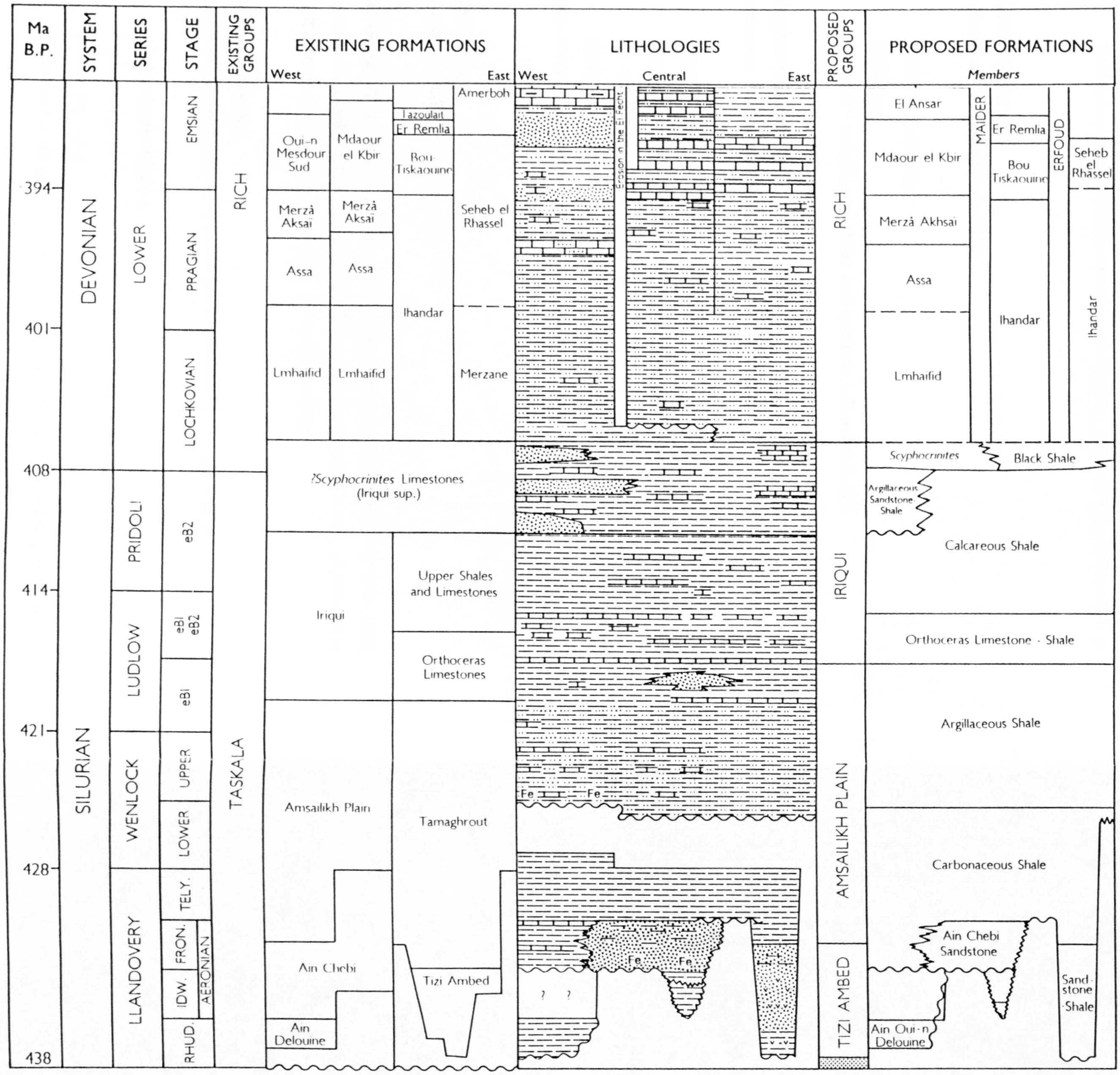


Figure 7. The lithostratigraphic framework for the Silurian System showing the comparison between the published lithostratigraphy and that proposed by the Robertson Group (1985).

Ain Delouine Formation.

(Published equivalent: Ain Delouine Formation).

Age: Latest Ordovician (*G. persculptus* Zone)- Rhuddanian.

Thickness: Upto 6m in the type section.

Lithology: Well indurated laminated mudstones, greenish grey, violet, pink or mauve-white in colour.

Sandstone-Shale Formation.

(Published equivalent: Tizi Ambed Formation?).

Age: Rhuddanian-Aeronian.

Thickness: Unknown.

Lithology: Sandstones and siliceous shales with epiclastic volcanic elements.

Ain Chebi (Sandstone) Formation.

(Published equivalent: Ain Chebi Formation).

Age: Aeronian.

Thickness: Very variable over short lateral distances, upto 40m in the type section but upto 200m further to the west.

Lithology: Sandstone, normally grey, violet or yellowish in colour. Ferruginous nodules occur towards the base and the sequence fines upwards with numerous clay partings towards the top.

Amsailikh Plain Group.

(Published equivalent: Taskala Group [part]).

The black mud deposits of the lower formation of this group represent maximum flooding of the Early Silurian transgression. However, continued deposition of coeval arenaceous sediments, attributable to the underlying Tizi Ambed Group, do occur locally, for example at Iriqui.

Carbonaceous Shale Formation.

(Published equivalent: Amsailikh Plain Formation [part], Tarnaghrout Formation [part]).

Age: Aeronian-early Wenlock.

Thickness: ? The thickest sections occur in the Plains du Draa of the central and eastern Anti Atlas.

Lithology: Carbonaceous and graptolitic black-grey shales. The shales are white-pink when weathered. This formation is believed to be the oldest potential source rock in the region.

Argillaceous Shale Formation.

(Published equivalent: Amsailikh Plain Formation [part], Tamaghrout Formation [part]).

Age: Wenlock-early Ludlow.

Thickness: Unknown.

Lithology: Generally grey, micaceous shale with rare intercalations of carbonate nodules. Grey-white shales, argillaceous sandstones and iron rich arenites are less common. The Argillaceous Shale Formation is generally distinguished from the underlying Carbonaceous Shale Formation by its less homogeneous, lighter coloured micaceous lithology. However in the Tazzarine area, the former is a black organically rich shale which sits on a much reduced thickness of the Carbonaceous Shale Formation. The graptolitic faunas present indicate a mid Wenlock-lower Ludlow age for these sediments which suggests that the early Silurian maximum flooding occurred later in this area.

Iriqui Group.

(Published equivalent: Taskala Group [part]).

Orthoceras Limestone-shale Formation.

(Published equivalent: Orthoceras Limestone Formation)

Age: Late Ludlow.

Thickness: Upto approximately 30m.

Lithology: Normally black argillaceous limestones with abundant orthoconic cephalopods, intercalated with shales. This forms the most easily recognisable marker horizon in the Silurian sequence.

Calcareous Shale Formation.

(Published equivalents: Upper Shales and Limestone Formation, ?*Scyphocrinites* Limestones Formation).

Age: Late Ludlow-?early Gedinnian.

Thickness: Unknown. The Formation is thickest in the Akka/Foum el Hassan region.

Lithology: Grey calcareous shales.

Argillaceous Sandstone Shale Member.

Age: Pridoli?

Thickness: Unknown.

Lithology: Argillaceous fine sandstone.

Scyphrocrinites Member.

Age: Early Lochkovian?

Thickness: Unknown.

Lithology: Sandy limestones and calcareous sandstones with *Scyphrocrinites*. This member forms a useful marker horizon at the top of the Calcareous Shale Formation from Ain (oui-n) Delouine in the south-west to the Erfoud region in the ENE.

Black Shale Member.

Age: Early Lochkovian?

Thickness: Unknown.

Lithology: Black organic rich shale. This can be found to ENE of the South Atlas region towards the top of the Calcareous Shale Formation.

The Devonian lithostratigraphic nomenclature proposed by the Robertson Group in their South Atlas study follows Hollard's and other workers ideas in being split up into three major east-west tectonically related regions, namely the Draa, Maider and Tafilalt. The well section from which the majority of the Devonian samples analysed in the present study came, Oum Doul-1, lies to the west of the Anti Atlas region. It is the Devonian lithostratigraphy of this western region that is described below. The lithological descriptions and formation thicknesses given are based on data from Oum Doul-1.

Rich Group.

(Published equivalent: Rich Group [part]).

Lmhaifid Formation.

(Published equivalent: Lmhaifid Formation).

Age: Gedinnian-early Siegenian.

Thickness: Greater than 407m.

Lithology: Grey and brownish grey mudstones with occasional intercalated white or light grey sandstones. Both of these lithologies are locally calcareous.

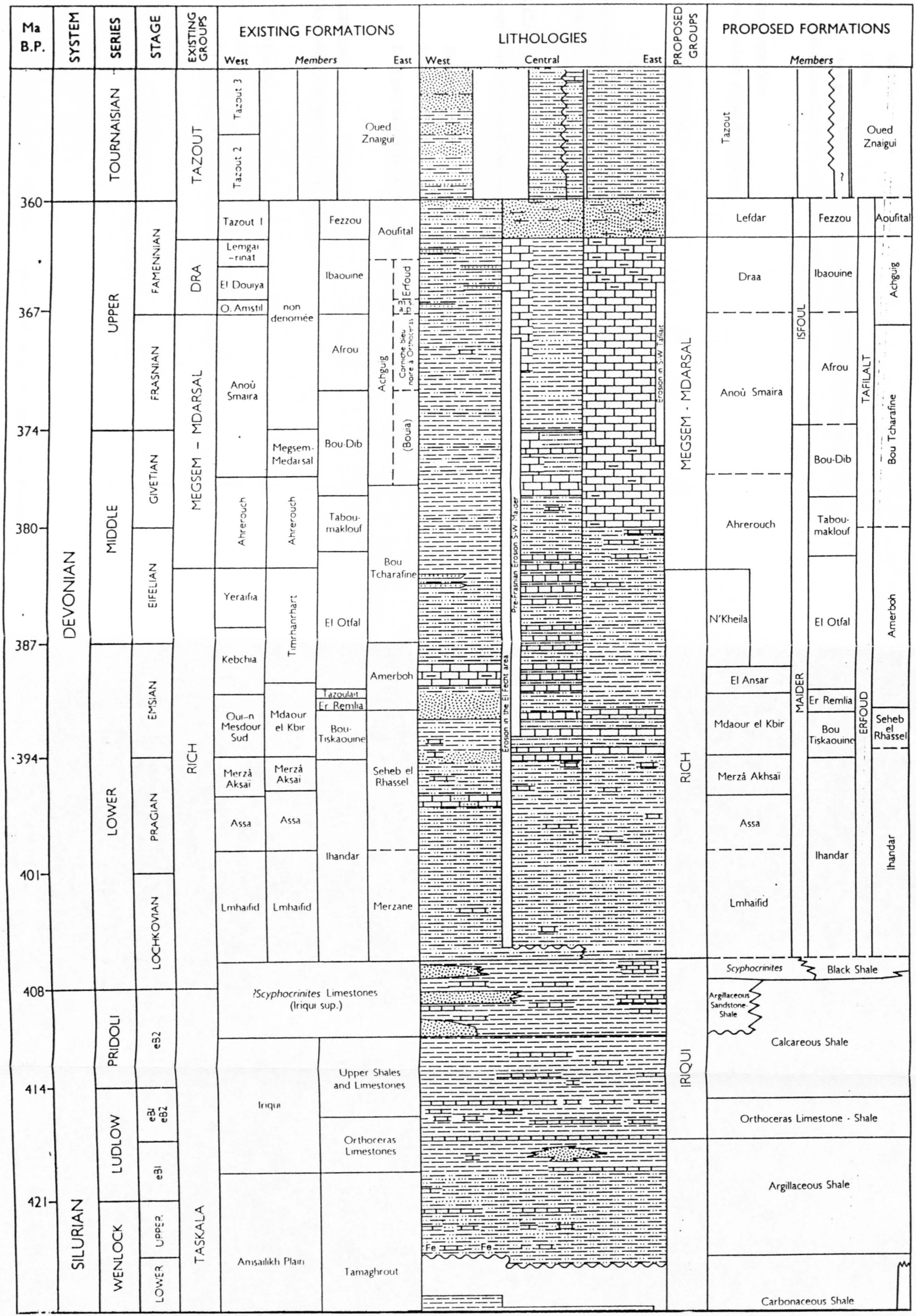


Figure 8. The lithostratigraphic framework for the Devonian System showing the comparison between the published lithostratigraphy and that proposed by the Robertson Group (1985).

Assa Formation.

(Published equivalent: Assa Formation).

Age: Siegenian.
Thickness: 190m.
Lithology: Dark grey mudstones with occasional intercalated white or yellowish brown sandstones. Both of these lithologies are locally calcareous.

Merza Akhsai Formation.

(Published equivalent: Akhsai Formation).

Age: Late Siegenian.
Thickness: 145m.
Lithology: Intercalated dark grey mudstones and white and light grey sandstones with light to medium grey limestones beds towards the top of the formation. Iron staining is evident in the sandstone lithology

Mdaour el Kbir Formation.

(Published equivalent: Mdaour el Kbir Formation).

Age: Emsian.
Thickness: 150m.
Lithology: Dark grey mudstones with common fine grained, calcareous sandstones.

El Ansar Formation.

(Published equivalent: Kebchia Formation [part]).

Age: Emsian.
Thickness: 150m.
Lithology: Dark grey mudstones with common fine grained, calcareous sandstones.

N'Kheila Formation.

(Published equivalent: Kebchia Formation [part], Yeraifia Formation).

Age: Late Emsian-Eifelian.
Thickness: 345m.
Lithology: A coarsening upward sequence with carbonaceous dark grey mudstones predominating at the base with fine grained, calcareous silty sandstones more common towards the top.

Megsem-Mdarsal Group.

(Published equivalent: Megsem-Mdarsal Group, Draa Group).

Ahrerouch Formation.

(Published equivalent: Ahrerouch Formation).

Age: Latest Emsian-Givetian.

Thickness: 200m.

Lithology: Medium to dark grey mudstones which are occasionally silty and calcareous with minor silty, calcareous, fine sandstones.

Anou Smaira Formation.

(Published equivalent: Anou Smaira Formation).

Age: Givetian-Frasnian.

Thickness: 1000m.

Lithology: Dark grey, carbonaceous mudstones with rare fine sandstone interbeds.

Draa Formation.

(Published equivalents: O. Amstil Formation, El Douiya Formation, Lemgairinat Formation).

Age: Famennian.

Thickness: 264m.

Lithology: Medium to dark grey or brownish grey, carbonaceous mudstones with rare fine light grey sandstone interbeds.

Lefdar Formation.

(Published equivalent: Tazout 1 Formation).

Age: Late Famennian.

Thickness: 157.

Lithology: Dark grey, carbonaceous mudstones with rare fine sandstone interbeds.

No group names have been proposed by the Robertson Group for their Carboniferous lithostratigraphic framework.

Tazout Formation.

(Published equivalent: Tazout 2 Formation, Tazout 3 Formation).

Age: Tournasian.

Thickness: 239m.

Lithology: Light grey and brownish grey calcareous fine to medium grained sandstones with intercalated medium to dark grey or olive grey mudstones.

Chapter 2. Aims and Objectives.

The aims and objectives of the thesis fall into two categories. The first category includes those that were set out at the start of the project which are essentially the reasons for the conception of the project by my sponsors, Simon Petroleum Technology (SPT). The second set of aims and objectives are those which arose during the course of the study.

The initial aims and objectives.

1. The primary aim of the project is to extract palynomorph assemblages from the Ordovician to Devonian macrofossil dated field samples from the Anti Atlas of Morocco, in order to calibrate the palynomorph assemblages against the macrofossil assemblages.

2. To refine techniques for the palynological preparation of the Lower and middle Palaeozoic rocks with a view to their application in the field of industrial palynology.

3. To produce a palynological zonation for the Ordovician to Devonian interval.

Aims and objectives arising during the course of the project.

1. To select additional samples (field or well) to those that are macrofossil dated, with suitable lithologies for palynology, to fill in the stratigraphic gaps between the macrofossil dated samples made available.

2. To establish the lithostratigraphic position of the field samples utilised with the aid of field note books, the Robertson Group South Atlas Study report (1985) and the geological maps of Morocco.

3. To refine the technique of oxidising palynological preparations by the use of fuming Schulz's solution.

4. To analyse the practicability of suprageneric schemes currently in use for the acritarchs and chitinozoans.

5. To adopt a generic and specific taxonomy for the acritarchs and chitinozoans that is practicable to palynologists working with a light microscope alone (i.e. not with SEM) which conforms with the rules of the ICBN.

6. To make general palaeoenvironmental interpretations of the site of deposition of the samples using the assemblages recorded, paticularly from the relative abundances of palynomorph groups.

Chapter 3. Techniques.

Palynological processing procedure.

The procedure for the palynological preparation of rock samples for the present study is illustrated in the accompanying flowchart (fig. 9). The techniques employed are practical and time-efficient, notably the oxidation of the thermally mature samples. These time-efficient techniques are seen as flexible for use in future academic research or for use in the time conscious field of industrial palynology.

Between 20 and 50g of dry rock, (depending on the quantity of rock available and the lithology; shales 20-30g, siltstones and sandstones 30-50g) were crushed to pea size or smaller fragments with a pestle and mortar. The rock was then tested for the presence of calcium carbonate (CaCo3) with dilute (10%) hydrochloric acid (HCl). If the sample reacted, it was immersed in 35% HCl until the effervescent reaction was complete. The sample was then decanted several times until neutral.

The non calcareous sample was then immersed in approximately 100-200ml of 40% hydrofluoric acid to break down the silicate minerals. It was left to stand in the fume cupboard for a period of between two days and three weeks. The sample was stirred twice daily and the HF replaced weekly in the cases where the rock was more indurated.

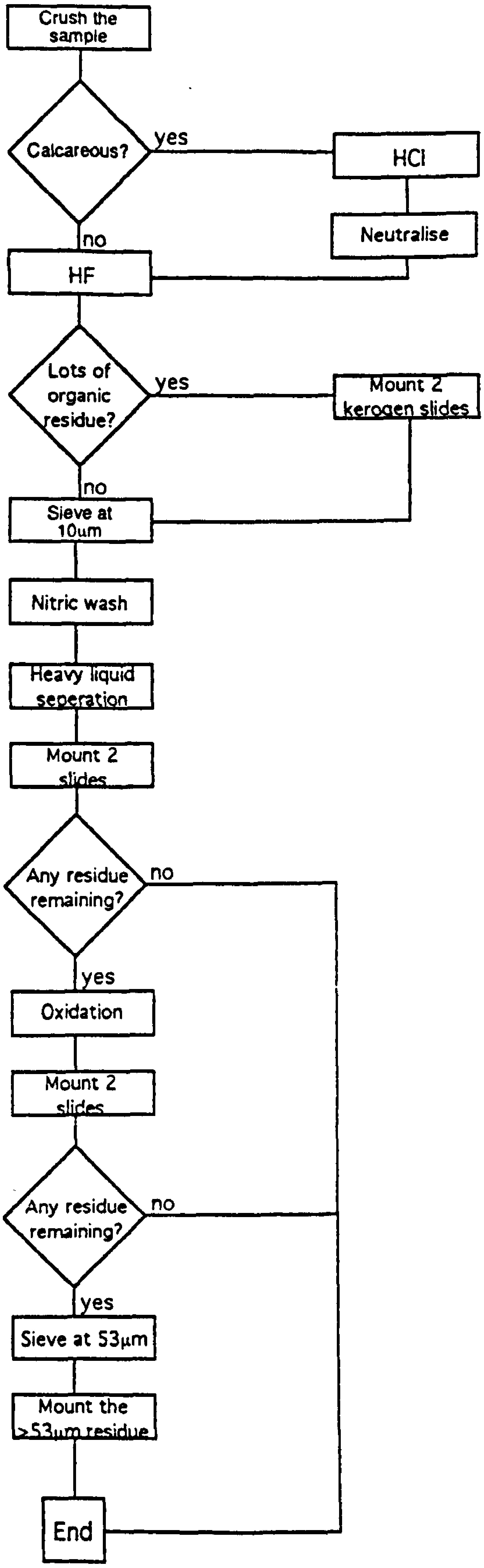
Recent developments in microwave rock digestion technology, a technique currently under investigation at Sheffield University, has shown that the time taken for this part of the processing procedure can be drastically shortened, rock digestion usually taking less than 20 minutes. This technique, which was not available for the present study, will surely become more widely used in the near future.

Post the HF digestion, the sample was sieved through a 10um nylon mesh. If abundant organic residue was retained by the sieve, two kerogen slides were mounted (see below for the slide mounting procedure).

The 10um plus residue was then oxidised for between 30 minutes to 1 hour in 70% nitric acid. This was done primarily to remove any pyrite in the sample that may occur within the palynomorphs. The presence of pyrite within the palynomorphs would cause them to sink during heavy liquid separation. The sample was then neutralised.

The organic residue was separated from the remaining mineral matter using heavy liquid separation. The sample was pipetted into a centrifuge tube and the heavy liquid, zinc chloride (SG 1.54) added. The tube was centrifuged for approximately 15 minutes at 2000 RPM. The floating organic residue was then

Figure 9. Palynological processing flowchart.



transferred to a glass beaker, acidified slightly with two drops of HCl and sieved until neutral. Two slides of the residue were then mounted.

If any sample remained, further oxidation of the sample was carried out. The Ordovician, Silurian and Lower Devonian field samples prepared in the present study were found to be of high thermal maturity and required intense oxidation. Extended oxidation using Schulze's solution was found to be unsuccessful in attempting to bring about some degree of transparency of the palynomorphs. Breakage occurred prior to them becoming transparent using this oxidation agent. However, a technique using fuming Schulze's solution, commonly employed on the high maturity Carboniferous assemblages of southern Eire (Higgs and other workers) which was recently developed upon by researchers at Southampton University (R. Knight and P. Lake pers. comm. 1990) proved to be very successful. The solution is composed of fuming nitric acid (98%) saturated with potassium chlorate. The blood red coloured fuming Schulze's solution was added to the organic residue for between five and 15 minutes. This achieved a more than adequate degree of transparency, with limited breakage, for detailed taxanomic analyses of the palynomorphs. This technique was found to be of particular value in chitinozoan analysis as thinning of the vesicle revealed the detail of surface ornamentation in many specimens. Mounted and unmounted residues treated with fuming Schulze's are apparently prone to reversion back to a the black, opaque condition if subjected to prolonged atmospheric temperatures (R. Knight & P. Lake pers. comm. 1989). For this reason, the residues and slides are presently stored in a refrigerator. Samples treated with fuming Schulze's approximately two years ago have not yet reverted under refrigerated conditions.

The Devonian core samples from Oum Doul-1 were found to respond better to normal Schulze's solution than did the field samples. The downhole samples were oxidised with normal Schulze's for a maximum of 16 hours with samples from the uphole Late Devonian interval only requiring approximately five minutes oxidation.

Research into microwave stimulated oxidation of palynological residues, also at Sheffield University, is presently being developed . Initial results suggest that acid concentration and oxidation time can both be greatly reduced using the microwave technique (S. Ellin & D. McLean pers. comm. 1990-1992). The research is ongoing.

An additional two slides, as a minimum, were mounted after the major oxidation stage.

If any residue was remaining, it was split using a 53um sieve to isolate the chitinozoa. The 53um plus fraction was then mounted on a slide.

Slide mounting: The neutral organic residue was immersed in poly-vinyl alcohol (PVA) to disperse the palynomorphs and pipetted onto a cover slip positioned on a hot plate. The cover slip, when dry, was then mounted on a biological slide using petropoxy 154 as the mounting medium.

Analytical procedure.

The preparation procedure employed produced upto four sets of slides for each sample:

1. Post HF kerogen slides.
2. Post nitric slides.
3. Schulze's or fuming Schulze's slides.
4. 53um slides.

For every sample, post nitric slides were mounted, with Schulze's or fuming Schulze's slides made up if any residue remained. The slide from which a palynomorph count was made was selected from one of these two sets, selection depending on which contained the better preserved palynomorphs. A standard count of 250 palynomorphs (acritarchs, chitinozoans, prasinophytes and spores) was made from the selected slide and at least two, and upto five slides were scanned for additional or well preserved photogenic specimens. The 53um slides, if available, were also scanned for supplementary chitinozoan taxa.

Photography.

The photomicrographs of the palynomorphs were taken on a Reichert-Jung Polyvar microscope with an 80B colour correction filter. Kodak Kodacolour Gold 100 or 200 ASA film was used and the films were processed at Masterlab Ltd., Sheffield. The final plates were printed by Mr. B. Piggot, University of Sheffield.

Computer applications.

The computing package *Tilia* has been used to generate the illustrations of the presence and relative abundances of palynomorphs recorded and the cluster analyses of the assemblages from the samples analysed. The manuscript has been produced using the IBM compatable word processing applications *Word 5.1* and *Word for Windows*.

Chapter 4. The Acritarcha Evitt 1963.

Introduction.

The first collective name for this group of microfossils, prior to the introduction of the term acritarch, was the 'hystrichospheres'. The Group Acritarcha was erected by Evitt (1963) in order to accommodate the numerous miscellaneous hystrichospheres that were not assignable to recognised plant groups at that time e.g. the Dinophyceae, the Prasinophyceae, and the land plant spores. Since 1963, several groups of morphotypes within the Acritarcha have been reinterpreted as having affinity to recognised plant groups, some of these interpretations, in my opinion, are correct, some are incorrect. The Acritarcha can be viewed as an amorphous amoeboid collection of microfossils that we should aim to reduce in size. This we should do by reassigning morphotypes within it that, on the basis of research can be reassigned, without question, to a recognised biological group.

The Group Acritarcha (Evitt 1963) was originally defined as "Small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed b a wall of single or multiple layers and chiefly of organic composition; symmetry, shape, structure, and ornamentation varied; central cavity closed or communicating with the exterior by varied means, for example: pores, a slit like or irregular rupture, a circular opening (the pylome)." This definition was restricted by Fensome *et al.* (1990) to account for the introduction of the colonial spheromorph group, the Cryptarcha Diver & Peat (1979, p.404). The restricted definition of Fensome *et al.* (1990, p.3) is as follows: "unicellular, or apparently unicellular, non colonial organic-walled microfossils of unknown or highly questionable affinity, occurring in palynological assemblages".

The acritarchs are a polyphyletic group of fossils (Evitt 1963; Downie, Evitt & Sarjeant 1963) which are commonly the dominant group of microfossils in Palaeozoic rocks. Various aspects of the group, including morphology, possible biological affinity and classification are discussed in the following sections.

Acritarch morphology.

The morphological terminology adopted for the description of the Acritarcha has been somewhat inconsistent. Several glossaries of terms have been published, e.g. Lister 1970, Kjellstrom 1971a. Unfortunately, these glossaries include some dinoflagellate cyst terms for acritarch morphological features that are potentially misleading. The functional implications of some of the dinoflagellate cyst terms used e.g. cyst, cingulum, if applied to acritarchs, may be interpreted as having a dinoflagellate style of function for the acritarch specimen in question. The potential for this type of confusion to arise can be avoided by using terms that have no implication for the mode of life of the acritarchs, as we are presently unaware of the true affinities of forms included in this group. The alternative terms used here are those already available so as to keep the dictionary of descriptive terms to a minimum.

A glossary of terms follows which is drawn from three sources, the published glossaries of Kjellstrom (1971) and Lister (1970) mentioned above with the addition of information personally conveyed by Professor C. Downie.

Central body: The test minus the processes. Synonymous with vesicle.

Cluster: Discoid or spherical shaped agglomeration of similar individuals.

Distal: In an outward direction from the geometric centre of the vesicle. A term commonly used with reference to the processes.

Epibystra: A circular opening positioned at the apex of a cone shaped process.

Epityche: A flap-like opening at the lateral margin if a flattened vesicle.

Equatorial split: An opening formed be the splitting of a spherical vesicle into two equal hemispheres.

Heteromorphic: Processes having a variable morphology on a specimen.

Homomorphic: Processes having the same morphology on a specimen.

Lipped pylome: Circular opening of the vesicle with a raised rim at the margin.

Longitudinal split: A slit-like opening running parallel to the longitudinal axis of the vesicle.

Marginal split: A slit-like opening at the lateral margin of a flattened vesicle.

Medium split: An opening formed by the splitting of an elongated vesicle into two more or less equal halves.

Opening: A regularly shaped aperture in the wall of the vesicle. It is commonly regarded as the aperture through which the vesicle contents (the protoplasm) escaped to continue the life cycle of the acritarch, i.e. having a similar function as the archaeopyle in dinoflagellate cysts.

Operculum: The part of the vesicle wall lost in the formation of a pylome, an epityche or an epibystra.

Ornament: Projections on, or sculpture of the test. Elements 2um in height and less are considered to be ornamentation. Ornamentation may be scabrate, granulate, baculate, echinate or in the form of ridges.

Process: A prominent projection from the vesicle, here considered to be greater than 2um in height.

Process base: That part of the process adjacent to the vesicle. The process base may be angular, curved or constricted.

Process branching: The furcation of the process distally. Branching may be bifurcate, trifurcate, palmate, ramusculose/multifurcate, floreate or digitate.

Process distribution: Processes distribution may be regular, apical, linear, bipolar or unipolar

Process shaft: That part of the process between the process base and the process termination. The shaft may be conical, cylindrical or inflated.

Process termination: The distal part of the process. The process termination may be accuminate, truncated, capitate, bulbous, rounded or, branched.

Proximal: In an inward direction towards the geometric centre of the vesicle. A term commonly used with reference to the processes.

Pylome: A circular opening of the vesicle.

Plug: An accumulation of organic matter at the base of a process dividing the process cavity from the vesicle interior.

Stigmata: An opening of the vesicle in the centre of one of the flattened surfaces of a flattened vesicle.

Test: The organic test as a whole.

Test shape: The overall shape of the acritarch. The terms used here are acanthomorphic with a rounded vesicle, acanthomorphic with a polygonal vesicle, acanthomorphic with an elongated vesicle, polygonal, spherical, fusiform, cylindrical, flattened or discoid.

Vesicle: The test minus the processes. Synonymous with central body.

Vesicle communication: The separation or non-separation of the process cavity from the interior of the vesicle.

Figure 10. Acritarch morphology.

a. A briefly labelled specimen of *Diexallophasis* sp.

Test shape.

- b. Acanthomorph with rounded vesicle
- c. Acanthomorph with polygonal vesicle
- d. Polygonal
- e. Spherical
- f. Acanthomorph with elongated vesicle
- g. Fusiform
- h. Cylindrical
- i. Flattened
- j. Discoid

Opening types.

- k. Pylome, with the corresponding operculum
- l. Lipped pylome
- m. Epibystra
- n. Stigmata
- o. Marginal split
- p. Epityche
- q. Medium split
- r. longitudinal split
- s. Equatorial split

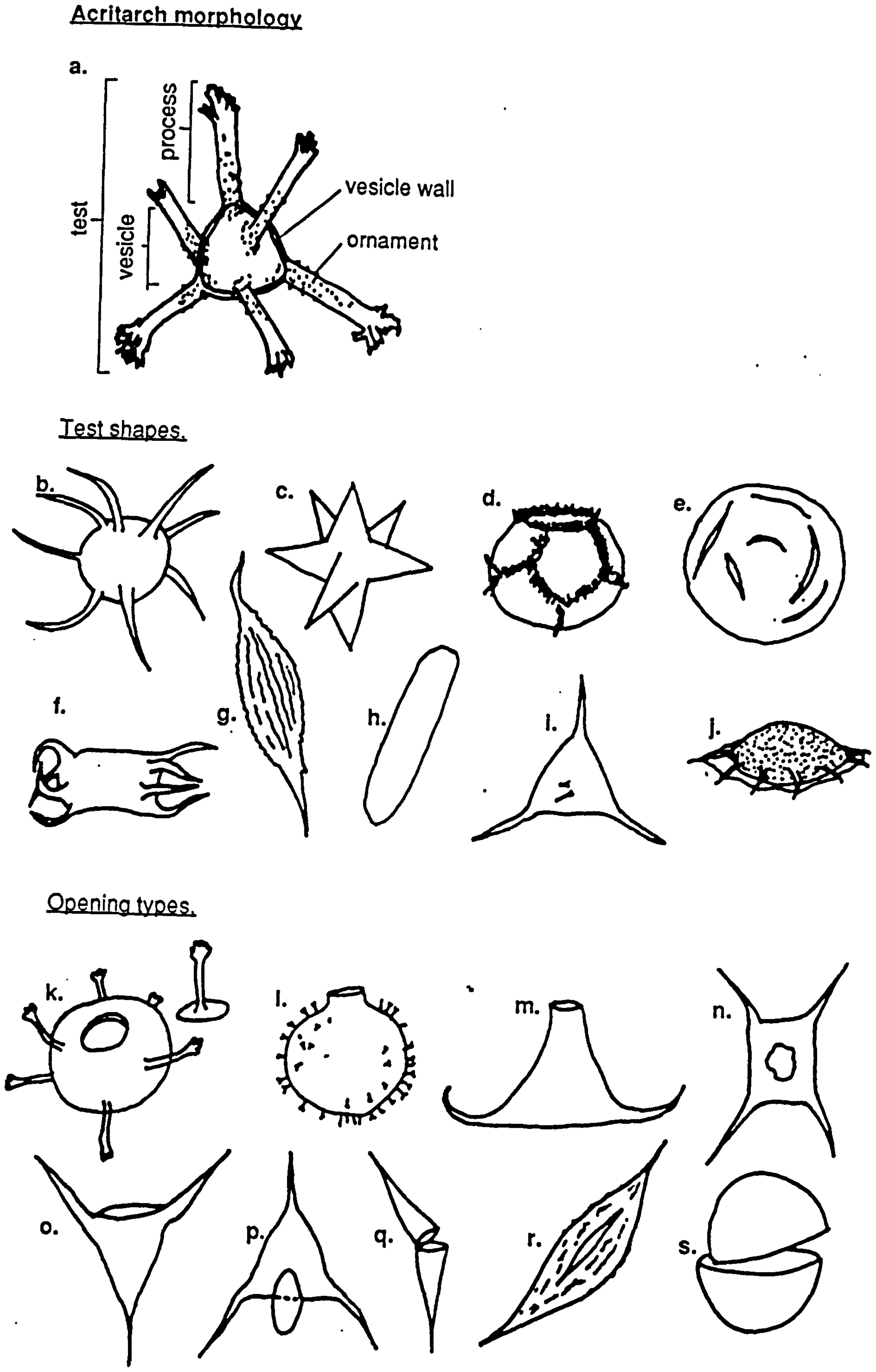


Figure 11. Acritarch morphology (continued).

Processes to vesicle relationship.

a. Free communication between the process cavity and the vesicle
b. Solid processes
c. Sealed. The process cavity is sealed from the vesicle by the inner wall layer.
d. Plugged. The base of the process cavity is plugged by an accumulation of organic matter

Processes distribution.

e. Regular
f. Apical
g. Linear
h. Bipolar
i. Unipolar

Process base.

j. Angular
k. Curved
l. Constricted

Process shaft.

m. Conical
n. Cylindrical
o. Inflated

Process terminations.

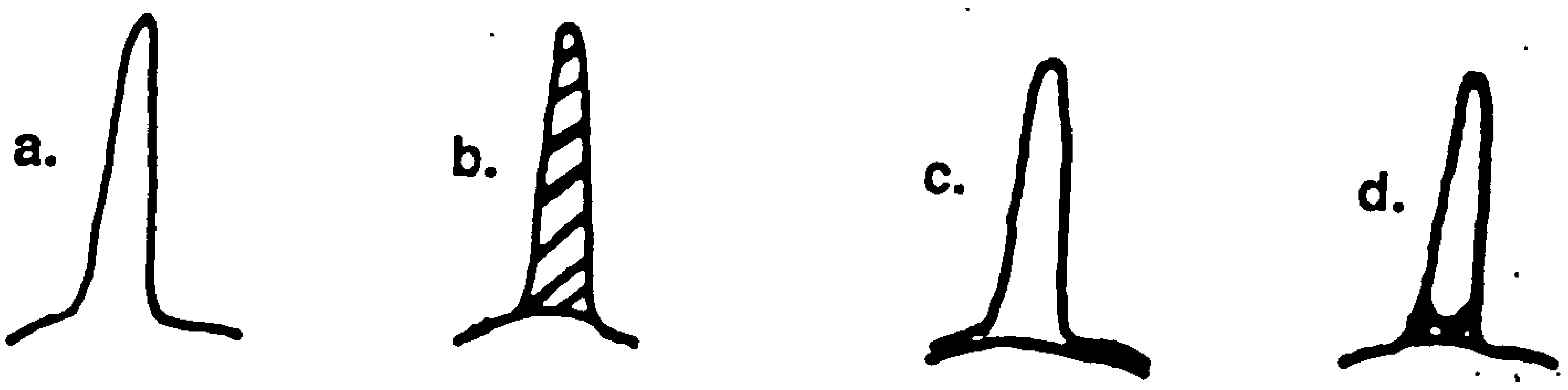
p. Accuminate.
q. Truncated.
r. Capitate.
s. Bulbous.
t. Rounded.

Process branching.

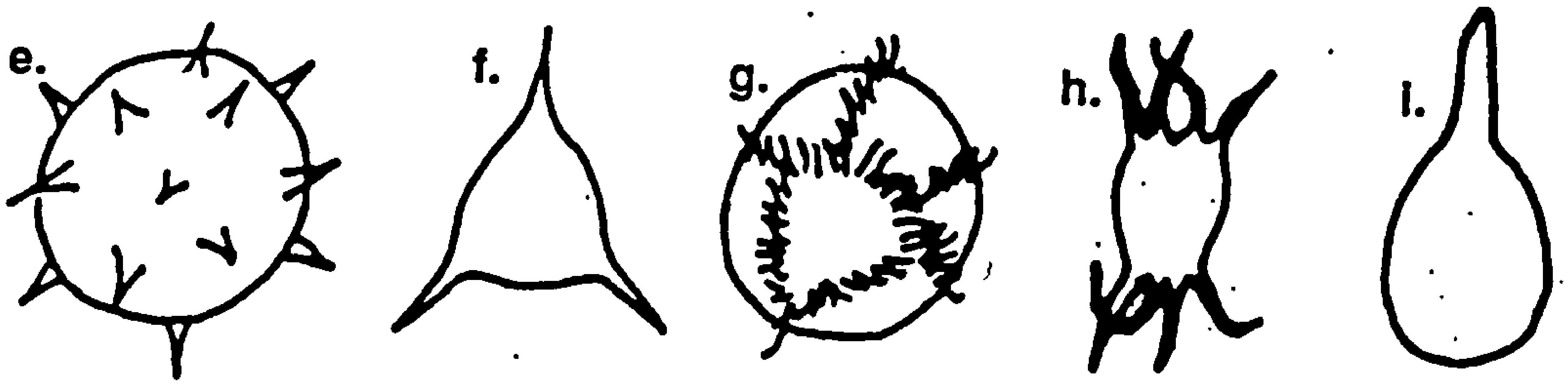
u. Simple, not branched.
v. Bifurcate.
w. Trifurcate.
x. Palmate.
y. Ramusculose or multifurcate.
z. Floreate.
aa. Digitate.

Acritarch morphology cont.

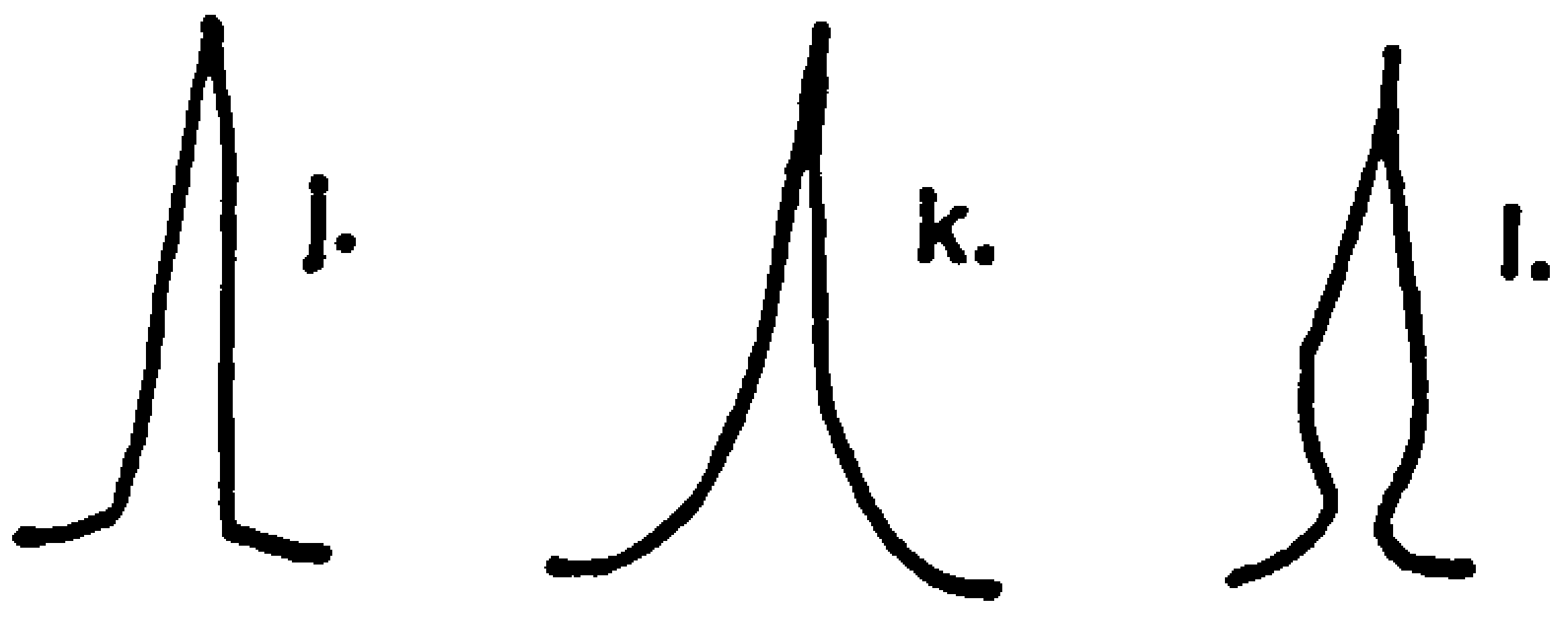
Process-vesicle relationship.



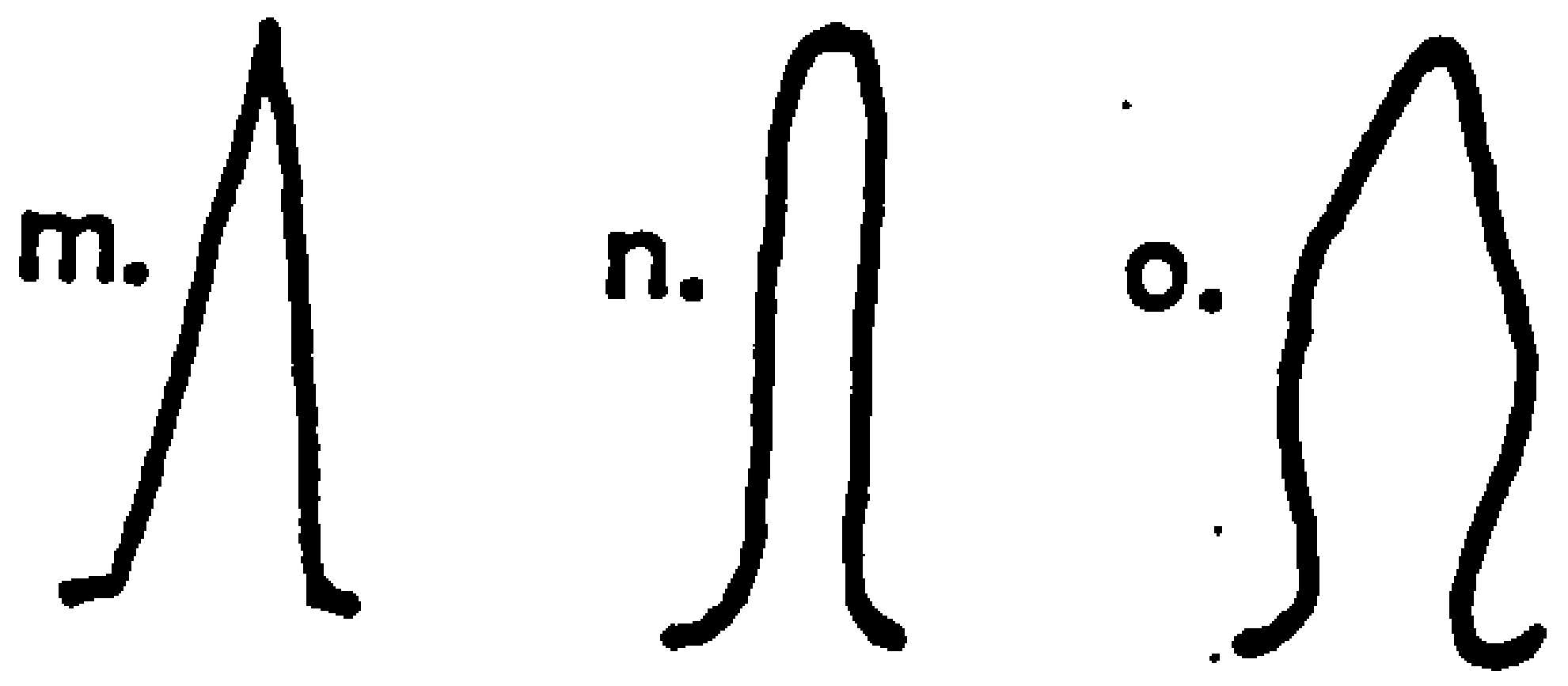
Distribution of the processes.



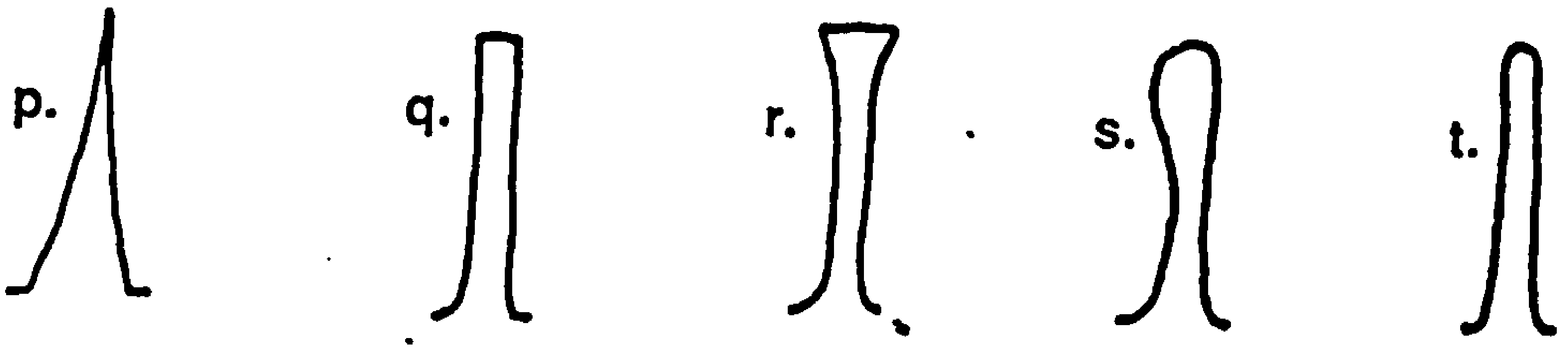
Process bases.



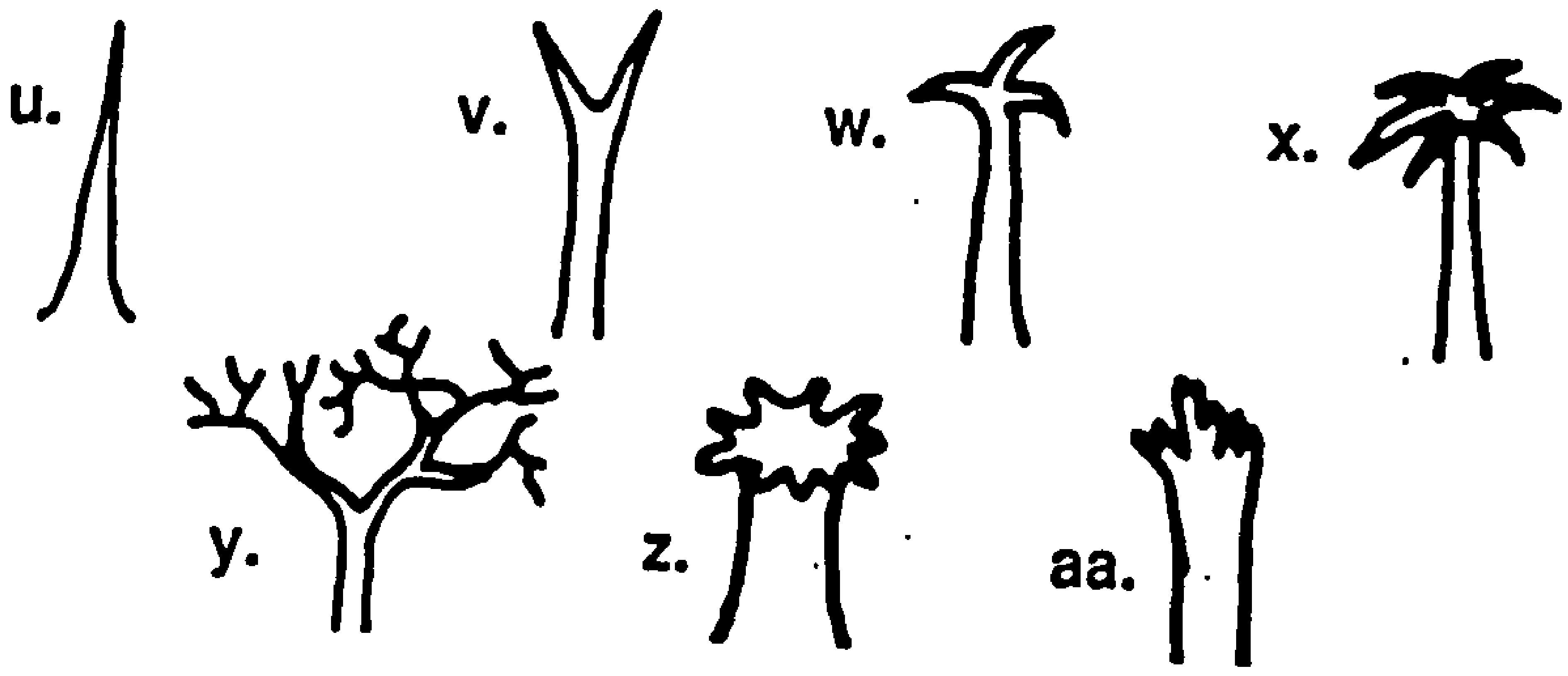
Process shafts.



Process terminations.



Process branching.



Wall: The organic wall of the test which consists of one or more layers. Where two wall layers occur, they are simply referred to as the inner and outer layers. If three layers occur, the middle layer is referred to as such.

Biological affinity.

Acritarchs are, by nature of their definition, a group of microfossils of unknown or uncertain affinity. However, many acritarchs show closely comparable morphological features to recognised microfossil groups.

The Dinophyceae show a remarkable similarity in morphology to many genera presently included in the Acritarcha. This similarity was investigated to a considerable extent by Lister (1970) who proposed tabulation configurations for species of *Cymbosphaeridium* which he recorded from the Ludlow of Shropshire. The anomalous occurrence of *Arpylorus* Calandra 1964 emend. Sarjeant 1978 in the Silurian, which is considered to be a dinoflagellate cyst genus (Lentin & Williams 1989; Fensome *et al.* 1990), suggests that perhaps more genera of acritarchs may be demonstrated to be closely related to the dinoflagellates by future research.

A number of acritarchs show close morphological similarities to the phycoma stage in the life cycle of some prasinophyte genera. Although some genera that were originally included in the acritarchs are now universally accepted as prasinophytes, e.g. *Tasmanites* Newton 1875, *Pterospermella* Eisenack 1975, many are still in dispute (Colbath 1979; 1983), see the Prasinophycean algae chapter herein.

Comparison and transfers of acritarchs to the Chlorophyta is also apparent in the literature (Tappan 1980). A notable genus which is relevant to this study is *Deflandrastrum* Combaz 1962. This is a four celled form which, although appearing superficially similar to the present day *Pediastrum*, can not be placed in the Chlorophyta without question. For this reason *Deflandrastrum* is included in the Acritarcha here.

Spheromorphic acritarchs with low ornamentation or a smooth vesicle wall may in some cases be related to the land plants. From middle Ordovician records and younger, the time of land plants development, it is quite possible that such spherical bodies may be alete miospores of land plant origin. Detailed investigation of the wall ultrastructure of such bodies would have to be undertaken to elucidate such questions.

Acritarch classification.

For purely practical reasons, Evitt (1963) recommended that the Acritarcha should be treated under the same classificatory code as the dinoflagellates which is the International Code of Botanical Nomenclature (ICBN). Earlier, Downie, Williams & Sarjeant (1961) had proposed that fossil organic shelled microplankton, which included the dinoflagellates and the then named hystrichospheres, should be classified as plants and subject to the rules of the ICBN. Evitt, in 1963, endorsed this view.

Prior to the introduction of the Acritarcha, several family names were in use for the hystrichospheres e.g. Leiosphaeridae Eisenack 1954, Hystrichosphaeridae Wetzel 1933, Diplotestidae Cookson & Eisenack 1960. In order to reorganise the suprageneric framework post the introduction of the group Acritarcha, Downie, Evitt & Sarjeant (1963) published 13 subgroups of acritarchs. The subgroups were recognised as not conforming to the rules of the ICBN by the authors but were proposed as a purely mechanical means of suprageneric grouping. A list of the 13 subgroups of Downie Evitt & Sarjeant follows with an indication of the corresponding pre 1963 family names follows. The present systematic position of the subgroup is indicated if it is no longer included in the Acritarcha.

Subgroup ACANTHOMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Hystrichosphaeridae (pars) Wetzel 1933a.

Subgroup POLYGONOMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Hystrichosphaeridae (pars) Wetzel 1933a.

Subgroup SPHAEROMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Leiosphaeridae Eisenack 1954.

Subgroup NETROMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Netromorphitae Eisenack 1938a.

Subgroup DIACROMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Dicrodiaceae Timofeev 1958, the Diornatosphaeridea Downie 1958 and the Trachydiacrodidae Deflandre & Deflandre-Rigaud 1962.

Subgroup HERKOMORPHITAE Downie, Evitt & Sarjeant 1963. Some authors believe that all species that are accommodated in this subgroup are assignable to the Class Prasinophyceae Round 1971, e.g. Tappan 1981. The present author believes only some of the species included here can be justifiably transferred at the present time.

Subgroup PTEROMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Pterospermopsidae (pars) Eisenack 1954a. Species included here are now assignable to the Class Prasinophyceae.

Subgroup PRISMATOMORPHITAE Downie, Evitt & Sarjeant 1963.

Subgroup OOMORPHITAE Downie, Evitt & Sarjeant 1963.

Subgroup STEPHANOMORPHITAE Downie, Evitt & Sarjeant 1963. Species included here are now included in the Class Dinophyceae Fritsch 1929.

Subgroup DISPHAEROMORPHITAE Downie, Evitt & Sarjeant 1963.

Subgroup DINETROMORPHITAE Downie, Evitt & Sarjeant 1963, equivalent to the Diplotestidae (pars) Cookson and Eisenack 1960. Species included here are now included in the Class Dinophyceae.

Subgroup PLATYMORPHITAE Downie, Evitt & Sarjeant 1963. Species originally assigned here are now included in the Class Dinophyceae.

In addition to the initial 13 subgroupings, Staplin Jansonius & Pocock 1965 published the subgroups Baltisphaeritae, which is essentially a subset of the Acanthomorphitae, the Leiosphaeritae, which is identical to the Sphaeromorphitae and the Tasmanatae which is equivalent to the family Tasmanaceae Sommer 1956. In 1967, Seagroves published the subgroup Schizomorphitae which incorporated spheromorphs with an equatorial split. Brito introduced the subgroups Scutellomorphitae (Brito 1967a) and the Retractomorphitae (Brito 1969), the former to accommodate *Maranhites* type forms, the latter for *Triangulina* type forms. The only other subgroupings that have been published are the Reticulasphaeromorphitae Sinha 1969 which includes reticulate spheromorphs, as the name implies, and the Coryphomorphitae Vavrdova 1973 which includes pad shaped forms with decorated apices.

In 1979, Cramer & Diez published a comprehensive key to genera which utilises some of the subgroupings published previously. They divided the acritarchs into three broad units as follows:

Unit 1. Sphaeromorphitae: Unit consisting of spheromorphs with a smooth or little ornamented vesicle wall.

Unit 2. Those acritarchs that do not belong to the spheromorphs (Unit 1) and the acanthomorphs (Unit 3).

Unit 3. Acanthomorphitic acritarchs: Acritarchs possessing processes. This overwhelmingly large unit was subdivided into three subunits.

a. The Netromorphitae. Fusiform acanthomorphs.
b. Diacromorphitae Acanthomorphs with a bipolar distribution of processes.
c. Acanthomorphitae. Acanthomorphs with a regular distribution of processes.

The main criticism of this key is the total disregard for the method of opening as a morphological feature of the acritarchs. It would appear likely from comparison with other algal groups, e.g. the Dinophyceae, that this phenomenon is biologically significant and should, therefore, not be ignored.

An unpublished suprageneric scheme of Downie, personally conveyed to the students on the 1988-89 palynology M.Sc. course at the University of Sheffield, has some very interesting aspects. The scheme splits the acritarch genera into 19 complexes based not only on morphology, as did the scheme of Downie, Evitt & Sarjeant 1963, but on both morphology and their distribution in time. The restriction of a particular morphotype to a relatively narrow time interval may well indicate a biological relationship between taxa falling into that complex. Providing further information as to the possible biological relationship between taxa is probably the major benefits of constructing a morphological suprageneric scheme. As for the other supposed benefit of a suprageneric scheme, i.e. rapid location and retrieval of taxa, it is hard to imagine a purely morphological scheme in which taxa are more easily located than in a system where taxa are listed alphabetically.

The author believes that the suprageneric ordering of acritarchs on a morphological basis will only create problems for future workers wishing to use this piece of work. The published scheme of Downie, Evitt & Sarjeant 1963 is far from ideal, as indicated by the additional work of Downie (pers. comm. 1989). This suggests that alterations will be made or alternative schemes will be used by future workers. Evolution of such artificial suprageneric schemes leads to frustration and time wasting for workers wishing to locate a particular taxon buried in a scheme that is out of date. For these reasons, acritarch taxa are listed alphabetically in this thesis.

Acritarch systematics.

In this section all taxa are listed alphabetically for the reasons outlined in the previous chapter. All size dimensions given are based on five specimens measured, unless stated otherwise.

Synonomy for the Acritarcha largely follows that of Fensome *et al* 1990. However, where there is disagreement with this publication, remarks are made under the taxa concerned. Selective synonomy lists for these controversial taxa are included.

The ages stated here for the holotypes of the species are those sited by their authors.

Group Acritarcha Evitt 1963.

Genus *Acanthodiacrodium* Timofeev 1958 emend. Deflandre & Deflandre-Rigaud 1962.

Synonomy: 1961, *Priscotheca,* Deunff, p.42-43.

Type species: *Acanthodiacrodium dentiferum* Timofeev 1958.

Generic description: Timofeev 1958, p.831; Deflandre & Deflandre-Rigaud 1962, p.194.

Remarks: The genus *Actinodissus* Loeblich & Tappan 1978 includes species with a thinner wall than those included in *Acanthodiacrodium*. *Priscotheca* Deunff 1961 is here considered to be a junior synonym of the *Acanthodiacrodium* as suggested by Cramer & Diez (1979).

Acanthodiacrodium amplium Rasul 1979.

Plate 1, figs.1 & 2.

Description: Rasul 1979, p.64, pl.2, fig.1.

Holotype: Rasul 1979, pl.2, fig.1. Age: Tremadoc.

Remarks: *Acanthodiacrodium amplium* differs from *A. computulum* Rasul 1979 by having broader and longer processes.

Acanthodiacrodium angustizonale Burmann 1968.

Plate 1, figs.3 & 4.

Description: Burmann 1968, p.641, pl.1, fig.8.

Holotype: Burmann 1968, pl.1, fig.8. Age: Late Llanvirn.

Remarks: Morphologically similar species include *A. plenum* Timofeev 1959 and *A. aciferum* Timofeev 1959. The former appears to have less rigid processes and a more spherical central body. *Acanthodiacrodium aciferum* has a very similar body shape and process morphology to *A. angustizonale* but, from the illustration of the holotype by Timofeev 1959, it appears to have considerably fewer processes.

Acanthodiacrodium constrictum (Deunff) Downie & Sarjeant 1965.

Plate 1, figs.5 & 6; pl.14, fig.1.

Description: Deunff 1961a, p.43-44, pl.3, fig.8; for an English translation see Eisenack, Cramer & Diez 1979, p.13.

Holotype: Deunff 1961a, pl.3, fig.8. Age: Tremadoc.

Remarks: Specimens of *A. constrictum* recorded here have a varying degree of equatorial constriction. In addition to those closely resembling the holotype, a considerable number of specimens included here have a similar morphology to *A.* (*Diornatosphaera*) cf. *constrictum sensu* Deunff 1961 which has a less marked constriction of the central body at the girdle.

Acanthodiacrodium costatum Burmann 1968.

Plate 1, figs.9, 10 & 11.

Description: Burmann 1968, p.640, pl.1, fig.5.

Holotype: Burmann 1968, pl.1, fig.5. Age: Late Llanvirn.

Remarks: *Acanthodiacrodium costatum* is distinguished from the majority of *Acanthodiacrodium* species by the presence of longitudinally arranged ribs in the region of the girdle. *Acanthodiacrodium latizonale* Burmann 1968 and *A. rectinerve* Burmann 1968 also possess ribs but these two species differ by having more prominent spines than *A. costatum*. *Acanthodiacrodium tasselii* Martin 1968 also possesses feint ribs but the processes of this species are also longer and greater in number.

Acanthodiacrodium raia (Deunff) Eisenack Cramer & Diez 1979.

Plate 1, figs.7 & 8.

Synonomy: 1961, *Priscotheca raia*, Deunff, p.42-43, pl.3, fig.2.

Description: Deunff 1961a, p.42-43, pl.3, fig.2; for English translation see Eisenack, Cramer & Diez 1979, p.20.

Holotype: Deunff 1961a, pl.3, fig.2. Age: Tremadoc.

Remarks: Fensome *et al.* 1990 retained the genus *Priscotheca* Deunff 1961, of which *'P. raia'* is the type species, for the sole reason that Volkova 1988 published another species in that genus. The present author sides with Cramer & Diez 1979 in this case (p.89) in discarding the genus *Priscotheca* and accommodating all species of that genus within *Acanthodiacrodium*.

A number of species whose morphology varies only slightly from that of *A. raia* have been split on very minor variations in the shape of the base of the process, shape of the central body and size. Susceptibility of these elongate forms to folding and distortion in compression makes splitting of this group of morphotypes on such characteristics rather arbitrary. The species *A. prismatic* (Deunff) Eisenack, Cramer & Diez 1979, *A. minima* (Deunff) Eisenack, Cramer & Diez 1979 and *A. compliant* (Deunff) Eisenack, Cramer & Diez 1979 are all closely comparable and require biometrical analysis of their populations to establish the legitimacy and the scope of these species within this complex of forms.

Acanthodiacrodium selectum Timofeev 1959.

Plate 2, figs.1 & 2.

Description: Timofeev 1959b, p.75, pl.6, fig.34.

Holotype: Timofeev 1959b, pl.6, fig.34. Age: Late Cambrian.

Remarks: Specimens assigned here have a rather thick, robust wall.

Acanthodiacrodium uniforme Timofeev 1959.

Plate 2, figs.3, 4 & 5.

Synonomy:	1959, *Acanthorytidodiacrodium serotinum* Timofeev, p.82, pl.7, fig.9.
	1959, *Acanthorytidodiacrodium diffusum* Timofeev, p.86, pl.7, fig.27.

Description: Timofeev 1959b, p.69, pl.6, fig.2.

Holotype: Timofeev 1959b, pl.6, fig.2. Age: Mid-Late Cambrian.

Remarks: Of the 51 species of *Acanthodiacrodium* and 34 species of '*Acanthorytidodiacrodium*' (the majority of the species originally described in *Acanthorytidodiacrodium* are now accommodated in *Acanthodiacrodium*, [Fensome *et al.* 1990]) described by Timofeev (1959) from the Soviet Cambrian, there is much room for synonomy as one might expect.

Specimens have an ovoidal central body with rounded apices. Spine length varies between 2-8um in length and breakage of the spines is common. The girdle occupies approximately 1/4-1/3 of the length of the body. There are no longitudinal ribs or striations in the region of the girdle. The vesicle is 30-45um in length.

Acanthodiacrodium costatum Burmann 1968 is similar in overall shape but differs in having ribs in the area of the girdle.

Acanthodiacrodium varvrdovae Cramer & Diez 1977.

Plate 2, fig.6.

Description: Cramer & Diez 1977a, p.343, pl.5, figs.4, 5 & 9.

Holotype: Cramer & Diez 1977a, pl.5, fig.5. Age: Early Arenig.

Remarks: A morphologically similar species is *A. petrovi* Timofeev 1959 which differs in having markedly fewer processes at each pole.

Acanthodiacrodium cf. *vulgare* Timofeev 1959 *ex* Downie & Sarjeant 1965.

Plate 2, fig.10.

Holotype: Timofeev 1959b, pl.7, fig.27. Age: Late Cambrian.

Remarks: Compare with Timofeev 1959b, p.86, pl.7, fig.27 and Downie & Sarjeant 1965, p.81. Specimens assigned here have a squat cylindrical central body, a girdle occupying approximately 1/3 of the body length and short stout processes at the poles. Specimens are 35-40um in length.

The holotype of *A. vulgare* has a similar body shape and process morphology to *A.* cf. *vulgare* but it has noticeably fewer processes. The type material is also larger in size, the central body ranging in length between 51-40um compared to 35-40um in length here.

Acanthodiacrodium sp. 1.

Plate 2, figs.7, 8 & 9.

Description: Acanthomorphic acritarchs with processes concentrated at each pole of the central body. The central body has a strongly polygonal aspect as a result of the conical shaped '*Goniosphaeridium* type' processes. The body is as broad as it is long (the length ranges between 22-31um). The girdle is poorly defined and occupies approximately 1/4 of the length of the central body. The processes are cone shaped, upto 10um long and upto 7um wide at the base tapering distally to truncated or accuminate tips. The wall is composed of a single wall layer and the processes communicate freely with the central body. The wall is smooth. No regular form of opening is apparent.

Remarks: This species has similar process morphology and a similar polygonal aspect to the central body as has *A. constrictum* described above. However, *Acanthodiacrodium* sp. 1 has a more equidimensional central body and little, if any, constriction at the girdle.

Acanthodiacrodium sp. 2.

Plate 2, figs. 11-14.

Description: Acanthomorphic acritarchs with processes concentrated at each pole of the central body. The central body is flattened (as in *Veryhachium*) and has a strongly polygonal aspect as a result of the '*Polygonium* type' processes. The body is generally equidimensional. The girdle occupies approximately 3/4 of the central body and the length of the body ranges between 22-29um. Processes are long, upto 15um in length, with broad polygonal bases and accuminate tips. The wall is composed of a single wall layer and the processes communicate freely with the central body. The wall is smooth. No regular form of opening is apparent.

Remarks: This species is distinguished from other species of *Acanthodiacrodium* by the flattened polygonal body and 'whip-like' processes. It closely resembles some of the *Polygonium* spp. observed from the Tremadoc-Arenig aged samples in the present study. The most notable similarity is with *P. gracile* vars. 2 & 3 described below. This form also has a polygonal central body but they differs in having a more regular distribution of processes.

Genus *Actinodissus* Loeblich & Tappan 1978.

Type species: *Actinodissus longitaleosus* Loeblich & Tappan 1978.

Generic description: Loeblich & Tappan 1978, p.1236-1238.

Remarks: *Actinodissus* is distinguished from *Acanthodiacrodium* in possessing a thinner vesicle wall.

Actinodissus rectinerve (Burmann) comb. nov.

Plate 14, figs.2, 3 & 4; pl.40, figs.1, 2 & 3.

Synonomy: 1968, *Acanthodiacrodium rectinerve* Burmann, p.641, pl.1, fig.7; pl.7, fig.5.

Description: Burmann 1968, p.641, pl.1, fig.7; pl.7, fig.5.

Holotype: Burmann 1968, pl.1, fig.7; pl.7, fig.5. Age: Late Llanvirn.

Remarks: This thin walled, granulate diacrodian species described from the Llanvirn by Burmann (1968) is better accommodated in the genus *Actinodissus*. Species within the genus *Acanthodiacrodium* are generally more robust in appearance with a thicker wall. In addition, *Acanthodiacrodium* species generally occur in older sediments (usually Late Cambrian-Arenig in age) than the thinner walled *Actinodissus* species.

Actinodissus sp. 1.

Plate 31, fig.1.

Description: Acanthomorphic acritarchs with processes concentrated at each pole of the central body. The body is elongate ellipsoidal and measures 35-40um in length and 20-25um wide at the girdle, the girdle occupying approximately 1\4 of the length of the body. Each pole has a concentration of about 20 processes measuring between 10-15um in length and upto 3um wide at their base. The processes are simple with accuminate tips and they communicate freely with the central body. The wall is thin and composed of a single layer with a smooth or granulate surface. No regular form of opening is apparent.

Remarks: *Actinodissus crassus* Loeblich & Tappan 1978 has a more equidimensional central body and has a longer and more slender processes than *Actinodissus* sp. 1. The former also differs in possessing striations on the central body. *Actinodissus longitaleosus* Loeblich & Tappan 1978 has more straight sided processes which gives a more polygonal aspect to the shape of the central body of this species. In addition processes are longer, more slender and are ornamented with fine grana. *Actinodissus ubuii* (Martin) Fensome *et al.* 1990 has shorter spine-like processes and a striate central body.

Actinodissus sp. 2.

Plate 14, fig.5.

Description: Acanthomorphic acritarchs with the processes concentrated at each pole of the central body. The body is elongate ellipsoidal and measures 35-44um in length and 25-35um wide at the girdle. The girdle occupies approximately 1\3 of the length of the body. Each pole has a concentration of about 15 processes measuring up to 15um in length and up to 4um wide at the base. The processes are broad with accuminate tips and they communicate freely with the central body. The wall is thin and composed of a single layer and the wall surface is granulate. No regular form of opening is apparent.

Remarks: This species is very similar in morphology to *Actinodissus* sp. 1 but differs in having broader, more blunt processes and a broader central body.

Genus *Actinophasis* Loeblich & Wicander 1976.

Type species: *Actinophasis complurilata* Loeblich & Wicander 1976.

Generic description: Loeblich & Wicander 1976, p.5-6.

Remarks: This genus is similar to the genus *Multiplicisphaeridium*. Species within it are distinguished by the presence an ornament of radially arranged striations on the central body centred about the base of the processes. The genus *Stelliferidium* has a very similar ornamentation on the central body but can be distinguished by the presence of a pylome.

Actinophasis cf. *complurilata* Loeblich & Wicander 1976.

Plate 120, figs.1-4.

Holotype: Loeblich & Wicander 1976, pl.1, fig.3. Age: Late Gedinnian.

Remarks: compare with *Actinophasis complurilata* Loeblich & Wicander 1976, p.6, pl.1, figs.1-3. Specimens included here strongly resemble the type material. However, the processes are slightly shorter and the central body is slightly more rounded in the specimens recorded here.

Genus *Ammonidium* Lister 1970.

Type species: *Ammonidium microcladum* (Downie) Lister 1970.

Generic description: Lister 1970, p.48-48.

Remarks: The genus *Ammonidium* encompasses acanthomorphic acritarch species with processes that are equifurcate at the distal terminations. The wall may be smooth or sculptured. *Multiplicisphaeridium* differs by having heteromorphic processes that branch in a more elaborate manner.

Ammonidium? *alloiteauii* (Deunff) Deunff 1976.

Plate 149, fig.1; pl.153, figs.1 & 2; pl.163, fig.1; pl.172, fig.1; pl.180, figs.1 & 2.

Description: Deunff 1955, p.148, pl.4, fig.3.

Holotype: Deunff 1955, pl.4, fig.3. Age: Middle Devonian.

Remarks: This species is a moderately thick walled form and commonly appears dark in coloration in palynological preparations. *Ammonidium* sp. 1 (herein) is morphologically very similar. However, this older form, recorded here from Wenlock aged sediments, has broader, more stout processes. *Multiplicisphaeridium raspum* (Cramer) Eisenack, Cramer & Diez 1973 has longer processes than *A*? *alloiteauii* that furcate in a less ordered manner.

Ammonidium grosjeanii (Stockmans & Williere) Martin 1981.

Plate 172, figs.2-6; pl.180, fig.3.

Description: Stockmans & Williere 1962, p.87-88, pl.2, fig.17, text-fig.6.

Holotype: Stockmans & Williere 1962, pl.2, fig.17. Age: Frasnian.

Remarks: This species has a similar morphology to *A. microcladum*, however it has processes which are more robust, having thicker shafts and thicker distal pinnae.

Ammonidium microcladum (Downie) Dorning 1981.

Plate 57, figs.2 & 3; pl.72, fig.1; pl.81, figs.1, 2 & 3.

Description: Downie 1963, p.645, pl.91, fig.3; pl.92, fig.6, text-fig.3g.

Holotype: Downie 1963, pl.92, fig.6. Age: Wenlock.

Remarks: The intraspecific variation within *A. microcladum* reported by Le Herrise (1989, p.83) indicates that *A. waldronense* (Tappan & Loeblich) Dorning 1981 may be a junior synonym of this species. *Salopidium granuliferum* (Downie) Dorning 1981 has a similar gross morphology to *A. microcladum* but differs in having simple as opposed to equifurcate process tips.

Ammonidium cf. *ludloviense* Lister 1970 *ex* Dorning 1981.

Plate 57, figs.1 & 4.

Holotype: Lister 1970, pl.1, fig. 14. Age: Wenlock-Ludlow.

Remarks: Compare with Lister 1970, p.50, pl.1, figs.6, 12-14. The two specimens recorded here have processes with expanded bases that merge with the central body, as in *A. ludloviensis*. The central vesicle is faintly granulate. The specimens observed have capitate process terminations which differs from the combination of capitate and minutely furcate process terminations of the holotype. Specimens here are also slightly larger than the type material, the central body measuring upto 50um in diameter. *Ammonidium listeri* Smelror 1986 also has expanded process bases but possesses a greater number of processes.

Ammonidium sp. 1.

Plate 78, figs.1-4.

Description: Acanthomorphic acritarchs which have a rigid spherical central body measuring between 32-38um in maximum diameter. There are more than 50 short evenly distributed processes present. They measure between 3-7um in length and upto 4um wide at the base. They taper distally and possess a combination of capitate, equifurcate bifid and\or equifurcate trifid tips. The process to body ratio is approximately 1:8. The wall is composed of a single layer and is smooth. The processes appear to communicate freely with the central body. Opening of the vesicle is by medium split.

Remarks: This species is morphologically similar to *Ammonidium*? sp.1 *sensu* Hill 1974 (Ph.D. thesis), 1974 and 1984. Specimens recorded in the present study have a slightly thicker, more robust wall. *Ammonidium*? sp.1 Hill *sensu* Le Herisse 1989 (p.84, pl.5, fig.6) is also very similar in morphology to *Ammonidium* sp.1.

Of the formally published species, *A*? *alloiteauii* is the most comparable. *Ammonidium*? *alloiteauii*, described from the Devonian of North America, differs in possessing more straight sided and longer processes.

Ammonidium sp. 2.

Plate 104, figs.1-5; pl.114, figs.1 & 4.

Description: Acanthomorphic acritarchs which have a subspherical central body measuring between 40-50um in maximum diameter. There are more than 50 slender evenly distributed processes present. They measure approximately 8um in length and are 1-2um wide at the base. They taper very slightly distally and possess a combination of capitate, equifurcate bifid and equifurcate trifid tips. The process to body ratio is approximately 1:6. The wall is composed of a single layer which under high magnification appears to be vacuolate with many hundreds of small (1um in diameter) subspherical vacuoles. Opening of the vesicle is by medium split.

Remarks: The thin processes and the distinctive vacuolate wall structure distinguish this taxon. *Ammonidium microcladum* is a comparable form by way of the form of the processes. However, *A. microcladum* has a more dense distribution of processes, the processes also being longer relative to the diameter of the central body.

Genus *Arbusculidium* Deunff 1968.

Type species: *Arbusculidium destombesii* Deunff 1968.

Generic description: Deunff 1968a, p.101-102.

Remarks: *Arbusculidium* is comparable to the genus *Dicrodiacrodium*. Both genera include species with filamentous processes at one pole of the elongated vesicle. However, the opposite pole to that possessing the filamentous elements in *Dicrodiacrodium* species possesses a single process with a furcate distal termination in contrast with the several simple processes at the opposite pole in *Arbusculidium* species.

Arbusculidium filamentosum (Vavrdova) Vavrdova 1972.

Plate 14, figs.8, 9 & 10.

Description: Vavrdova 1965, p.335-336, pl.4, fig.1.

Holotype: Vavrdova 1965, pl.4, fig.1. Age: Arenig.

Remarks: Specimens recorded here closely resemble the type specimens described by Vavrdova.

Genus *Baltisphaeridium* Eisenack 1958 *ex* Eisenack 1959 emend. Eisenack 1969.

Type species: *Baltisphaeridium longispinosum* (Eisenack ex O. Wetzel) Eisenack 1959.

Generic description: Eisenack 1969, p.249.

Remarks: *Baltisphaeridium* is distinguished from *Micrhystridium* by having the communication between vesicle and processes blocked proximally. The processes communicate freely with the vesicle in *Micrhystridium*. The genus *Baltisphaerosum* Turner 1984 differs from *Baltisphaeridium* in the method by which the vesicle opens. In the former, opening is by medium split and in the latter by means of a pylome.

Baltisphaeridium anfractum Playford 1977.

Plate 137, fig.1; pl.153, fig.3; pl.163, fig.2, 3 & 5.

Description: Playford 1977, p.11, pl.1, figs.1-8.

Holotype: Playford 1977, pl.1, fig.1. Age: Emsian.

Remarks: This species is characterised by the relatively small central body (17-35um) and the very long (30-60um), flexible, slender processes.

Baltisphaeridium archaicum Cramer & Diez 1972.

Plate 58, fig.1; pl.72, fig.2.

Description: Cramer & Diez 1972, p.148, pl.31, figs.3 & 4.

Holotype: Cramer & Diez 1972, pl.31, figs.3 & 4. Age: Early Llandovery.

Baltisphaeridium cf. *cantabricum* Cramer 1964.

Plate 81, fig.5.

Holotype: Cramer 1964, pl.4, fig.15. Age: Ludlow-Siegenian.

Remarks: Compare with Cramer 1964, p.290-291, pl.4, figs.15-16. Specimens included here have the same overall dimensions, the same process number and distribution, and the same central body to process ratio as the holotype. However, the inner body is noticeably thicker in the specimens observed here.

Baltisphaeridium distentum Playford 1977.

Plate 163, figs.4 & 6.

Description: Playford 1977, p.12-13, pl.1, figs.13 & 14; pl.2, figs.1-5.

Holotype: Playford 1977, pl.2, fig.1. Age: Emsian.

Baltisphaeridium hirsutoides (Eisenack) Eisenack 1959.

Plate 3, figs.1, 2 & 3; pl.14, fig.7.

Description: Eisenack 1951, p.189-190, pl.3, fig.8.

Holotype: Eisenack 1931, pl.5, fig.19.

Neotype: Eisenack 1951, pl.3, fig. 8. Age: Late Ordovician.

Baltisphaeridium klabavense (Vavrdova) Kjellstrom 1971.

Plate 31, figs.2, 3 & 6.

Description: Vavrdova 1965, p.353, pl.2, fig.1, text-fig.1.

Holotype: Vavrdova 1965, pl.2, fig.1. Age: Arenig.

Remarks: Deunff 1977 recorded this taxon from the Llanvirn aged Tachilla shales from Morocco.

Baltisphaeridium longispinosum subsp. *delicatum* Turner 1984.

Plate 14, figs.11 & 12.

Description: Turner 1984, p.99-100, pl.6, figs.1 & 7.

Holotype: Turner 1984, pl.6, fig.7. Age: Caradoc.

Remarks: These forms with rather delicate processes commonly show evidence of mechanical damage in the poorly preserved material observed.

Baltisphaeridium sp. 1

Plate 40, fig.1.

Description: Acanthomorphic acritarchs which have a rigid spherical central body measuring between 29-32um in maximum diameter. There are approximately 15 evenly distributed, simple processes which are 15-20um in length, upto 3um wide at the base and taper distally to accuminate tips. The process to body ratio is approximately 1:1.5. The wall is composed of a single layer. The central body is relatively thick walled and has a granulate ornamentation. The processes are smooth. No regular form of opening is apparent.

Remarks: *Baltisphaeridium bulbosum* Kjellstrom 1971 is larger in size, has a smooth central body and has broader based processes.

Baltisphaeridium sp. 2.

Plate 40, fig.2.

Description: Acanthomorphic acritarchs with a rigid spherical central body measuring between 20-23um in maximum diameter. There are approximately 15 evenly distributed simple processes. They are upto 30um in length, upto 3um wide at the base and they taper distally to accuminate tips. The process to body ratio is approximately 1.5:1. The wall is composed of a single layer and is smooth or very finely granulate. No regular form of opening is apparent.

Remarks: *Baltisphaeridium* sp.1 differs in the processes length to central body ratio. Processes are longer and the central body is smaller in *Baltisphaeridium* sp. 2.

Baltisphaeridium? sp. 3.

Plate 58, figs.2 & 3.

Description: Acanthomorphic acritarchs with a rigid spherical central body measuring between 35-50um in maximum diameter. There are approximately 7-15 evenly distributed simple processes. The processes are upto 45um in length, upto 4um wide at the base and they taper distally to accuminate tips. The process to body ratio is approximately 1.2:1. The wall appears to be composed of two wall layers. The layers are closely appressed over the central body, the outer layer forming the processes. The central body has a granulate or rugulate ornament and the processes are smooth. No regular form of opening is apparent.

Remarks: This taxon is distinguished by the relatively dark coloured, thick walled central body. The wall structure is similar to that of some of the *Cymbosphaeridium* species recorded at the same stratigraphic level in this study. However, specimens included here have simple process terminations in contrast to the denticulate terminations of *Cymbosphaeridium* species.

Baltisphaeridium? sp. 5.

Plate 180, figs.4-7.

Description: Acanthomorphic acritarchs which have a rigid subspherical central body measuring between 16-30um in maximum diameter. There are approximately 10-20 evenly distributed simple processes. The processes are upto 15um in length, upto 3um wide at the base and they taper distally to accuminate tips. The process to body ratio is approximately 1:1.2. The wall appears to be composed of two wall layers. The layers are closely appressed over the central body and the base of the processes, the outer layer forming the process shaft and tip. The vesicle wall of the central body and the processes is smooth. The opening of the vesicle is by "double pylome" which forms by the loss of two subcircular portions of the vesicle wall which lie adjacent to each other prior to pylome formation. Each pylome is surmounted by a single process.

Remarks: The distinctive "double pylome" excystment mechanism is the most diagnostic feature of this taxon. Assignment to the genus *Baltisphaeridium* is questioned due to the presence of this unique form of opening.

Baltisphaeridium\Baltisphaerosum sp.

Plate 31, fig.12.

Remarks: This large form of *Baltisphaeridium* or *Baltisphaerosum* (central body 72um in diameter) has plugged, granulate processes that measure at least 35um in length (the processes are all broken). The single specimen observed closely resembles *Baltisphaerosum dispar* Turner 1984, however the central body is markedly smaller in *B. dispar* and the diagnostic medium split style of opening is not discernible.

Genus *Baltisphaerosum* Turner 1984.

Type species: *Baltisphaerosum christoferi* (Kjellstrom) Turner 1984.

Generic description: Turner 1984, p.101-102.

Remarks: *Baltisphaerosum* Turner 1984 is distinguished from *Baltisphaeridium* by having a medium split style of opening. Species of *Baltisphaeridium* open by means of a pylome (Turner 1984, p.102).

Baltisphaerosum onniense Turner 1984.

Plate 31, figs.2, 3 & 6.

Description: Turner 1984, p.104-105, pl.5, figs.2 & 5.

Holotype: Turner 1984, pl.5, fig.5. Age: Caradoc.

Genus *Buedingisphaeridium* Schaarschmidt 1963 emend. Lister 1970.

Type species: *Buedingisphaeridium permicum* Schaarschmidt 1963.

Generic description: Lister 1970, p.59-61.

Remarks: The genus *Lophosphaeridium* has an ornament of solid tubercles in contrast to the hollow tubercular elements of *Beudingisphaeridium*. *Trichosphaeridium* has an ornament of fine hair-like echinae. *Tylotopalla* may have short stumpy elements similar to those in *Beudingisphaeridium* but it differs in having additional ornament in the viscinity of the elements.

Buedingisphaeridium lunatum Le Herisse 1989.

Plate 58, fig.7; pl.81, fig.4.

Description: Le Herisse 1989, p.87-88, pl.5, figs.14-15.

Holotype: Le Herisse 1989, pl.5, fig.14. Age: Llandovery.

Buedingisphaeridium sp. 1.

Plate 58, fig.6.

Description: Subspherical acritarchs with numerous short pyramidal outgrowths. The maximum diameter of the body ranges between 26-35um. The hollow conical processes are closely spaced and number approximately 100. They are 3-4um high and 3-5um wide at the bases. The process to body ratio is approximately 1:9. The wall is composed of a single layer, the processes communicate freely with the central body. The wall is smooth to scabrate and no regular form of opening is apparent.

Remarks: *Tylotopalla pyramidale* (Lister) Dorning 1981 appears morphologically identical from the description and illustration of the holotype given by Lister (1970, p.61). However, re-examination of the holotype by Dorning (1981) revealed that the processes of the holotype are ornamented with echinae which justifies his transfer of this species to *Tylotopalla*. *Tylotopalla deerlijkianum* (Martin) Le Herisse 1989 has striate ornamentation at the base of the processes.

Genus *Caldariola* Molyneux 1988.

Type species: *Caldariola glabra* (Martin) Molyneux 1988.

Generic description: Molyneux 1988, p.57.

Remarks: In their erection of the genus *Caldariola*, Molyneux & Rushton (1988, p.56-57) discuss in considerable detail the complex of Lower Ordovician genera with large polar openings or pylomes, namely *Cymatiogalea*, *Priscogalae*, *Stelliferidium* and *Caldariola*. The present author follows their interpretation of these genera (p.57, 4th paragraph).

Caldariola glabra (Martin) Molyneux 1988.

Plate 3, fig.12.

Description: Martin 1972, p.22, pl.4, fig.8; pl.5, fig.17.

Holotype: Martin 1972, pl.5, fig.17. Age: Tremadoc.

Remarks. The two specimens recorded here accord well with the description of the type material.

Genus *Candelasphaeridium* Deunff 1978.

Type species: *Candelasphaeridium insolitum* Deunff 1978.

Generic description: Deunff 1978, p.115.

Candelasphaeridium cf. *insolitum* Deunff 1978.

Plate 128, fig.6?; pl.149, figs.3-6.

Holotype: Deunff 1978, pl.1, fig.11. Age: Early Gedinnian.

Remarks: Compare with Deunff 1978, p.115, pl.1, figs.8-14. The poorly preserved specimens of *C.* cf. *insolitum* that have been recorded in the present study have fewer processes than the type specimens. The original description states that 12-25 processes are present in this species, upto 10 processes are present on specimens recorded here.

Genus *Comasphaeridium* Staplin Jansonius & Pocock 1965.

Type species: *Comasphaeridium cometes* (Valensi) Staplin Jansonius & Pocock 1965.

Generic description: Staplin, Jansonius & Pocock 1965, p.192.

Remarks: This genus is distinguished by the high density of solid processes on the central body.

Comasphaeridium denseprocessum Cramer & Diez 1977.

Plate 15, fig.11.

Description: Cramer & Diez 1977a, p.346, pl.2, figs.10 & 11.

Holotype: Cramer & Diez 1977a, pl.2, fig.11. Age: Early Arenig.

Remarks: The processes of this form are less in number and are broader than those of *C. pratulum* Cramer & Diez 1977 and *C. tonsum* Cramer & Diez 1977.

Comasphaeridium cf. *denseprocessum* Cramer & Diez 1977.

Plate 31, figs.10 & 11.

Holotype: Cramer & Diez 1977, pl.2, fig.11. Age: Early Arenig.

Remarks: Compare with Cramer & Diez 1977, p.346, pl.2, figs.10 & 11. Processes are thinner and more numerous in the specimens observed here than in the type material of *C. denseprocessum*. *Comasphaeridium pratulum* Cramer & Diez 1977 has thinner and more numerous processes than *C.* cf. *denseprocessum*.

Comasphaeridium hirtum Le Herisse 1989.

Plate 58, figs.8 & 9.

Description: Le Herisse 1989, p.89, pl.6, figs.8-10.

Holotype: Le Herisse 1989, pl.6, fig.10. Age: Aeronian, Llandovery.

Remarks: *Comasphaeridium caesariatum* Wicander 1974, described from the Upper Devonian of Ohio, USA has longer processes than *L. hirtum*. *Filisphaeridium brevispinosum* Lister 1970 is a comparable species in terms of the morphology of the processes and the central body. It differs in the number and density of processes present, processes being fewer and more sparsely distributed.

Genus *Coryphidium* Vavrdova 1972.

Type species: *Coryphidium bohemicum* Vavrdova 1972.

Generic description: Vavrdova 1972.

Coryphidium almohadillum? Cramer & Diez 1976.

Plate 15, fig.7.

Description: Cramer & Diez 1976b, p.204, pl.23, figs. 8 & 11.

Holotype: Cramer & Diez 1976b, pl.23, fig.8. Age: Late Arenig.

Remarks: This striate form has short accuminate spines. Preservation is rather poor and there is some question as to the primary form of the spines.

Cramer & Diez 1976b illustrated and compared the 9 species of *Coryphidium* published to that date. Similar species with surface striations are *C. elegans* Cramer *et al.* 1974, *C. miladum* Cramer & Diez 1976 and *C. bohemicum* Vavrdova 1972. *Coryphidium elegans* differs by having longer processes, *C. miladum* has processes with wide bases and capitate tips and *C. bohemicum* has short, stout, branching processes.

Coryphidium elegans Cramer *et al.* 1974.

Plate 31, figs.4 & 5.

Description: Cramer *et al.* 1974, p.184, pl.27, figs 12-19.

Holotype: Cramer *et al.* 1974, pl.27, fig.16. Age: Late Arenig-Early Llanvirn.

Remarks: Similar species with surface striations are *C. almohadilla* Cramer & Diez 1976, *C. miladum* Cramer & Diez 1976 and *C. bohemicum* Vavrdova 1972. The former two species have shorter more stout processes and the latter has processes with wide bases and capitate tips.

Coryphidium ramiferum? Cramer & Diez 1976.

Plate 15, fig.8.

Description: Cramer & Diez 1976, p.206, pl.23, figs.16 & 24.

Holotype: Cramer & Diez 1976, pl.23, fig.16. Age: Early Arenig.

Remarks: The poorly preserved specimens recorded here are questionably assigned to this species.

Coryphidium cf. *tadlum* Cramer & Diez 1976.

Plate 15, figs.1-6.

Holotype: Cramer & Diez 1976b, pl.23, fig.4. Age: Late Arenig.

Remarks: Compare with Cramer & Diez 1976b, p.206, pl.23, figs.3, 4, 15, 18 & 19. Specimens observed here differ slightly from *C. tadlum* in the nature of the process terminations. Process tips here tend to be accuminate rather than club-like as in the type material. *Coryphidium elegans* has a similar body shape and process shape but has striations on the central body.

Genus *Crassiangulina* Jardine *et al.* 1972.

Type species: *Crassiangulina tesselita* Jardine *et al.* 1972.

Generic description: Jardine *et al.* 1972, p.295.

Remarks: The genus *Crassiangulina* is, to date, monospecific, the single species, *C. tesselita*, having a rather broad range of morphology.

Crassiangulina tesselita Jardine *et al.* 1972.

Plate 180, fig.9; pl.187, figs.1 & 2; pl.191, fig.1.

Description: Jardine *et al.* 1972, p.295-296, pl.1, figs.1 & 2.

Holotype: Jardine *et al.* 1972, pl.1, figs.1. Age: Late Devonian.

Remarks: This species has a simple but distinctive morphology. It has a polygonal vesicle with between three and upto as many as eight 'reinforced' angles. The angles are reinforced by thickenings of the vesicle wall.

Genus *Craterisphaeridium* Deunff 1981.

Type species: *Craterisphaeridium sprucegrovense* (Staplin) emend. Turner 1986.

Generic description: Deunff 1981, p.67.

Remarks: *Craterisphaeridium inuncans* Deunff 1981 was stated as the type species for the genus by Deunff (1981). However, this species is considered to be a junior synonym of *C. sprucegrovense* which is now the correct name for the type.

Species assigned to this genus are acanthomorphic forms with branched processes. These forms have craters present in the wall of the central body forming a foveolate ornamentation. A very similar genus morphologically is *Hapsidiopalla* Playford 1977 emend. Wicander & Wood 1981 which differs in possessing a reticulate, as opposed to a foveolate, ornamentation on the vesicle wall.

Craterisphaeridium sprucegrovense (Staplin) emend. Turner 1986.

Plate 153, figs.4-7; pl.163, figs.7, 8 & 9; pl.164, fig.1; pl.172, figs.7-10; pl.187, figs.4 & 5; pl.191, figs.2-5

Description: Turner 1986, p.602-606.

Holotype: Staplin 1961, pl.49, fig.6. Age: Late Devonian.

Remarks: The descrete pitting of the vesicle wall is only apparent under high magnification when observed using light microscopy. This species is closely similar to some species of *Hapsidiopalla*, e.g.

H. chela Wicander & Wood 1981 and *H. invenusta* Wicander & Wood 1981 but differs in the presence of a foveolate rather than reticulate vesicle wall.

Genus *Crystallinium* Vanguestaine 1978 *ex* Fensome *et al.* 1990.

Type species: *Crystallinium ovillense* (Cramer & Diez) Fensome *et al.* 1990.

Generic description: Vanguestaine 1978, p.270.

Remarks: Fensome *et al.* (1990) validated the genus by designating a validly published species as the type. By designating the invalid species *Dictyotidium cambriense* as the type species of the genus *Crystallinium*, Vanguestaine had not fulfilled this obligation.

Crystallinium ovillense (Cramer & Diez) Fensome *et al.* 1990.

Plate 3, figs.4, 5 & 6.

Description: Cramer & Diez 1972a, p.44, pl.2, figs.4, 7 & 10.

Holotype: Cramer & Diez 1972a, pl.2, fig.4. Age: Middle Cambrian.

Genus *Cymatiogalea* Deunff 1961 emend. Deunff 1964.

Type species: *Cymatiogalea margaritata* Deunff 1961.

Generic description: Deunff 1961a, p.41-42; Deunff 1964a, p.121.

Remarks: The interpretation of this genus by Molyneux & Rushton (1988, p.56-57) is accepted here.

Cymatiogalea deunffii Jardine *et al.* 1974.

plate 3, figs.7-10; pl.16, fig.4?

Description: Jardine *et al.* 1974, p.123, pl.1, figs.7 & 8; for an English translation see Eisenack, Cramer & Diez 1979, p.97.

Holotype: Jardine *et al.* 1974, pl.1, fig.7. Age: Arenig.

Cymatiogalea cf. *deunffii* Jardine *et al.* 1974.

plate 3, fig.11.

Remarks: Compare with Jardine *et al.* 1974, p.123, pl.1, figs.7 & 8. Specimens included here have grana and echinae ornamenting the membranous outer wall layer.

The specimens observed differ from *C. deunffii* in having minor sculptural elements developed on the outer wall layer.

Cymatiogalea cf. *margaritata* Deunff 1961.

Plate 4, figs.1 & 2.

Holotype: Deunff 1961a, p.42, pl.1, fig.1. Age: Tremadoc.

Remarks: Compared with Deunff 1961a, p.42, pl.1, fig.1. The specimens observed here have slightly thinner and slightly longer processes than the holotype.

Cymatiogalea bellicosa Deunff 1961 has thicker, more sturdy processes which are fewer in number than in *C.* cf. *margaritata.*

Cymatiogalea messaoudii Jardine *et al.* 1974.

Description: Jardine *et al.* 1974, p.123, pl.2, figs.5 & 6; for an English translation see Eisenack, Cramer & Diez 1979, p.105.

Holotype: Jardine *et al.* 1974, pl.2, fig.5. Age: Tremadoc.

Remarks: Within this species, two morphological varieties have been recognised:

Cymatiogalea messaoudii var. A.

Plate 4, figs.3 & 4; pl.15, figs.12 & 13.

Remarks: Included here are atypical forms with very elaborate and densely packed processes with fenestrate terminations.

Cymatiogalea messaoudii var. B.

Plate 4, figs.5-8.

Remarks: Included here are forms closely resembling the holotype of the species with fewer and relatively simple processes compared to var. A.

Cymatiogalea multarea (Deunff) Eisenack, Cramer & Diez 1973.

Plate 16, fig.1.

Description: Deunff 1961a, p.41, pl.1, fig.5; for an English translation see Eisenack, Cramer & Diez 1973, p.229.

Holotype: Deunff 1961a, pl.1, fig.5. Age: Tremadoc.

Cymatiogalea velifera (Downie) Martin 1969.

Plate 16, figs.2 & 3.

Description: Downie 1958, p.340, pl.17, fig.2; Martin 1969 p.133.

Holotype: Downie 1958, pl.17, fig.2. Age: Tremadoc.

Remarks: Only seven specimens are recorded here, all are poorly preserved. However, they do appear to have the characteristic bifurcating and trifurcating process tips and the vela between processes that are characteristic of this species.

Cymatiogalea sp. 1.

plate 4, figs.9-13.

Synonomy: 1988, *Cymatiogalea messaoudii*, Molyneux & Rushton, pl.5, fig.c.
1989, *Cymatiogalea messaoudii*, Mette, pl.3, figs.13-16.

Description: Polygonal acritarchs with a complex double wall layered structure. The inner body is subspherical in shape, relatively thick walled and smooth. It has a maximum diameter of 28-35um. The outer wall layer is relatively thin and is 'pinched up' into elaborately ornamented linear crests. The crests are 7-10um in height and have short furcating processes at their apices, these being an additional 2-7um in height. The crests are arranged into polygons dividing the vesicle into fields. The intracrest areas are smooth. The vesicle opens by means of a pylome.

Remarks: This species shows minor variation in the height of the crests and the processes ornamenting the crests. The variation is considered insufficient to justify the proposal of any varieties within this species.

Comparable species include *C. messaoudii* and *C. gorkae* Raucher 1974. The former has a similar structure to the outer wall layer but the field boundaries are defined by prominent processes composed of the outer wall with low crests draped between them. In contrast, *Cymatiogalea* sp. 1 has fields defined by crests with minor processes ornamenting the crest apices. *Cymatiogalea gorkae* appears to have delicate processes ornamenting the field boundaries as in *Cymatiogalea* sp. 1 but differs in that the processes support an outer membranous network.

Cymatiogalea? sp.

Plate 16, figs.5-8.

Remarks: Five specimens of this taxon have been recorded from sample DW 294. Specimens are small (less than 35um in central body diameter), possess the characteristic pylome of *Cymatiogalea* species and have slender processes with branched terminations. The processes are approximately 10um long, 1um wide and branch distally upto the second order.

Ornamentation of the central body is not apparent on the dark specimens recorded, hence their questioned assignment to the genus *Cymatiogalea*. Lighter coloured specimens may reveal a *Stelliferidium* type ornamentation. Unfortunately no material for further oxidation of sample DW 294 remains.

Genus *Cymbosphaeridium* Lister 1970.

Type species: *Cymbosphaeridium bikidium* Lister 1970.

Generic description: Lister 1970, p.63.

Remarks: This genus includes acanthomorphic acritarch species with two wall layers. The wall layers are closely appressed on the central body, giving it a relatively dark coloration. The outer layer forms the hollow tubiform processes which are relatively light in colour. The process terminations are denticulate. A common feature is the presence of a pylome, the operculum of which possesses a single or several process.

Cymbosphaeridium bikidium Lister 1970.

Plate 81, figs.8-12.

Description: Lister 1970, p.64-65, pl.6, figs.1-9, text-figs.18a-c, f, k, 21.

Holotype: Lister 1970, pl.6, fig.1. Age: Ludlow.

Remarks: The central body of this species is smooth. *Cymbosphaeridium pilar* var. *pilar* Cramer 1964 has a coarsely granular body with the grana adjacent to each other. *Cymbosphaeridium pilar* var. *scabratum* Cramer 1970 also has a granular body, the grana being more widely spaced in this variety of the species. *Cymbosphaeridium pilar* var. 1 (herein) has a faintly granular body and is larger in size than *Cymbosphaeridium bikidium.*

Cymbosphaeridium cariniosum (Cramer) Jardine *et al.* 1972.

Plate 82, figs.1-5.

Description: Cramer 1964, p.284, pl.1, fig.13, text-fig.14, nos.7 & 8.

Holotype: Cramer 1964, pl.1, fig.13. Age: Ludlow.

Remarks: This species is included in the genus *Cymbosphaeridium* here on the basis of its wall structure, the species having a double wall layer, the outer layer forming the processes, and also because it possesses a pylome. The species is distinct from other species in the genus in possessing a greater number of processes. The processes are also much shorter than in the other *Cymbosphaeridium* species.

Cymbosphaeridium pilar Cramer 1964.

Description: Cramer 1964, p.286, pl.1, figs.1 & 2, text-fig.14, no.1.

Holotype: Cramer 1964, pl.1, fig.1. Age: Ludlow.

Remarks: *Cymbosphaeridium gueltaense* Jardine *et al.* 1974 is described as being almost identical to *C. pilar*, differing only in lacking a pylome, a diagnostic characteristic of *C. pilar*. Jardine *et al.* (1974) had probably observed unexcysted specimens of *C. pilar* which they described as *C. gueltaense*. *Cymbosphaeridium gueltaense* is probably therefore a junior synonym of *C. pilar*.

Two published varieties of *C. pilar* have been recorded in the present study.

Cymbosphaeridium pilar var. *pilar* Cramer 1964.

Plate 114, fig.2; pl.120, figs.5, 6 & 7; pl.121, figs.1-4; pl.128. fig.3?, 4 & 5; pl.137, figs.2-5 & 7; pl.149, fig.2.

Description: Cramer 1964, p.286, pl.1, figs.1 & 2, text-fig.14, no.1.

Holotype: Cramer 1964, pl.1, fig.1. Age: Ludlow.

Remarks: This variety of *C. pilar* is distinguished by the presence of coarse, closely spaced or adjacent grana on the central vesicle. *Cymbosphaeridium pilar* var. *scabratum* has more widely spaced grana. *Cymbosphaeridium bikidium* has a smooth central body.

Cymbosphaeridium pilar var. *scabratum* Cramer 1970.

Plate 82, fig.6; pl.104, figs. 6? & 7?; pl.128, fig.2?

Description: Cramer 1970, p.167, pl.18, fig.252-255, text-fig.52f.

Holotype: Cramer 1970, pl.18, fig.252. Age: Silurian.

Remarks: This variety of *C. pilar* is distinguished by the presence of widely spaced grana on the central body. *Cymbosphaeridium pilar* var. *pilar* has closely spaced, coarse grana. *Cymbosphaeridium bikidium* has a smooth central body.

Cymbosphaeridium pilar var. 1.

Plate 82, figs.7 & 8.

Remarks: This variety of *Cymbosphaeridium pilar* is distinguished by its large size, central body less than 45um in diameter, and the faintly granular body wall. *Cymbosphaeridium* cf. *ravum* is similarly large in size but differs by having a coarsely scabrate central body wall.

Cymbosphaeridium cf. *ravum* (Downie) Dorning 1981.

Plate 59, figs.1, 3 & 5.

Holotype: Downie 1963, pl.91, fig.6. Age: Wenlock.

Remarks: Compare with Downie 1963, p.643, pl.91, fig.6, text-fig.3c. Specimens observed here fall within the upper part of the size range given for the species by Downie. The texture of the wall of the central body appears to be more coarsely scabrate in the specimens observed here than on the holotype. This could be due to the poor preservation of the present material.

Cymbosphaeridium sp. 1.

Plate 104, figs.8-11.

Description: Acanthomorphic acritarchs which have a spherical central body measuring between 34-45um in maximum diameter. There are approximately 40 evenly distributed processes, measuring 8-13um in length and upto 5um wide at the base, which branch distally in a ramusculose manner. The process length to body diameter ratio is approximately 1:4. The wall is composed of two layers that are closely appressed over the central body which gives the central body a relatively dark coloration. The processes are composed of the outer wall layer only and are consequently relatively light in colour. The central body wall is thick (> 1um) and has a granulate ornamentation. The processes are smooth. Opening of the vesicle is by a pylome.

Remarks: Specimens included here have the same wall structure, the same number and distribution of processes and are of similar dimensions to *C. cariniosum*. However, the processes shafts are thicker and the process terminations branch in a more complex manner in the specimens included here. Dispite the poor preservation, surface ornament is apparent on some specimens which appears to be granulate.

Genus *Dactylofusa* Brito & Santos 1965b emend. Cramer 1970.

Type species: *Dactylofusa maranhensis* Brito & Santos 1965b.

Generic description: Brito & Santos 1965b, p.12 & 20; Cramer 1970, p.79 & 80.

Remarks: *Eupoikilofusa* Cramer 1970 is considered to be a junior synonym of *Dactylofusa*, for arguments see Fensome *et al.* 1990, p.179, 213 & 214.

Dactylofusa ctenista (Loeblich & Tappan) Fensome *et al.* 1990.

Plate 41, figs.5 & 6.

Synonomy: 1988, *Eupoikilofusa striata*, Elaouad-Debbaj, pl.2, figs.1-6.

Description: Loeblich & Tappan 1978, p.1263, pl.8, figs. 8-9.

Holotype: Loeblich & Tappan 1978, pl.8, figs.8-9. Age: Ashgill.

Remarks: Specimens recorded here are slightly smaller (132-171um in length) than in the type material (170-193um). The species is distinguished by the slender fusiform vesicle with accuminate poles and the longitudinal ribs that are restricted to the central region of the vesicle. Comparable species include *D. anolata* (Loeblich & Tappan) Fensome *et al.* 1990, which has a more dense ornamentation, *D. platynetrella* (Loeblich & Tappan) Fensome *et al.* 1990 which has a broader central vesicle, *D. squama* (Deunff) Fensome *et al.* 1990 which has very feint longitudinal ridges and *D. striata* (Staplin, Jansonius & Pocock) Fensome *et al.* 1990 which has a more squat vesicle shape with less pointed poles.

Dactylofusa striatifera (Cramer) Fensome *et al.* 1990.

Plate 121, fig 5?

Description: Cramer 1964, p.35-36, pl.2, figs.9 & 13.

Holotype: Cramer 1964, pl.2, fig.9. Age: Early Gedinnian.

Remarks: Poorly preserved specimens of *D. striatifera* are included here.

Dactylofusa striatifera var. *striatifera* (Cramer) Fensome *et al.* 1990.

Plate 85, figs.9, 10 & 11; pl.128, figs.8 & 9.

Description: Cramer 1964, p.35-36, pl.2, figs.9 & 13.

Holotype: Cramer 1964, pl.2, fig.9. Age: Early Gedinnian.

Remarks: *Dactylofusa striatifera* var. *stericula* (Cramer & Diez) Fensome *et al.* 1990 differs from *D. striatifera* var. *striatifera* in having a broader fusiform vesicle with a greater number of longitudinal striations.

Genus *Daillydium* Stockmans & Williere 1969.

Type species: *Daillydium pentaster* (Staplin) Playford *in* Playford & Dring 1981.

Generic description: Stockmans & Williere 1969, p.33.

Remarks: The type species for the genus designated by Stockmans & Williere (1969), *D. quadradactylites*, is considered to be a junior synonym of *D. pentaster* (according to Playford *in* Playford & Dring 1981). For this reason, *D. pentaster* is now the correct name for the type species of *Daillydium*. However, the nomenclatural type of the genus remains the holotype of *D. quadradactylites*.

Daillydium pentaster (Staplin) Playford *in* Playford & Dring 1981.

Plate 173, figs.2 & 3; pl.180, figs.10 & 13; pl.191, fig.6.

Description: Staplin 1961, p.416, pl.49, fig.18.

Holotype: Staplin 1961, pl.49, fig.18. Age: Late Devonian.

Remarks: As mentioned above, *D. quadradactylites* is considered to be a junior synonym of *D. pentaster*. The only other species of *Daillydium* published to-date, *D. foveolatum* Deunff 1981, differs in possessing an ornament foveolae on the wall of the inner body.

Genus *Daisypilula* Loeblich & Wicander 1976.

Type species: *Daisypilula compacta* Loeblich & Wicander 1976.

Generic description: Loeblich & Wicander 1976, p.26.

Remarks: This genus is distinguished by the presence of a subspherical central body with a cover of matted solid processes of varying length. A similar genus is *Carminella* Cramer 1968 which differs in possessing a cylindrical outer membrane which encloses the processes.

Daisypilula compacta Loeblich & Wicander 1976.

Plate 137, fig.11.

Description: Loeblich & Wicander 1976, p.10, pl.3, fig.1.

Holotype: Loeblich & Wicander 1976, pl.3, fig.1. Age: Late Gedinnian.

Remarks: The only other species described in the genus *Daisypilula* to-date, *D. storea* Wicander & Loeblich 1977, differs in having a much smaller vesicle diameter and mat width and having a much thinner vesicle wall.

Genus *Dateriocradus* Tappan & Loeblich 1971.

Type species: *Dateriocradus monterossae* (Cramer) Pothe de Baldis 1981.

Generic description: Tappan & Loeblich 1971, p.394.

Remarks: *Dateriocradus polydactylus* Tappan & Loeblich 1971 was initially stated as the type species for the genus. However, this species is considered to be a junior synonym of *D. monterossae* (see Eisenack, Cramer & Diez 1976, p.185). Thus, *D. monterossae* is the correct name for the type species of *Dateriocradus* but the nomenclatural type of the genus remains the holotype of *D. polydactylus*, i.e. Tappan & Loeblich 1971, pl.5, fig.1.

The genus *Dateriocradus* includes species with a three sided, slightly inflated central body with processes at the apices. The processes branch distally to a minimum of the second order and commonly in a ramusculose fashion. The genus *Frankea* has a similar shape to the central body and the same distribution of processes but differs in that the processes branch in a palmate manner. *Oppilatala* differs by having a rounded-subrounded central body.

Dateriocradus lindus (Cramer & Diez) comb. nov.

Plate 128, figs.7, 10 & 11.

Synonomy: 1976, *Multiplicisphaeridium lindum*, Cramer & Diez, p.85, pl.1, figs.4, 6 & 8, not 1-3, pl.2, fig.11.

Description: Cramer & Diez 1976, p.85, pl.1, figs.4, 6 & 8, not 1-3, pl.2, fig.11.

Holotype: Cramer & Diez 1976, pl.1, fig.6. Age: Emsian.

Remarks: The illustrations of the type specimens given by Cramer & Diez (1976) shows two morphotypes within their taxon. The holotype and three of the additional specimens illustrated (pl.1, figs. 4, 6 & 8, pl.2, fig.11) have a three-sided vesicle with three processes present positioned at the apices of the vesicle. A fourth process may be present. The distal terminations of the processes are ramusculose. The other group (pl.1, figs.1-3) have a subspherical central body with more numerous processes. The former group of morphotypes, which include the holotype, are better accommodated in the genus *Dateriocradus* than *Multiplicisphaeridium* due to the morphology of the vesicle and the distribution of processes.

Dateriocradus monterossae (Cramer) Pothe de Baldis 1981.

Plate 72, figs.6 & 7.

Description: Cramer 1969, p.490, pl.70, figs.5-7, text-fig.10f.

Holotype: Cramer 1969, pl.70, fig.5. Age: Late Llandovery.

Remarks: *Dateriocradus polydactylus* Tappan & Loeblich 1971 is considered to be a junior synonym of *D. monterossae* (Eisenack Cramer & Diez 1976, p.185). Morphologically similar species in terms of wall structure and process form are *Oppilatala eoplanktonica* (Eisenack) Dorning 1981 and *O.*

ramusculosa (Deflandre) Dorning 1981. They both differ from *D. monterossae* in the distribution of processes. Processes are positioned at the apices of the subtriangular central body in *D. monterossae* in contrast with the more random distribution of processes in the *Oppilatala* species. A useful pictorial comparison of *D. monterossae* and some morphologically similar species is given by Cramer 1970, p.125, text-fig.39. *Dateriocradus tenuatum* (Burmann) has more polygonal central body than *D. monterossae.*

Dateriocradus tenuatum (Burmann) Comb. nov.

Plate 32, fig.1.

Synonomy: 1970, *Vogtlandia tenuatum,* Burmann p.293, pl.3, fig.3; pl.4, fig.2.1976, *Multiplicisphaeridium tenuatum,* Eisenack, Cramer & Diez, p.485-486.

Description: Burmann 1970, p.293, pl.3, fig.3; pl.4, fig.2; for an English translation see Eisenack, Cramer & Diez 1976, p.285-286.

Holotype: Burmann 1970, pl.3, fig.3. Age: Late Arenig- Early Llanvirn.

Remarks: This species is transferred to the Genus *Dateriocradus* as it possesses a three sided central body and has processes positioned at the apices of the body which branch distally in a ramusculose manner.

This species is similar in body shape and process distribution to species of *Frankea.* However, species of *Frankea* differs by having palmate pinnae at the process terminations, *Dateriocradus monterossae* has deeper furcation of the distal part of the processes.

Genus *Deflandrastrum* Combaz 1962.

Type species: *Deflandrastrum millepiedi* Combaz 1962.

Generic description: Combaz 1962, p.1977.

Remarks: The species included here are forms composed of four cells that are positioned about a circular or quadrate central lumen. Each elongated triangular cell is joined to two adjacent cells at the basal apices. This acritarch genus is comparable with the chlorophyte genus *Pediastrum,* however it differs in the number and arrangement of cells.

Deflandrastrum millepiedi? Combaz 1962.

Plate 82, fig.9.

Description: Combaz 1962, p.1977-1978, fig.1.

Holotype: Combaz 1962, fig.1. Age: Silurian.

Remarks: The single specimen recorded is poorly preserved. The radial spines are damaged, hence the questioned assignation to the species.

Deflandrastrum authierae Combaz 1962 has a more elongate form to the triangular cells than *D. millepiedi*. *Deflandrastrum speciosum* Deflandre 1967 has a much larger central lumen than the other species in the genus.

Genus *Demorhethium* Loeblich & Wicander 1974.

Type species: *Demorhethium lappaceum* Loeblich & Wicander 1974.

Generic description: Loeblich & Wicander 1974, p.708.

Remarks: This genus is quite distinct from any other by way of the short, distally open processes with denticulate terminations. *Demorhethium* is, at present, a monospecific genus.

Demorhethium cf. *lappaceum* Loeblich & Wicander 1974.

Plate 137, figs.6, 8 & 11.

Holotype: Loeblich & Wicander 1974, fig.2. Age: Late Gedinnian.

Remarks: Compare with Loeblich & Wicander 1974, p.708-711, figs.1-6. Specimens recorded here are closely similar to the illustrations of the type material given by Loeblich & Wicander 1974. However, there are more than the stipulated number of processes for the species present on the specimens here. Processes number eight or more here compared to five to seven processes on the type specimens. In addition, the ornament of baculae is less prominent on the present specimens.

Genus *Dicrodiacrodium* Burmann 1968.

Type species: *Dicrodiacrodium ancoriforme* Burmann 1968

Generic description: Burmann 1968, p.643; for English translation see Eisenack Cramer & Diez 1979, p.203.

Remarks: The genus *Arbusculidium* is comparable to *Dicrodiacrodium*. Both genera include species with filamentous processes at one pole of the elongated vesicle. However, the opposite pole to that possessing the filamentous elements in *Dicrodiacrodium* species possesses a single process with a furcate distal termination in contrast with the several simple processes at the opposite pole in *Arbusculidium* species.

Dicrodiacrodium ancoriforme var. *minutum* Burmann 1968.

Plate 16, figs.11 & 12; pl.32, fig.2.

Description: Burmann 1968, p.644, pl.5, fig.5; for an English translation see Eisenack Cramer & Diez 1979, p.207.

Holotype: Burmann 1968, pl.5, fig.5. Age: Late Llanvirn.

Remarks: This form is distinguished by the relatively broad, ribbed central body, the single 'apical' process, the flattened 'antapex' with the fine anastomosing mesh and its relatively small size. The 'apical' process is broken in all the specimens observed.

Of the five species of *Dicrodiacrodium* published to date, two have a single 'apical' process, namely *D. ancoriforme* and *D. normale* Burmann 1968. From the original descriptions and illustrations of these two species, they would appear to be synonymous.

Genus *Dictyotidium* Eisenack 1955 emend. Staplin 1961.

Type species: *Dictyotidium dictyotum* (Eisenack) Eisenack 1955.

Generic description: Eisenack 1955, p.179; Staplin 1961, p.417.

Remarks: The prasinophyte genus *Cymatiosphaera* Wetzel 1933 *ex* Deflandre 1954 differs from *Dictyotidium* in possessing membranous outgrowths from the vesicle that divide it into polygonal fields. In *Dictyotidium* the field dividers are non-membranous ridges. *Alveosphaera* Kiryanov 1978 differs from *Dictyotidium* by having a very thick, double wall layered vesicle with very small polygonal fields.

Dictyotidium cf. *arctum* Kiryanov 1978.

Plate 59, fig.6.

Holotype: Kiryanov 1978, pl.4, fig.7. Age: Late Llandovery.

Remarks: Compare with Kiryanov 1978, p.39, pl.4, figs.6, 7 & 9. Specimens assigned here differ from the type material of this species in size only. The specimens observed are 39-40um in diameter, the type material ranges between 18-30um in diameter. *Dictyotidium dictyotum* differs in having a diameter of 60-100um. *Dictyotidium stenodictyum* Eisenack 1965 is also larger in size and has a greater number of small fields on the vesicle.

Dictyotidium coarctatum (Kiryanov) Colbath 1983.

Plate 60, fig.4; pl.72, figs.4 & 5; pl.82, figs.10 & 11; pl.105, figs.1, 2 & 3; pl.137, fig.10.

Description: Kiryanov 1978, p.24-25, pl.7, figs. 1 & 4; emend. Colbath 1983, p.257-258.

Holotype: Kiryanov 1978, pl.7, figs.4. Age: Late Silurian.

Remarks: Colbath's emended description of the species broadened the size dimensions from 58-64um (Kiryanov 1978, p.24) to 25-70um (Colbath 1983, p.257). A broad range of specimens in terms of size has consequently been accommodated in this species. The fields on the vesicle in the species *D. arctum*, *D. dictyotum* and *D. stenodictyum* Eisenack 1965 are broader than on *D. coarctatum*.

Dictyotidium dictyotum (Eisenack) Eisenack 1955.

Plate 59, figs.2 & 4; pl.83, figs.2 & 4; pl.105, figs.4 & 6; pl.114, fig.3; pl.138, fig.2?

Description: Eisenack 1938, p.27-28, pl.3, figs.8a-c.

Holotype: Eisenack 1938, pl.3, fig.8a (lost according to Kiryanov [1978, p.40-41] and Eisenack, Cramer & Diez [1979, p.162]). Age: Silurian.

Remarks: Specimens assigned accord well with the description and illustration of the type material.

Dictyotidium stenodictyum Eisenack 1965

Plate 60, figs.3 & 6; pl.72, fig.8; pl.121, fig.8.

Description: Eisenack 1965, p.264, pl.22, figs.2-3.

Holotype: Eisenack 1965, pl.22, fig.2. Age: Llandovery.

Remarks: The fields on the vesicle of *D. stenodictyum* are smaller than on *D. dictyota* and *D. arctum*. The greater numbers of ridges dividing the fields gives the vesicle a rigid structure. There are thickenings of the wall at the triple junctions of the ridges.

Dictyotidium sp. 1.

Plate 60, figs. 1, 5 & 7.

Description: A species of *Dictyotidium* with a thick vesicle wall. The vesicle measures 55-80um in maximum diameter and the wall is 4-9um wide. The vesicle surface is reticulate with the vesicle surface divided into many hundreds of polygonal fields. The fields measure between 2-5um across. The ridges dividing the fields are less than 1m high and less than 1m wide. The thick vesicle wall makes for a rigid structure, however, broad thick fold are present. No regular form of opening is apparent.

Remarks: This species has similarly small fields on the vesicle to *D. coarctatum* but can be distinguished by the thick vesicle wall. *Alveosphaera locellata* Kiryanov 1978 has a similarly thick vesicle wall and a similar vesicle diameter to *Dictyotidium* sp. 1 but differs in possessing broader, more rigid muri dividing more regular polygonal fields on the vesicle.

Dictyotidium sp. 2.

Plate 60, fig.2; pl.83, figs.1 & 3; pl.105, fig.8; pl.114, fig.5; pl.138, fig.1.

Description: A species of *Dictyotidium* with a thick vesicle wall. The vesicle measures 100-160um in maximum diameter and the wall is approximately 1um thick. The vesicle surface is reticulate with the vesicle surface divided into polygonal fields. The fields measure between 8-18um across. The ridges dividing the fields are less than 2um high and less than 2um wide. The wall may be markedly thickened at the triple junctions of the ridges. No regular form of opening is apparent.

Remarks: This taxon differs from *D. dictyotum* in the diameter of the vesicle. Specimens included here are between 100-160um in maximum diameter which is greater than the sizes given in the diagnosis of *D. dictyotum* (60-100um) by Eisenack. Gonal thickenings of the vesicle wall are another notable feature of *Dictytidium* sp. 2.

Genus *Diexallophasis* Loeblich 1970.

Type species: *Diexallophasis denticulata* (Stockmans & Williere) Loeblich 1970.

Generic description: Loeblich 1970, 1970a, p.714.

Remarks: The contention that the type species, *D. denticulata*, is a junior synonym of *D. remotum* (Deunff) Playford 1977, (Playford 1977, p.19; upheld by Fensome *et al.* 1990, p.197-198) is rejected here as the polygonal shape of the central body of the latter is distinguishable from the more rounded central body of the former.

This group of acritarchs represents a good example of a morphological continuum of forms. The morphological continuity, in process length and branching, sphericity of the central body and the degree of ornamentation has resulted in a complex of species and subspecies, of essentially the same morphotype being published. In the interest of practicability, the present author considers there to be two dominant species in the genus *Diexallophasis*; *D. denticulata* in which the central body is rounded to subrounded and *D. remota* in which the central body is polygonal. Variations within these species are considered to be at the subspecies or variety rank.

The genus *Evittia* includes very similar morphotypes in terms of general outline, process shape and ornamentation, but differs by including forms with flattened veryhachid type bodies rather than the central body being inflated. This differentiation is rather unsatisfactory as compression can be very misleading. Species of *Evittia* are very similar in form to the species *Diexallophasis remota*.

The genus *Estiastra* includes species in which the processes are cone shaped, the processes merging proximally, as in the genus *Goniosphaeridium*. Adjacent processes merge to form sharp angles between each other and no distinct central body apparent.

Diexallophasis denticulata (Stockmans & Williere) Loeblich 1970.

Plate 61, figs.4-7; pl.72, fig.9; pl.83, fig.5; pl.84, fig.1; pl.105, figs.5, 7 & 9; pl.121, figs.9 & 10; pl.129, figs.1 & 2; pl.138, figs.3 & 5-9; pl.149, figs.7 & 8; pl.153, figs.8 & 10?

Synonomy: 1963, *Veryhachium denticulata*, Stockmans & Williere, p.458, pl.1, fig.4, text-fig.13.
1973, *Multiplicisphaeridium denticulatum*, Eisenack Cramer & Diez, p.587-591.

Description: Stockmans & Williere 1963, p.458, pl.1, fig.4, text-fig.13.

Holotype: Stockmans & Williere 1963, pl.1, fig.4. Age: Silurian.

Remarks: Included here are specimens of *Diexallophasis* with a rounded central body. Specimens not assigned to a variety of this species are either too poorly preserved or of too few numbers to warrant subdivision at the subspecies level.

Diexallophasis denticulata var. *gotlandica* (Cramer) Comb. nov.

Plate 40, figs.11 & 12.

Synonomy: 1970, *Diexallophasis gotlandica*, Cramer, p.138-140, pl.10, fig.151, pl.20, fig.302; text-fig.43b.

Description: Cramer 1970, p.138-140, pl.10, fig.151, pl.20, fig.302; text-fig.43b.

Holotype: Cramer 1970, pl.19, fig.151. Age: Silurian.

Remarks: This variety is characterised by the spherical central body, the relatively simple processes with shallow furcations and a relatively low denticulate ornament.

Diexallophasis denticulata var. *granulatispinosa* (Downie) Comb. nov.

Plate 61, figs.1, 2 & 3.

Synonomy: 1963, *Baltisphaeridium granulatispinosum*, Downie, p.640-641, pl.91, figs.1 & 7, text-fig.3c.
1970, *Evittia granulatispinosa*, Lister, p.67.

1973, *Multiplicisphaeridium granulatispinosum*, Eisenack Cramer & Diez, p.643.

Description: Downie 1963, p.640-641, pl.91, figs.1 & 7, text-fig.3c.

Holotype: Downie 1963, pl.91, figs.1. Age: Wenlock.

Remarks: This new combination is proposed to accommodate a variety of *D. denticulata* specimens that appear to be restricted stratigraphically to the late Llandovery-early Wenlock in the samples studied. The specimens observed are almost identical in morphology to the holotype of this taxon.

Diexallophasis denticulata var. *rigida* (Cramer) Comb. nov.

Plate 83, fig.6.

Synonomy: 1966, *Diexallophasis remota* forma *rigida*, Cramer, p.36-37, pl.3, figs.6-8.

Description: Cramer 1966, p.36-37, pl.3, figs.6-8.

Holotype: Cramer 1966, pl.3, fig.7. Age: Silurian.

Remarks: This variety of *D. denticulata* is distinguished by its large size (upto 150um including the processes) and the long rigid processes.

Diexallophasis denticulata var. A.

Plate 106, figs.1-6; pl.114, figs.6, 7 & 8.

Remarks: Specimens included here have the same broad range of process morphology as *Diexallophasis denticulata* var. *denticulata* (Stockmans & Williere) Loeblich 1970. However, *D. denticulata* var. A has a thicker wall (ca. 2um) and a more descrete echinate ornamentation on the central body and on the processes.

Multiplicisphaeridium amphitrite Deunff, Lefort & Paris 1971, described from the late Ludlow of France, is of very similar morphology to this variety of *Diexallophasis denticulata* and could possibly be synonymous.

Diexallophasis remota (Deunff) Playford 1977.

Plate 84, fig.5; pl.107, figs.3 & 4; pl.122, fig.5; pl.164, figs.2, 5 & 6; pl.173, figs.1 & 5; pl.180, figs.11 & 12.

Description: Deunff 1955, p.146, pl.4, fig.8.

Holotype: Deunff 1955, pl.4, fig.8. Age: Wenlock-Givetian.

Remarks: Included here are specimens of *Diexallophasis* with a polygonal central body. Specimens not assigned to a variety of this species are either too poorly preserved or of too few numbers to warrant subdivision at the subspecies level.

Diexallophasis remota var. *remota* (Deunff) Fensome *et al.* 1990.

Plate 84, figs.3 & 4; pl.107, figs.1 & 2; pl.115, figs.1, 2 & 3; pl.139, figs.2 & 4; pl.149, figs.9 & 10; pl.164, pl.3 & 4

Description: Deunff 1955, p.146, pl.4, fig.8.

Holotype: Deunff 1955, pl.4, fig.8. Age: Wenlock-Givetian.

Remarks: The specimens of *D. remota* var. *remota* recorded here measure upto 110um in total diameter. This variety has four-six processes, four of which are positioned at the apices of the flattened polygonal central body. The processes are echinate and striate and the process terminations are denticulate with shallow (<5um) furcation at the tips.

The specimens observed strongly resemble the holotype. Also comparable are specimens recorded by Deunff (1966) as *Veryhachium remotum* from the Devonian of Tunisia.

Diexallophasis remota var. *rabiosum* (Cramer) comb. nov.

Plate 129, fig.3; pl.139, figs.3 & 6; pl.149, figs.11 & 12; pl.153, fig.9?

Synonomy:

1964, *Veryhachium rabiosum*, Cramer, p.299, pl.5, fig.7; pl.6, figs.3 & 8, pl.7, figs.5, 8 & 9, text-fig.21b.
1967, *Evittia rabiosa*, Brito, p.477
1970, *Baltisphaeridium rabiosum*, Cramer, p.182-183.

1973, *Multiplicisphaeridium rabiosum*, Eisenack, Cramer & Diez, p.747-749.

Description: Cramer 1964, p.299, pl.5, fig.7, pl.6, figs.3 & 8, pl.7, figs.5, 8 & 9, text-fig.21b.

Holotype: Cramer 1964, pl.5, fig.7. Age: Siegenian-Emsian.

Remarks: This form is combined with *D. remota* as it possesses a flattened vesicle and has processes which have a granulate or echinate ornamentation and denticulate distal terminations. This particular variety has a large, quadrate central body and six processes, four of which are positioned at the apices of the vesicle. The processes are rather broad. *Diexallophasis remota* var. *remota* has an identical arrangement of the processes but differs in having thinner, more slender processes. The latter variety is also generally smaller in size.

Diexallophasis remota var. *thyrae* (Cramer) comb. nov.

Plate 173, fig.1; pl.180, 8, 11 & 12?

Synonomy: 1964, *Veryhachium thyrae*, Cramer, p.316-317, pl.12, figs.10 & 13.
1973, *Multiplicisphaeridium thyrea*, Eisenack, Cramer & Diez, p.809-810.
1984, *Exochoderma cleopatra*, Martin, p.55, pl.III, figs.1-6, 8 & 9.

Description: Cramer 1964, p.316-317, pl.12, figs.10 & 13.

Holotype: Cramer 1964, pl.12, figs.10. Age: Ludlow.

Remarks: This form is recombined here with *D. remota* due to the similarity of morphological features such as i. central body shape, ii. process terminations and iii. ornamentation with that species. The species *D. thyrae* is denoted to variety status within *D. remota* due to the broadening of the species *D. remota*, see p.76 and p.79.

Diexallophasis remota var. A.

Plate 115, figs.4, 5 & 6.

Remarks: This large variety of *D. remota*, upto 150um in total diameter, has four to six broad processes with a strongly polygonal central body. The processes are coarsely denticulate at the terminations and branch in the distal half. The wall is thick (> 1um) and sparsely ornamented with echinae.

Diexallophasis cf. *sanpetrensis* (Cramer) Dorning 1981.

Plate 78, figs.7 & 10

Holotype: Cramer 1964, pl.3, fig.16. Age: Ludlow.

Remarks: Compare with Cramer 1964, p.293-294, pl.3, figs.15-16, text-fig.18. This small form of *Diexallophasis*, measuring between 18-38um in diameter across the central body, is recorded here from samples from the *ludensis* (graptolite) Zone, latest Llandovery only. Specimens have a similar process to central body ratio and a similar degree of denticulation to *D. sanpetrensis*. Specimens here are smaller and have a slightly more polygonal aspect than the holotype.

Diexallophasis? sp. 1.

Plate 40, figs.8 & 9.

Remarks: Acanthomorphic acritarchs with a four-sided, slightly inflated central body. From the two poorly preserved specimens recovered, it appears probable that there would have been four short stout processes at the apices of central body (each specimen observed has only two fully preserved). The central body is 41-42um wide. The processes are 14-18um long, approximately 8um wide at the base and 4-5um wide distally. The distal tips have very shallow furcations less than 3um deep. The wall is composed of a single layer and the processes communicate freely with the central body. The body and processes are ornamented with grana and minute echinae.

A morphologically similar species is *Evittia sommeri* Brito 1967 which has deeper furcations in the distal extremities of the processes.

Genus *Duvernaysphaera* Staplin 1961.

Type species: *Duvernaysphaera tenuicingulata* Staplin 1961.

Generic description: Staplin 1961, p.414-415.

Remarks: The author agrees with Cramer & Diez 1972 (p.162) and Playford 1977 (p.21) that *Helios* Cramer 1974 is a junior synonym of *Duvernaysphaera*.

Duvernaysphaera gothica Martin 1967.

Plate 62, figs.1 & 2; pl.85, figs.1 & 2.

Description: Martin 1967, p.323, pl.1, figs.6 & 15.

Holotype: Martin 1967, pl.1, fig.15. Age: Silurian.

Remarks: *Duvernaysphaera aranaides* (Cramer) Cramer & Diez 1972 has a similar discoid vesicle shape, size, and approximately the same number of processes as *D. gothica*. It differs in the position of the processes. *Duvernaysphaera gothica* has a circle of processes radiating from the equator of the discoid central body, whereas the circle of processes of *D. aranaides* radiate from a position between the pole and the equator of the vesicle.

Duvernaysphaera radiata Brito 1967.

Plate 185, figs.4 & 5.

Description: Brito 1967, p.477, pl.1, figs.1 & 2.

Holotype: Brito 1967, pl.1, fig. 2. Age: ?Middle Devonian.

Duvernaysphaera sp.

Plate 78, figs.5 & 6.

Remarks: The two specimens included here have a similar structure to *D. aranaides*. It differs in possessing a greater number of processes, approximately 50, supporting the velum. *Duvernaysphaera aranaides* possesses approximately 10 processes.

Genus *Ephelopalla* Wicander 1974 emend. Martin 1981.

Type species: *Ephelopalla elongata* Wicander 1974.

Generic description: Wicander 1974, p.22, emend. Martin 1981, p.20-21.

Ephelopalla gorkae Martin 1981.

Plate 181, figs.1-6; pl.187, fig.3; pl.191, figs.7, 8 & 9.

Description: Martin 1981, p.22-23, pl.2, figs.1-3 & 5-7.

Holotype: Martin 1981, pl.2, figs.1. Age: Late Devonian.

Remarks: The well preserved specimens recorded in the present study accord well with the description and illustrations of the type material from Belgium.

Genus *Florisphaeridium* Lister 1970.

Type species: *Florisphaeridium castellum* Lister 1970.

Generic description: Lister 1970, p.74.

Remarks: This genus is distinguished from *Multiplicisphaeridium* by having floreate, as opposed to ramusculose, distal terminations of the processes.

Florisphaeridium toyetae (Cramer) Cramer & Diez 1976.

Plate 150, fig.1.

Description: Cramer 1964, p.302, pl.1, figs.14 & 15.

Holotype: Cramer 1964, pl.1, fig.15. Age: Middle Siegenian-Emsian.

Remarks: Specimens recorded here have processes that are shorter than on the holotype. However, specimens assigned to this species by Cramer & Diez in 1976 when they transferred the species to the genus *Florisphaeridium* are almost identical to those observed here.

Florisphaeridium sp.

Plate 129, fig. 4; pl.165, fig.2.

Remarks: The single folded specimen included here has approximately eight processes with floreate distal terminations. The central body is approximately 40um in diameter and processes are upto 13um in length.

Genus *Frankea* Burmann 1970.

Type species: *Frankea hamata* Burmann 1970.

Generic description: Burmann 1970, p.290; for an English translation see Eisenack, Cramer & Diez 1979, p.295.

Frankea sartbernardensis (Martin) Colbath 1986.

Plate 16, fig.13; pl.32, figs.3-6.

Description: Martin 1966b, p.434-435, text-figs.11-13.

Holotype: Martin 1966b, text-figs.12-13. Age: Arenig.

Remarks: The combination *F. sartbernardensis* was not validly published in Burmann 1970 (p.291) as the author did not fully reference the basionym.

Frankea hamata Burmann 1970 is very similar in morphology but differs in having only two pinnae at the distal terminations of the processes, *F. sartbernardensis* may have three or four. *Frankea hamulata* Burmann 1970 has three or more short stub-like pinnae.

Genus *Goniosphaeridium* Eisenack 1969 emend. Turner 1984.

Type species: *Goniosphaeridium polygonale* (Eisenack *ex* Eisenack) Eisenack 1969.

Generic description: Eisenack 1969a, p.256; Turner 1984, p.111-112.

Remarks: As discussed by Turner (1984, p.112), the morphological limits of the genus *Goniosphaeridium* are rather vague. Forms included here are smooth walled and have conical processes whose bases merge to form the poorly defined central body (i.e. the shape of the central body is dictated by the shape of the process bases). Forms included in the genus *Polygonium* have a polygonal, well defined central body with simple processes. Forms included in *Micrhystridium* have a round-ovate central body with simple processes. *Stellichinitum* and *Uncinisphaera* both have an ornament of echinae.

Goniosphaeridium cf. *connectum* Kjellstrom 1971.

Plate 5, figs.1, 2 & 3.

Holotype: Kjellstrom 1971a, pl.3, fig.5. Age: Middle Ordovician.

Remarks: Compare with Kjellstrom 1971a, p.44-45, pl.3, fig.5. Specimens assigned here are smaller (central body diameter 25-40um as opposed to 40-45um) and have more processes (15-20 rather than "about 10") than the material described by Kjellstrom. The illustration of the holotype by Kjellstrom (1971, pl.3, fig.5) is rather feint. The present author has been influenced in to comparing the specimens assigned here to *G. connectum* by the illustration of the species given in Eisenack, Cramer & Diez 1979, p.483.

Goniosphaeridium polygonale subsp. *pellucidum* (Timofeev *ex* Tynni) Fensome *et al.* 1990.

Plate 5, fig.8.

Description: Timofeev 1959b, p.40, pl.3, fig. 37.

Holotype: Timofeev 1959b, pl.3, fig. 37. Age: Early Ordovician.

Remarks: Specimens observed here have folded, rather flexible processes in contrast to the relatively rigid processes of the holotype as illustrated by Timofeev.

Goniosphaeridium polygonale subsp. *polygonale* (Eisenack) Fensome *et al.* 1990.

Plate 17, figs.1-4; pl.32, figs.7 & 8.

Synonomy: 1977, *Veryhachium splendens*, Paris & Deunff, pl.1, fig.4.

Description: Eisenack 1931, p.113, pl.4, figs.16-20; pl.5, fig.18. For further morphological information see Eisenack, Cramer & Diez 1979, p.499.

Holotype: Eisenack 1931, pl.4, fig. 19; lost according to Eisenack (1959a, p.199. Age: Silurian (the type material was taken from an erratic).

Goniosphaeridium polygonale var. A.

Plate 5, fig.9; pl.17, figs.6, 7 & 9.

Remarks: Acanthomorphic acritarchs which have a strongly polygonal central body ranging between 31um and 42um in maximum diameter. The processes have broad bases (upto 7um wide) that taper rapidly in the proximal half of the shaft and taper more gradually distally. Processes are 15-19um in length and have accuminate tips. The process length to central body diameter ratio is approximately 3:5. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth and no regular form of opening is apparent.

Remarks: This form is morphologically most similar to *G. polygonale* subsp. *polygonale*. The size and shape of the central body are almost identical, as is the process to central body size ratio. However, *G. polygonale* var. A has processes that are thinner distally and more numerous. *Goniosphaeridium polygonale* subsp. *pellucidum* has longer processes relative to the central body and the central body is markedly smaller.

Note: *Goniosphaeridium* sp.1 to sp.3 described below can be considered as a complex of *Goniosphaeridium* species which have a similar two-tier, galaeate processes. The three species described show variation in the number and dimensions of the processes.

Goniosphaeridium sp. 1.

Plate 5, fig.4

Description: Acanthomorphic acritarchs which have a strongly polygonal central body. The central body ranges between 20um and 25um in maximum diameter. There are approximately 20 processes that are galaeate in form. They have broad, inflated, bulbous bases (upto 10um wide) that taper rapidly to approximately half way up the shaft. The distal half of the shaft tapers more gradually to commonly truncated or to accuminate tips. Process are 10-14um in total length and the process to central body ratio is approximately 1:2. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth and no regular form of opening is apparent.

Remarks: The species is distinguished from those previously published by the galaeate processes. *Goniosphaeridium* sp. 2 has fewer more conical shaped processes. *Goniosphaeridium* sp. 3 has a greater number of processes and is larger in size.

Goniosphaeridium sp. 2.

Plate 5; fig.5.

Description: Acanthomorphic acritarchs which have a strongly polygonal central body. The central body ranges between 25um and 30um in maximum diameter. There are about 8-15 processes that are galaeate in form. They have broad conical bases (upto 15um wide) that taper rapidly to approximately half way up the shaft. The distal half of the shaft tapers more gradually to commonly truncated or to accuminate tips. Process are upto 18um in total length and the process to central body ratio is approximately 1:2. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth and no regular form of opening is apparent.

Remarks: This species differs from *Goniosphaeridium* sp. 1 by having fewer processes which are more conical as opposed to bulbous at their bases. A morphologically similar published species is *Stellinium octoaster* (Staplin) Jardine *et al.* 1974 which has a similar vesicle form and number of processes. This Late Devonian species, however, has crested processes.

Goniosphaeridium sp. 3.

Plate 5, fig.6.

Description: Acanthomorphic acritarchs having a strongly polygonal central body which ranges between 35um and 40um in maximum diameter. There are approximately 20-30 processes that are galaeate in form. They have broad conical bases (upto 8um wide) that taper rapidly to approximately half way up the shaft. The distal half of the shaft tapers more gradually to truncated or to rare accuminate tips. Process are upto 15um in total length and the process to central body ratio is approximately 2:5. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth and no regular form of opening is apparent.

Remarks: *Goniosphaeridium* sp. 1 is smaller in size and has fewer processes with more bulbous bases than this taxon.

Genus *Gorgonisphaeridium* Staplin, Jansonius & Pocock 1965.

Type species: *Gorgonisphaeridium winslowiae* Staplin, Jansonius & Pocock 1965.

Generic description: Staplin, Jansonius & Pocock 1965.

Remarks: An English translation of the restricted generic description proposed by Kiryanov (1978) is not available to the author. For this reason, the parameters of the genus utilised here are those stated in the original description by Staplin, Jansonius & Pocock (1965).

Of the 43 species of *Gorgonisphaeridium* considered to be valid at the present time (Fensome *et al.* 1990), 26 are described from the Middle to Late Devonian. It is apparent from personal observation of the illustrations of the holotypes of these Mid-Late Devonian species that these relatively simple, thick walled, acantho-morphotypes have been over-split. The thick, generally dark-coloured vesicle wall makes subdivision of these forms on the detail of the wall sculpture somewhat impractical. The group has, therefore, been subdivided into complexes of species in the interests of practicality for future usage of these morphotypes.

Gorgonisphaeridium ohioense Complex.

Plate 181, figs.8, 9 & 10; pl.187, figs.6 & 7; pl.192, figs.1-4

Remarks: Included here are forms with relatively long processes, i.e. with process to central body ratio greater than 6:1, and with simple process terminations. The central body is greater than 30um in maximum diameter.

The species *G. ohioense* (Winslow) Wicander 1974, *G. crinegerum* Deunff 1981, *G. elongatum* Wicander 1974 and *G. solidum* Jardine *et al.* 1974 are included in this complex. Transitional morphotypes, falling morphologically between these formally described species, are common in the material studied. It is for this reason that these forms are difficult to split practically and have, therefore, been grouped.

The *G. winslowiae* complex differs in possessing furcate process terminations.

Gorgonisphaeridium spicatum Complex.

Plate 182, figs.1, 2 & 3; pl.187, fig.10; pl.192, fig.6.

Remarks: Included here are forms with relatively short processes, i.e. the process to central body ratio is less than 6:1. The process termination are simple. The central body measures more than 30um in maximum diameter.

The species included in this complex are *G. spicatum* (Staplin) Staplin *et al.* 1965, *G. absitum* Wicander 1974, *G. disparatum* Playford 1977, *G. evexispinosum* Wicander 1974, *G. granatum* Playford 1977 and *G. pleurispinum* Wicander 1974. Although the descriptions and illustrations of the type specimens of these species suggest that these forms are easily recognisable, practical application of them was found to be very difficult due to the common occurrence of transitional morphotypes. The use of this group of species as the *G. spicatum* complex is thought to be of more practical value for future work.

A comparable species with this complex is *G. seperatum* Wicander 1974 which also has relatively short processes. This form, however, possesses bifid processes. *Gorgonisphaeridium telum* Wicander & Playford 1985 also has simple process terminations but is a much smaller species, measuring between 14-24um in vesicle diameter.

Gorgonisphaeridium telum Wicander & Playford 1985.

Plate 154, figs.1, 2 & 3; pl.165, figs.3 & 4; pl.192, figs.9 & 12.

Description: Wicander & Playford 1985, p.106-108, pl.3, figs.4 & 5.

Holotype: Wicander & Playford 1985, pl.3, figs.4. Age: Frasnian.

Remarks: This species is distinguished by the simple process terminations and the small size of the central vesicle which measures between 14um and 24um.

Gorgonisphaeridium winslowiae Complex.

Plate 192, fig.5.

Remarks: Included here are forms with relatively long processes, i.e. the process to central body ratio is greater than 1:6, with bifurcate and rarely trifurcate process terminations. The central body is greater than 30um in maximum diameter.

Species included here are *G. winslowiae* Staplin *et al.* 1965 and *G. furcillatum* Wicander and Playford 1985. The *G. ohioense* complex differs in possessing simple as opposed to furcate processes.

Gorgonisphaeridium? sp. 2.

Plate 187, figs.8 & 9; pl.191, figs.9, 11 & 12.

Remarks: Included here are acanthomorphic acritarchs with a spherical central body measuring between 25-45um in maximum diameter. The processes are simple and solid and measure upto 15um in length. The process to central body ratio is generally about 1:2. The vesicle wall is coarsely reticulate. No regular form of opening is apparent.

This form may be easily distinguished by the reticulum on the vesicle wall. The inclusion of such strongly reticulate forms in the genus *Gorgonisphaeridium* is questioned.

Gorgonisphaeridium? sp. 3.

Plate 187, figs.11 & 12.

Remarks: This taxon includes acanthomorphic acritarchs with a spherical central body measuring between 35-55um in maximum diameter. The processes are simple and solid and measure upto 20um in length. The process to central body ratio is generally about 1:2. The vesicle wall is vermiculate. No regular form of opening is apparent.

This form can be distinguished by the sinuous ridges or vermiculae ornamenting the vesicle wall. The inclusion of such ornamented forms in the genus *Gorgonisphaeridium* is questioned.

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

Type species: *Hapsidopalla sannemannii* (Deunff) Playford 1977.

Generic description: Playford 1977, pl.25 emend. Wicander & Wood 1981, p.42-43.

Remarks: *Hapsidopalla* is differentiated from the genus *Craterisphaeridium* by the presence of a reticulate, as opposed to a foveolate, ornamentation on the vesicle wall.

Hapsidopalla cf. *sannemanni* (Deunff) Playford 1977.

Plate 107, figs.5, 6, 8 & 9; pl.139, figs.10, 11 & 12.

Holotype: Deunff 1957, pl.13, fig.1. Age: Middle Devonian.

Remarks: Compare with Deunff 1957, p.6, pl.13, fig.1. Specimens recorded here have shorter and more slender processes than the type specimen.

Genus *Heliosphaeridium* Lister 1970.

Type species: *Heliosphaeridium clavispinulosum* Lister 1970.

Generic description: Lister 1970, p.76.

Remarks: The low ornamentation of the wall of these spheromorphs is expanded at the distal part of the element. *Lophosphaeridium* differs in possessing an ornament of solid tubercles. *Buedingisphaeridium* has conical tubercles that communicate freely with the vesicle cavity.

Heliosphaeridium cf. *citrinipeltatum* (Cramer & Diez) Dorning 1981.

Plate 62, figs.3, 4, 7 & 8.

Holotype: Cramer & Diez 1972, pl.35, fig. 58. Age: Early Llandovery.

Remarks: Compare with Cramer & Diez 1972, p.166-167, pl.35, figs.58-59. Specimens recorded have slightly lower ornament than that of the holotype of *H. citrinipeltatum*. The specimens observed have closely spaced 'donut-like' elements ornamenting the wall. The vesicle measures between 38um-50um in diameter.

Heliosphaeridium malvernensis Dorning 1981, *H. clavispinosum* Lister 1970 and *H. pseudodictyum* Lister 1970 all differ by possessing solid processes with blunt distal tips.

Genus *Impluviculus* Loeblich & Tappan 1969 emend. Martin 1975.

Type species: *Impluviculus milonii* (Deunff) Loeblich & Tappan. The vesicle is 38um-50um in diameter.

Generic description: Loeblich & Tappan 1969, p.48; Martin 1975, p.15.

Impluviculus? sp.

Plate pl.5, fig.7.

Remarks: Specimens are questionably assigned to the genus *Impluviculus* as the characteristic lid-like opening is not discernible in this dark coloured material.

Genus *Leiofusa* Eisenack 1938 emend. Combaz *et al.* 1967.

Type species: *Leiofusa fusiformis* Eisenack 1934 *ex* Eisenack 1938

Generic description: Eisenack 1938a, p.28; Combaz *et al.* 1967, p.297.

Leiofusa cf. *bernesgae* Cramer 1964.

Plate 62, fig.5.

Holotype: Cramer 1964 Cramer 1964, pl.2, fig.10. Age: Gedinnian.

Remarks: Compare with Cramer 1964, p.37, pl.2, fig.10. Specimens included here have a fusiform vesicle closely resembling the holotype, however, the processes are shorter in the specimens observed. *Leiofusa tumida* Downie 1959 has a slightly more rounded central body and longer processes.

Leiofusa estrecha Cramer 1964.

Plate 78, figs.12? & 13?; pl.85, figs.4, 5 & 6; pl.107, fig.7; pl.129, fig.6; pl.139, figs.5 & 13; pl.154, fig.10?

Description: Cramer 1964, p.36, figs.8 & 11.

Holotype: Cramer 1964, fig.11. Age: Early Gedinnian.

Remarks: Specimens of this large leiofusid species (upto 270um in length) are commonly broken in the material observed.

Leiofusa fusiformis Eisenack 1934 *ex* Eisenack 1938.

Plate 42, fig.4.

Description: Eisenack 1934, p.65-66, pl.4, fig.19.

Holotype: Eisenack 1934, pl.4, fig.19. Age: Silurian.

Remarks: Specimens included here are 110-150mm in length. *Leiofusa simplex* (Combaz) Martin 1975 would appear to have an almost identical morphology (by comparison of the photographic illustrations of the holotype) and is probably a junior synonym.

Leiofusa cf. *pittauae ex* Pittau 1985; Fensome *et al.* 1990.

Plate 6, fig.1.

Holotype: Pittau 1985, pl.9, fig.12. Age: Late Tremadoc-Early Arenig.

Remarks: Compare with Pittau 1985, p.188-189, pl.9, figs.9 & 12. Only the size dimensions of specimens observed here differ from the type material. The specimens here are 85-96um long here compared to 40-47um long in the type material. The species with the most similar vesicle form to *L.* cf. *pittauae* is *Dactylofusa squama* (Deunff) Rauscher 1973. This species is also of similar size but differs in possessing striae on the vesicle wall.

Leiofusa tumida Downie 1959.

Plate 62, fig.5.

Description: Downie 1959, p.65, pl.11, fig.5.

Holotype: Downie 1959, pl.11, fig.5. Age: Wenlock.

Remarks: *Leiofusa granulacutus* Loeblich 1970 has a similar shaped vesicle and process form, and is a similar size to *L. tumida*, however, the former has a granulate ornamentation on the wall.

Genus *Leiosphaeridia* Eisenack 1958 emend. Turner 1985.

Type species: *Leiosphaeridia baltica* Eisenack 1958.

Generic description: Eisenack 1958a, p.2-5; Turner 1985, p.116.

Leiosphaeridia microcystis Eisenack 1938 *ex* Eisenack 1958.

Plate 62, figs.9, 10 & 11.

Description: Eisenack 1958, p.8-9, pl.2, fig.6.

Holotype: Eisenack 1958, pl.2, fig.2. Age: Silurian.

Remarks: This species of *Leiosphaeridia* is distinguished by its size, 50-100um in diameter, and thick wall, 2-3um wide. *Leiosphaeridia Wenlockia* Downie 1959 has a thinner wall and has a diameter of 20-50um.

Leiosphaeridia wenlockia Downie 1959.

Plate 73, fig. 5.

Description: Downie 1959, p.65, pl.12, figs.2-4.

Holotype: Downie 1959, pl.12, fig.2. Age: Wenlock.

Remarks: Specimens included here are smooth thin walled spheromorph acritarchs with a maximum diameter of 20-50um.

Leiosphaeridia sp. 1.

Plate 62, fig.9; pl.122, fig.1.

Description: Spheromorphic acritarchs which have a thin (< 1um thick), smooth wall. The diameter of the vesicle ranges between 100-180um. No regular form of opening is apparent.

Remarks: This species is larger in size and has a thinner wall than *L. microcystis*.

Leiosphaeridia spp.

Plate 5, figs.10, 11 & 12; pl.18, fig. 1; pl.41, figs.1 & 2; pl.84, fig.6; pl.122, figs.2 & 4.

Remarks: Specimens assigned here are thin, smooth walled leiospheres that are commonly folded in an irregular manner. Opening of the vesicle may be by medium split or by irregular rupturing of the wall.

Genus *Leiovalia* Eisenack 1965 *ex* Gorka 1969 emend.

Type species: *Leiovalia ovalis* (Eisenack) Gorka 1969.

Emended description: Spheromorphic acritarchs which have an ovate central body. The wall is composed of a single layer and is smooth or ornamented with features of low relief (<2um high).

Remarks: The description has been emended to include the many species published in this genus that possess ornament (e.g. *L. scaberula* Loeblich & Tappan 1978). Eisenack 1965 (p.139) described the genus as one that included smooth walled species. *Leiosphaeridia* is spherical-subspherical with a smooth wall. *Lophosphaeridium* is spherical-subspherical with an ornamented wall. *Navifusa* is elongate ellipsoidal or cylindrical with rounded poles and has a smooth or ornamented wall. *Leiofusa* is elongate ellipsoidal, smooth walled and has accuminate poles.

Leiovalia sp. 1.

Plate 41; fig.7.

Description: Spheromorphic acritarchs which have an ovate vesicle measuring between 59-64um in length and 32-51um in width. The length to width ratio is approximately 1.5:1. The wall is single layered and is ornamented with grana (< 1um in diameter). No regular form of opening is apparent.

Remarks: *Leiovalia scaberula* is slightly larger and has a scabrate ornamentation composed of fine dimples and minute irregular elevations.

Genus *Lophosphaeridium* Timofeev 1959 *ex* Downie 1963 emend.

Type species: *Lophosphaeridium rarum* Timofeev 1959 *ex* Downie 1963.

Emended description: Spheromorphic acritarchs which have a spherical to subspherical vesicle. The wall is composed of a single layer and is ornamented with features of low relief (< 2um high).

Remarks: Lister 1970, p.61 gave an emended diagnosis of the genus that restricted it to include forms with solid tubercular ornament. The genus is broadened here to incorporate spheromorphs ornamented with any form of low relief ornamentation.

Lophosphaeridium citrinum Downie 1963.

Plate 63, fig.1.

Description: Downie 1963, p.630-631, pl.92, fig.3.

Holotype: Downie 1963, pl.92, fig.3. Age: Wenlock.

Remarks: The transfer of this species to the genus *Baltisphaeridium* by Stockmans & Williere (1974, p.12) is rejected here. The short spines on the vesicle are largely solid in this species which is a characteristic of species included in *Lophosphaeridiun*.

Lophosphaeridium sp. 1.

Plate 41, figs.3, 8 & 9.

Description: Spheromorphic acritarchs which have a subspherical vesicle measuring between 81-90um in maximum diameter. The wall is single layered, thin and commonly folded. The wall is ornamented with subpolygonal clusters of grana and baculae. The clusters are 2-4um in diameter and the elements within the clusters are approximately 1um in height. The non-ornamented boundaries between clusters are <1um wide. No regular form of opening is apparent.

Remarks: The ornament of subpolygonal clusters of elements distinguish this species. *Lophosphaeridium leptomolgion* Loeblich & Tappan 1978 is also a strongly ornamented species, however the ornamentation is of variably spaced grana and verrucae in that form.

Lophosphaeridium sp. 2.

Plate 42, fig. 12; pl.108, figs.1, 2 & 3.

Description: Spheromorphic acritarchs which have a subspherical vesicle measuring between 85-91um in maximum diameter. The wall is single layered, thin and commonly folded. The wall is scabrate, ornamented with minute granulate elements (<1um high) and fine fovea (<1um deep and <1um in diameter). No regular form of opening is apparent.

Remarks: This species has a very similar ornamentation to *Leiovalia scaberula* Loeblich & Tappan 1978 but differs in the shape of the vesicle.

Lophosphaeridium sp. 3.

Plate 42, fig.3.

Description: Spheromorphic acritarchs which have a subspherical vesicle measuring between 30-55um in maximum diameter. The wall is single layered, thick and occasionally folded. The wall is coarsely scabrate and ornamented with what appear to be a combination of grana, baculae and pila (all <2um high). No regular form of opening is apparent.

Remarks: The elements are not easy to distinguish because of the poor preservation. The pila make the wall surface appear 'hairy' in some specimens.

Lophosphaeridium sp. 4.

Plate 73, fig.2.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring between 65-75um in maximum diameter. The wall is single layered, thick (approximately 1um) and occasionally folded. The wall is ornamented with grana and baculae which are closely spaced (<2m between elements). The elements are approximately 2um in height and 2um in diameter. No regular form of opening is apparent.

Remarks: This species has a similar morphology to *Visbysphaera microspinosa*. However, the wall is thinner and the elements are more densely distributed on the vesicle than in *V. microspinosa*.

Lophosphaeridium sp. 5.

Plate 63, figs.2 & 3.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring between 25-30um in maximum diameter. The wall is single layered and ornamented with coarse baculae. The baculae are evenly spaced with approximately 2-3um between the elements. The baculae are 1-3um in height and approximately 3-4um in diameter. No regular form of opening is apparent.

Remarks: This species is distinguished by its small size and the coarse baculate ornament on the vesicle.

Lophosphaeridium sp. 6.

Plate 63, figs. 4 & 6.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring between 37-45um in maximum diameter. The wall is single layered, moderately thick (approximately 1um) and occasionally folded. The wall is ornamented with evenly spaced grana (<2um between elements) that are <1um in height and <2um in diameter. No regular form of opening is apparent.

Remarks: This species is distinguished by the evenly distributed, descrete grana and the rather rigid vesicle.

Lophosphaeridium sp. 7.

Plate 78, figs.8 & 9; pl.85, figs.3, 7 & 8; pl.108, fig.4.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring between 23-45um in maximum diameter. The wall is single layered, moderately thick, approximately 1um, and is commonly folded. The wall is ornamented with closely spaced, evenly distributed (<1um between elements) grana that are <1um in height and <1um in diameter. No regular form of opening is apparent.

Remarks: This species is distinguished by the dense, even distribution of grana and the small size of the vesicle.

Lophosphaeridium sp. 8.

Plate 86, fig.8.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring approximately 35um in maximum diameter (two specimens measured). The wall is thick (>1um) and single layered. It is ornamented with evenly distributed verrucae (>4um between the elements) that are >2um in height and >2um in diameter. No regular form of opening is apparent.

Remarks: The specimens included here strongly resemble *Tapajonites roxoi* Sommer & Van Boekel 1963 which was described from the Middle Devonian of Brazil. However, *T. roxoi* is approximately 140um in diameter compared to the diameter of approximately 35um of *Lophosphaeridium* sp.8. The genus *Tapajonites* has size limits of 100-200um for the species included within it, hence, specimens recorded here are assigned to the genus *Lophosphaeridium*.

Lophosphaeridium? sp. 9.

Plate 51, figs.3, 5 & 8.

Description: Spheromorphic acritarchs which have a spherical vesicle measuring 75-105um in maximum diameter. The wall is very thick (approximately 2um) and single layered. The wall has an unusual 'sponge-like' texture giving the vesicle surface a coarsely scabrate appearance. No regular form of opening is apparent.

Remarks: *Lophosphaeridium?* sp. 9 is only recorded from sample DJ 10. These morphotypes are questionably included in the genus *Lophosphaeridium* as it is debatable weather or not the coarsely scabrate surface of the wall should be considered as "ornamentation of low relief", the presence of which is a diagnostic feature of *Lophosphaeridium* species.

Genus *Maranhites* Brito 1965.

Type species: *Maranhites brasiliensis* Brito 1965.

Generic description: Brito 1965, p.1-2.

Maranhites britoi Stockmans & Williere 1969.

Plate 173, figs.4 & 6; pl.188, fig.1; pl.193, fig.1.

Description: Stockmans & Williere 1969, p.44-45, pl.2, figs.4 & 7.

Holotype: Stockmans & Williere 1969, pl.2, fig.4. Age: Early Famennian.

Remarks: This rather elaborate form of *Maranhites* has tabular extensions protruding from the lateral margin of the vesicle. The cells or pods are enclosed by a thin wall layer which are positioned between the tabular extensions from the vesicle. *Maranhites perplexus* Wicander & Playford 1985 has a similar morphology but is described as being consistently smaller in size than *M. britoi*.

Maranhites cf. *britoi* Stockmans & Williere 1969.

Plate 173, fig.7; pl.174, fig.2.

Holotype: Stockmans & Williere 1969, pl.2, fig.4. Age: Early Famennian.

Remarks: Compare with Stockmans & Williere 1969, p.44-45, pl.2, figs.4 & 7. These forms have thicker, more robust tabular extensions from the central body supporting the membranous pods than do specimens assigned to *M. britoi*.

Maranhites mosessii (Sommer) Brito 1967.

Plate 182, fig.8; pl.193, fig.2.

Description: Sommer 1956, p.458-461, figs.5-8.

Holotype: Sommer 1956, p.458-461, figs.5, 7 & 8.

Remarks: This species of *Maranhites* has a smooth, circular outer margin of the vesicle with large subcircular pods positioned on the inner wall. Morphologically similar species are *M. brasiliensis* Brito 1965 and *M. stockmansii* Martin 1981 emend. Martin 1984. These species also have a circular outline but differ in possessing smaller cells which are restricted to the outer margin of the vesicle.

Maranhites perplexus Wicander & Playford 1985.

Plate 193, fig.6.

Description: Wicander & Playford 1985, p.110, pl.3, figs.11a-b & 12.

Holotype: Wicander & Playford 1985, pl.3, figs.11a-b.

Remarks: This species has a similar morphology to *M. britoi* but can be distinguished by the larger size of the vesicle.

Maranhites stockmansii Martin 1981 emend. Martin 1984.

Plate 174, fig.1; pl.182, fig.6.

Description: Martin 1984, p.25, pl.7, figs.1, 3, 4-7 & 10.

Holotype: Martin 1981, pl.4, fig.10. Age: Early Famennian.

Remarks: This species is distinguished by the circular outline of the vesicle and the presence of minute pods which are restricted to lateral margin.

Maranhites cf. *stockmansii* Martin 1981 emend. Martin 1984.

Plate 174, figs.3 & 4.

Holotype: Martin 1981, pl.4, fig.10. Age: Early Famennian.

Remarks: Compare with Martin 1984, p.25, pl.7, figs.1, 3, 4-7 & 10. The pods of this form are restricted to the lateral margin of the vesicle as in *M stockmansii*, however, the pods are noticeably larger and more obtrusive in *M.* cf. *stockmansii.*

Maranhites sp. 1.

Plate 193, figs.3, 4 & 5.

Description: A species of *Maranhites* with a subcircular central body measuring between 65-100um in maximum diameter. The central body is moderately thick walled and is ornamented with a reticulum. The pods are positioned on the periphery of the central body and are ovate in shape. There is a thickening of the wall at the outer margin of the central body marking a boundary between it and the pods. There is little or no lateral extension of the central body between the pods. The pods are positioned closely adjacent to each other giving a gently undulating outline to this species.

Remarks: The reticulate ornamentation and the thickening of the wall at the outer margin of the central body distinguishes this species from the closely comparable *M. britoi.*

Maranhites sp. 2.

Plate 182, figs.4 & 7.

Description: A species of *Maranhites* with a subcircular central body measuring between 75-95um in maximum diameter. The central body is very thick walled and appears black in the material observed. The pods are positioned on the periphery of the central body and are subspherical to ovate in shape. There is little or no lateral extension of the central body between the pods.

Remarks: The absence of the lateral extensions of the central body between the pods is the major difference between this form and *Maranhites britoi.* This gives *Maranhites* sp. 2 a distinctly undulating outer margin in contrast with the smoother outer margin of *M. britoi.*

Genus *Marrocanium* Cramer *et al.* 1974.

Type species: *Marrocanium simplex* Cramer *et al.* 1974.

Generic description: Cramer *et al.* 1974b, p.59.

Remarks: Species included here have a four-sided veryhachid-shaped vesicle with a thin membrane extending between the processes.

Marrocanium simplex Cramer *et al.* 1974.

Plate 18, figs.3-8; pl.33, figs.1 & 2.

Description: Cramer *et al.* 1974, p.59, pl.26, figs.1-9.

Holotype: Cramer *et al.* 1974, pl.26, figs.1 & 2. Age: Late Arenig-Early Llanvirn.

Remarks: The thin transparent membrane or web extending between processes is poorly preserved in the specimens observed.

Marrocanium sp.

Plate 18, figs.9 & 10.

Remarks: Two specimens are recorded here. They have a rectangular shaped vesicle measuring approximately 35um in length and 28um wide. There are four processes at the apices of the vesicle measuring upto 17um in length. A poorly preserved membrane is present in the viscinity of the processes. The wall is ornamented with grana.

These forms can be distinguished from *Marrocanium simplex* by the presence of the granulate ornamentation on the wall of the central body and the processes.

Genus *Micrhystridium* Deflandre 1937 emend. Sarjeant 1967.

Type species: *Micrhystridium inconspicuum* (Deflandre) Deflandre 1937.

Generic description: Deflandre 1937b, p.79-80; Sarjeant 1967, p.204.

Remarks: *Micrhystridium* here encompasses species with well defined, round to ovate central bodies, simple processes that communicate freely with the central body and that have a smooth or scabrate wall. *Goniosphaeridium* has conical processes whose bases merge to form a poorly defined central body, i.e. the shape of the central body is dictated by the shape of the process bases. Species included in the genus *Polygonium* have a polygonal, well defined central body with simple processes. *Stellichinitum* and *Uncinisphaera* both have an ornamentation of echinae.

Micrhystridium aremorecanium (Paris & Deunff) Fensome *et al.* 1990.

Plate 6, figs.2 & 3.

Description: Paris & Deunff 1970, p.32, pl.2, fig.20; for English translation see Eisenack, Cramer & Diez 1979, p.445.

Holotype: Paris & Deunff 1970, pl.2, fig.20. Age: Llanvirn.

Micrhystridium henryii Paris & Deunff 1970.

Plate 18, figs.13 & 14.

Description: Paris & Deunff 1970, p.31, pl.2, figs.2, 10, 14-15, 18.

Holotype: Paris & Deunff 1970, pl.2, fig.14. Age: Llanvirn.

Micrhystridium inaffectilumium? Loeblich 1970.

Plate 18, figs.11 & 12.

Description: Loeblich 1970, p.728, figs.21E-D.

Holotype: Loeblich 1970, fig.21D. Age: Middle Silurian.

Remarks: Processes of the specimens observed here are slightly shorter than in the type material described from the Middle Silurian Maplewood Shale, New York, USA.

Micrhystridium stellatum Deflandre 1945.

Plate 86, fig.4; pl.140, fig.1; pl.174, fig.7.

Description: Deflandre 1945, p.65, pl.3, figs.16-19.

Holotype: Deflandre 1945, pl.3, fig.16. Age: Silurian.

Genus *Multiplicisphaeridium* Staplin 1961 emend. Turner 1984.

Type species: *Multiplicisphaeridium ramispinosum* Staplin 1961.

Generic description: Staplin 1961, p.410; Turner 1984, p.120.

Remarks: The genus *Piliferosphaera* has the same general morphology as *Multiplicisphaeridium* but differs in possessing an ornament of short spine-like pila on the central body. *Ammonidium* differs by having equifurcate processes. The genera *Baltisphaeridium*, *Micrhystridium* and *Salopidium* differ by having simple processes.

Multiplicisphaeridium bifurcatum Staplin, Jansonius & Pocock 1965.

Plate 42, figs.5 & 6.

Description: Staplin, Jansonius & Pocock 1965, p.182, pl.18, fig.13.

Holotype: Staplin, Jansonius & Pocock 1965, pl.18, fig.13. Age: Middle Ordovician.

Remarks: The delicate distal furcations are commonly damaged in the material observed. This taxon is very similar in morphology to species of *Ordovicidium* which have been recorded at the same stratigraphic level from which the present specimens have been recovered. *Multiplicisphaeridium bifurcatum* differs from these species by having slightly deeper and more elaborate distal process furcation.

Multiplicisphaeridium consolator Cramer & Diez 1977.

Plate 19, figs.1 & 2.

Description: Cramer & Diez 1977a, p.347, pl.3, fig.17.

Holotype: Cramer & Diez 1977a, pl.3, fig.17. Age: Early Arenig.

Remarks: *Multiplicisphaeridium multiradiale* (Burmann) Eisenack, Cramer & Diez 1976 differs in possessing more elaborate distal process terminations.

Multiplicisphaeridium crispum (Vavrdova) Comb. nov.

Plate 19, figs.3-6; pl.33, fig.3.

Synonomy: 1990, *Kladothecidum crispum*, Vavrdova, p.247-248, pl.IV, fig.3; text-fig.8.

Description: Vavrdova 1990, p.247-248, pl.IV, fig.3; text-fig.8.

Description of the material observed here: Acanthomorphic acritarchs which have a well defined subspherical central body measuring between 30-35um in maximum diameter. There are approximately 10-15 slender processes present which are upto 25um in length. The process bases are upto 5um wide and the shafts taper distally to branched distal terminations. Branching is restricted to the distal extremities of the processes where the pinnae furcate in a palmate manner upto the 3rd order. The process to central body ratio is approximately 4:5. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth to slightly granulose on the surface. No regular form of opening is apparent.

Remarks: Inclusion of this species in the genus *Kladothecidum* by Vavrdova 1986 is rather puzzling. Not only is the morphology that of a *Multiplicisphaeridium* species but there are also, what would appear to be a number of closely related species of *Multiplicisphaeridium* published from this stratigraphic level. Some of these closely related morphotypes have been observed in the present study. These include *M. consolator* Cramer & Diez 1977 which has a less well defined, more polygonal central body with shorter processes and *M. firmum* (Burmann) Fensome *et al.* 1990 which has a more polygonal central body and stout processes.

Multiplicisphaeridium firmum (Burmann) Fensome *et al.* 1990.

Plate 19, figs.7-11; pl.33, figs.4, 5 & 6?

Description: Burmann 1970, p.295, pl.5, figs. 3 & 4.

Holotype: Burmann 1970, pl.5, fig. 4. Age: Late Arenig-Early Llanvirn.

Remarks: The transfer of this species from *Adorfia* to *Multiplicisphaeridium* made by Cramer & Diez (1979, p.43) was legitimised by Fensome *et al.* (1990). The polygonal body and the short, stout processes with elaborate terminations distinguish this species. A similar species is *M. consolator* Cramer & Diez 1977 which was described from the Late Arenig of Morocco. Processes are broader and less elaborate at the distal terminations in *M. consolator. Multiplicisphaeridium multipugiunculatum* Cramer & Diez 1977 is also similar but it has many more processes than *M. firmum*.

Multiplicisphaeridium fisheri (Cramer) Lister 1970.

Plate 63, figs.7 & 8; pl.86, fig.7.

Description: Cramer 1968, p.65, pl.1, fig.1.

Holotype: Cramer 1968, pl.1, fig.1. Age: Late Llandovery.

Remarks: *Leptobrachion arbusculiferum* (Downie) Staplin, Jansonius & Pocock 1965 is of a similar size and has a similar process distribution to *M. fisheri* but has deeper and more complex furcation of the processes. *Multiplicisphaeridium ramispinosum* has slightly shorter processes and a more rounded central body. The more irregular body shape in *M. fisheri* is a reflection of the relatively thin wall of this species.

Multiplicisphaeridium inconstans Cramer & Diez 1977.

Plate 19, fig.13; pl.33, figs.7, 8 & 9.

Synonomy: 1977, *Evittia flosmaris*, Deunff, p.143, pl.1, fig.18, pl.2, figs.7, 9, 11 & 14.

Description: Cramer & Diez 1977a, p.347, pl.4, figs.5 & 8.

Holotype: Cramer & Diez 1977a, pl.4, fig.8. Age: Early Arenig.

Remarks: *Evittia flosmaris* Deunff 1977, described from the Llanvirn of the Anti Atlas region of Morocco appears to have an identical morphology to *M. inconstans* and is here considered to be a synonym. *Multiplicisphaeridium rayii* Cramer & Diez 1977 has a similar process morphology but differs by having a less well defined central body and by being much larger in size.

Multiplicisphaeridium cf. *inconstans* Cramer & Diez 1977.

Plate 19, fig.12.

Holotype: Cramer & Diez 1977a, pl.4, fig.8. Age: Early Arenig.

Remarks: Compare with Cramer & Diez 1977. Specimens included here have a thicker and more robust wall than *M. inconstans*. The branching of the processes is to the second order.

Multiplicisphaeridium lobeznum (Cramer) Eisenack, Cramer & Diez 1973.

Plate 130, figs.1 & 2; pl.140, fig.2; pl.150, fig.3

Description: Cramer 1964, p.296, pl.2, fig.15, pl.7, fig.3, text-fig.19, no.6.

Holotype: Cramer 1964, pl.2, fig.15. Middle Siegenian-Emsian.

Remarks: The contention of Colbath (1979, p.20-21), upheld by Fensome *et al.* (1990, p.348) that this species is a junior synonym of *M. cladum* Downie 1963 is rejected here. The photographic illustration and the line diagram of the holotype of *M. lobeznum* given by Cramer show a completely different style of process shaft and distal branching when compared to the holotype of *M. cladum*. *Multiplicisphaeridium lobeznum* is distinguished by the relatively small, spherical vesicle and the very complex, densely branched distal process terminations. *Multiplicisphaeridium ramispinosum* has less complex and less dense distal branching of the processes.

Multiplicisphaeridium ramispinosum Staplin 1961.

Plate 130, figs.4 & 5; pl.165, figs.6, 8 & 9; pl.174, figs.5 & 6; pl.182, fig.5; pl.188, fig.3; pl.193, figs.7, 8 & 9.

Description: Staplin 1961, p.411, pl.48, fig.24.

Holotype: Staplin 1961, pl.48, fig.24. Age: Late Devonian.

Remarks: This rather broad taxon has a spherical to subspherical vesicle with relatively sparsely distributed processes that branch distally in a ramusculose fashion. *Multiplicisphaeridium lobeznum* has a smaller vesicle with more complex and more densely ramusculose distal terminations to the processes. *Multiplicisphaeridium fisheri* has a less regular vesicle shape which reflects the thinner vesicle wall of that species.

Multiplicisphaeridium cf. *ramispinosum* Staplin 1961.

Plate 42, figs.4, 7, 8 & 9.

Holotype: Staplin 1961, pl.48, fig.24. Age: Late Devonian.

Remarks: Compare with Staplin 1961, p.411, pl.48, fig.24. The poorly preserved specimens included here have less complex distal terminations than the holotype of *M. ramispinosum*.

Multiplicisphaeridium raspum (Cramer) Eisenack, Cramer & Diez 1973.

Plate 130, fig.3; pl.140, figs.3 & 4; pl.150, fig.2; pl.154, fig.4; pl.165, fig.5.

Description: Cramer 1964, p.301, pl.4, figs.1-6 & 11.

Holotype: Cramer 1964, pl.4, fig.1. Age: Middle Siegenian-Emsian.

Remarks: This species rather conveniently accommodates forms which have a morphology that is transitional between *Ammonidium*? *alloiteauii*, which has shorter, less complex processes, and *Multiplicisphaeridium ramispinosum*, which has longer, more complex processes. The morphological variation observed here within *M. raspum* is almost identical to that represented by Cramer (1964) of the specimens from the type locality.

Multiplicisphaeridium rusticum? Martin 1973.

Plate 42, figs.10, 11 & 12.

Description: Martin 1973, p.11-12, pl.1, figs.28, 29, 32; pl.4, fig.131; pl.5, figs.150-153, 156, 163, 166, 169 & 170.

Holotype: Martin 1973, pl.5, figs.150, 156 & 166. Age: Early Llandovery.

Remarks: The specimens assigned here are rather poorly preserved.

Multiplicisphaeridium variabile (Lister) Dorning 1981.

Plate 108, figs.6-9; pl.116, figs.1, 2 & 3.

Description: Lister 1970, p.87-88, pl.11, figs.4-7, 9 & 10, text-figs.25d & 26c.

Holotype: Lister 1970, pl.11, fig.10. Age: Ludlow.

Remarks: Specimens included here have a small central vesicle (16-24um in diameter) with processes that branch in a ramusculose manner. Branching occurs in the distal half of the process, upto the fourth order.

Multiplicisphaeridium cf. *saharicum* Lister 1970.

Plate 86, figs.5 & 6; pl.108, fig.5.

Holotype: Lister 1970, pl.12, fig.4. Age: Ludlow.

Remarks: Compare with Lister 1970, p.94, pl.12, figs.2, 3 & 4. Specimens recorded here have a thicker wall (ca. 2um thick) than in the type material which was described by Lister from the Welsh Borderlands.

This species appears superficially similar to *Cymbosphaeridium cariniosum*. However, the two species differ by way of their wall structures, *C. cariniosum* having two wall layers, *Multiplicisphaeridium* cf. *saharicum* having a single thick layer. *Multiplicisphaeridium raspum* (Cramer) Eisenack, Cramer &

Diez 1973 is also morphologically similar but differs in the processes being of greater length and being greater in number.

Multiplicisphaeridium sp. 1.

Plate 108, figs.10, 11 & 12.

Synonomy: 1971, *Multiplicisphaeridium arbusculiferum*, Deunff, Lefort & Paris, p.11.

Description: Acanthomorphic acritarchs which have a subspherical central body measuring between 35-45um in maximum diameter. There are approximately 10-15 slender processes which are upto 35um in length. The process bases are upto 7um wide and the shafts taper distally to branched distal terminations. Branching occurs in the distal two thirds of the processes. Branching is ramusculose, upto the 4th order. The process to central body ratio is approximately 3:4. The wall is composed of a single layer and the processes communicate freely with the central body. The wall is smooth to slightly granulose on the surface. No regular form of opening is apparent.

Remarks: This form appears to be identical to the specimens described as *Multiplicisphaeridium arbusculiferum* (Downie) by Deunff, Lefort & Paris 1971, from the late Ludlow of France. Comparison with the holotype of *M. arbusculiferum* (now *Leptobrachion arbusculiferum* [Downie] Dorning 1981) shows that Deunff, Paris & Lefort (1971) incorrectly assigned the specimens they illustrated to this species, in the opinion of the present author.

Multiplicisphaeridium? sp. 2.

Plate 165, figs.7, 10, 11 & 12.

Description: Acanthomorphic acritarchs which have a polygonal central body measuring between 23-35um in maximum diameter. There are approximately 10-20 slender processes which are upto 20um in length. The process bases are upto 4um wide and the shafts taper distally to branched distal terminations. Branching occurs in the distal half of the processes. Branching is ramusculose, upto the 4th order. The process to central body ratio is approximately 4:5. The wall appears to be composed of a single layer but the nature of communication between the processes and the central body is not clear from the specimens observed. The wall is smooth on the surface. No regular form of opening is apparent.

Remarks: This acanthomorphic form with a polygonal central body is not typical of forms included in the genus *Multiplicisphaeridium*, hence the questioned assignation. The wall relationship between the processes and the central body is not clear in the thermally altered specimens observed, some specimens appear to have solid processes and some don't. This form appears to be comparable to *Dateriocradus* sp. B of Playford 1977 which he described from the Devonian of Ontario.

Genus *Muraticavia* Wicander 1974.

Type species: *Muraticavia enteichia* Wicander 1974.

Generic description: Wicander 1974, p.14.

Remarks: *Muraticavia* differs from *Polyedryxium* in lacking serrated edges and projections from the vesicle.

Muraticavia sp. 1.

Plate 185, figs.7-11; pl.188, fig.9; pl.196, figs.2 & 3.

Description: Acritarchs with an apparently disc or flattened star shaped central body reinforced with thickened ribs that radiate from the poles of the vesicle to the equator. The ribs number between six and ten and commonly extend beyond the equator to support a membranous fringe. The total diameter of the vesicle ranges between 39-53um. No regular form of opening is apparent.

Remarks: These morphologically distinct palynomorphs show a considerable range of morphology. Study of larger populations may justify the proposal of several species within the range of morphology illustrated here. Other species in the genus from the Middle to Late Devonian include the type species *M. enteichia* Wicander 1974 and *M. munifica* Wicander & Wood 1981. Both of these species have a more spherical outline to the vesicle which is divided into pentagonal fields as opposed to the pseudo-triangular fields of *Muraticavia* sp. 1.

Genus *Navifusa* Combaz *et al.* 1967 *ex* Eisenack 1976.

Type species: *Navifusa navis* (Eisenack) Eisenack 1976.

Generic description: Combaz *et al.* 1967, p.293.

Remarks: Included here are fusiform acritarch species with rounded poles. The genus *Leiofusa* has accuminate tips at each pole of the vesicle.

Navifusa bacilla (Deunff) Playford 1977.

Plate 154, fig.9; pl.166, figs.6 & 7.

Description: Deunff 1955, p.148, pl.4, fig.2.

Holotype: Deunff 1955, pl.4, fig.2. Age: Middle Devonian.

Remarks: Included here are cigar-shaped acritarchs with a smooth vesicle wall. This species has a more elongate vesicle form than *N. minuta.*

Navifusa minuta (Deunff) Eisenack, Cramer & Diez 1979.

Plate 154, figs.5 & 7; pl.183, fig.3.

Description: Deunff 1955, p.148, pl.4, fig.5.

Holotype: Deunff 1955, pl.4, fig.5. Age: Middle Devonian.

Remarks: Specimens here are fusiform in shape with rounded poles. They differ from *N. bacilla* in having a broader, more squat vesicle shape.

Genus *Neoveryhachium* Cramer 1970.

Type species: *Neoveryhachium carminae* (Cramer) Cramer 1970.

Generic description: Cramer 1970, p.110-112.

Remarks: *Neoveryhachium* is distinguished from the genus *Veryhachium* by the presence of rectangular striations on the vesicle. Species of *Veryhachium* have a smooth vesicle wall.

Neoveryhachium carminae (Cramer) Cramer 1970.

Plate 86, fig.8.

Description: Cramer 1964, p.307,309, pl.14, fig.16, pl.16, figs.1-3, text-fig.28, no.1.

Holotype: Cramer 1964, pl.16, fig.1. Age: Ludlow-early Gedinnian.

Remarks: *Neoveryhachium carminae* is a relatively small species of *Neoveryhachium* with four processes positioned at the apices of the quadrate vesicle. A fifth process may be present. *Neoveryhachium mayhillense* Dorning 1981 is larger in size.

Genus *Onondagella* Cramer 1966

Type species: *Onondagella asymmetrica* (Deunff) Cramer 1966.

Generic description: Cramer 1966, p.86-87.

Remarks: The genus *Onondagella* is distinguished from *Veryhachium* by possessing three sturdy processes, one of which is commonly broader. This broader process houses the opening to the vesicle which is by means of an epibystra. The genus *Triangulina* differs by having a double layered wall with a cavation between the wall layers at the apices of the three sided vesicle.

Onondagella asymmetrica (Deunff *ex* Deunff) Cramer 1966.

Plate 154, fig.11; pl.155, figs.1 & 2; pl.166, figs.3, 5 & 8.

Description: Deunff 1961, p.217.

Holotype: Deunff 1954, fig.15. Age: Devonian.

Remarks: *Onondagella asymmetrica* is distinguished by the pointed distal terminations of the processes. Specimens included here are almost identical to those recorded from the La Vid Shales (Emsian-lower Couvinian) of Leon, Spain by Cramer & Diez (1976).

Onondagella deunffii Cramer 1966

Plate 78, fig.11; pl.86, figs.9, 10 & 11; pl.87, figs.1 & 2; pl.109, figs.1 & 2; pl.122, fig.7; pl.130, figs. 8 & 12; pl.140, fig.5.

Description: Cramer 1966, p.87-88, pl.2, figs.12 & 13, text-fig.2 (16).

Holotype: Cramer 1966, pl.2, 13. Age: ?Ludlow-?Gedinnian.

Remarks: *Onondagella asymmetrica* differs from *O. deunffii* by possessing sharp, as opposed to blunt, process tips.

Onondagella sp.1.

Plate 140, figs.6-9.

Synonomy: 1986, *Pulvenosphaeridium* sp., Al-Ameri, pl.1, fig.6.

Description: A species of *Onondagella* with a rounded-triangular shaped vesicle. The vesicle has a maximum diameter of between 60-85um. One of the apices of the vesicle houses an epibystra which forms the opening to the vesicle. The other two apices have a rounded morphology. The wall of the vesicle is thick (> 1um) and appears to be smooth.

Remarks: This species of *Onondagella* can be differentiated from other species in the genus by the much reduced apices not housing the epibystra. Both *O. deunffii* and *O. asymmetrica* posses processes at these positions.

An identical morphotype to *Onondagella* sp. 1, recovered from the Lower Devonian of North Africa, was assigned to the genus *Pulvinosphaeridium* by Al-Ameri 1986. The presence of an epibystra suggests that this form is better accommodated in *Onondagella*.

Genus *Oppilatala* Loeblich & Wicander 1976.

Type species: *Oppilatala vulgaris* Loeblich & Wicander 1976.

Generic description: Loeblich & Wicander 1976, p.19.

Remarks: The genus *Multiplicisphaeridium* differs from *Oppilatala* in lacking proximal plugs at the base of the processes. The genus *Cymbosphaeridium* opens by means of a pylome which differs from the simple rupture style of opening in *Oppilatala*. The genus *Dateriocradus* differs from *Oppilatala* in possessing a three sided central body.

Oppilatala eoplanktonica (Eisenack) Dorning 1981.

Plate 87, figs.3 & 6.

Description: Eisenack 1955, p.178-179, pl.4, fig.14.

Holotype: Eisenack 1955, pl.4, fig.14. Age: Late Ludlow.

Remarks: *Oppilatala ramusculosa* (Deflandre) Dorning 1981 has a higher central body diameter to process length ratio and a greater depth of furcation of the processes than *O. eoplanktonica*. *Dateriocradus monterossae* differs by having a three sided central body. Useful comparative illustrations of these morphologically similar species is given by Cramer 1970, p.125, text-fig.39. *Oppilatala insolita* (Cramer & Diez) Dorning 1981 appears to be of identical morphology to *O. eoplanktonica* and may well be a junior synonym.

Oppilatala eoplanktonica-ramusculosa Complex.

Plate 73, figs.3, 4 & 6.

Remarks: Specimens assigned here are poorly preserved forms with the same general morphology as the *O. eoplanktonica-O. ramosculosa* complex of morphotypes (see Cramer 1970, p.125, text-fig.39a & b). Specimens are too poorly preserved to be assigned to one of these two species.

Oppilatala? *frondis* (Cramer & Diez) Dorning 1981.

Plate 64, figs.2, 3, 5 & 7.

Description: Cramer & Diez 1972, p.152, pl.32, figs.18 & 19.

Holotype: Cramer & Diez 1972, pl.32, fig.19.

Remarks: Priewalder (1987, p.47) questioned the assignment of this species to the genus *Oppilatala*. In the present material, the presence or absence of plugs at the base of the processes, this being the feature that distinguishes *Oppilatala* species from *Multiplicisphaeridium* species, is questionable. *Oppilatala eoplanktonica* and *O. ramusculosa* both have longer and fewer processes than *O? frondis*. *Multiplicisphaeridium cladum* (Downie) Eisenack 1969 differs by possessing processes with broad bases that taper distally.

Genus *Ordovicidium* Tappan & Loeblich 1971.

Type species: *Ordovicidium elegantulum* Tappan & Loeblich 1971.

Generic description: Loeblich & Tappan 1971, p.398.

Remarks: The genus *Peteinosphaeridium* differs by having vela ornamenting the process shafts. *Multiplicisphaeridium* differs by having processes that communicate freely with the central body.

Ordovicidium cf. *heteromorphicum* (Kjellstrom) Loeblich & Tappan 1978.

Plate 20, figs.1, 2 & 3.

Holotype: Kjellstrom 1971a, pl.4, fig.2. Age: Middle Ordovician.

Remarks: Compare with Kjellstrom 1971a, p.53, pl.4, fig.2. Specimens observed here are smaller than *O. heteromorphicum* (central body 25-40um compared to 67-76um in the type material).

Genus *Orygmahapsis* Colbath 1987.

Type species: *Orygmahapsis fistulosa* (Colbath) Colbath 1987.

Generic description: Colbath 1987, p.66.

Remarks: *Orygmahapsis* differs from the genera *Dictyotidium*, *Melikeriopalla* and *Alveosphaera* in possessing a pseudopore in the centre of each field.

Orygmahapsis fistulosa (Colbath) Colbath 1987.

Plate 109, figs.6, 7 & 8; pl.116, fig.4.

Description: Colbath 1983, p.259, figs.34-36.

Holotype: Colbath 1983, figs.35 & 36. Age: Silurian.

Remarks. *Orygmahapsis fistulosa* has a considerably greater number of fields than the only other species in the genus at the present time, *O. magnata*.

Genus *Ozotobrachion* Loeblich & Drugg 1968.

Type species: *Ozotobrachion palidodigitatus* (Cramer) Playford 1977.

Generic description: Loeblich & Drugg 1968, p.130.

Remarks: This genus differs from *Veryhachium* in having processes that do not communicate with the central body. The processes in species of *Ozotobrachion* are tabular in form and may be open distally. The genus *Triangulina* has processes that taper distally to a simple tip.

Ozotobrachion furcillatus (Deunff) Playford 1977.

Plate 140, figs.10, 11 & 12; pl.155, fig.3; pl.166, figs.1 & 2.

Description: Deunff 1955, p.146, fig.18.

Holotype: Deunff 1955, fig.18. Age: Middle Devonian.

Remarks: *Ozotobrachion palidodigitatus* (Cramer) Playford 1977 differs in possessing a triangular shaped vesicle with fewer and broader processes than *O. furcillatus*.

Ozotobrachion palidodigitatus (Cramer) Playford 1977.

Plate 109, fig.3?; pl.130, fig.6; pl.141, figs.1 & 2; pl.150, fig.4.

Description: Cramer 1966, p.247, pl.1, fig.8, text-fig.3, no.5.

Holotype: Cramer 1966, pl.1, fig.8. Age: Gedinnian-Emsian.

Remarks: *Ozotobrachion dactylos* Loeblich & Drugg 1968, described from the Late Gedinnian of Oklahoma, USA is considered to be a junior synonym of *O. palidodigitatus* (Fensome *et al.* 1990). *Ozotobrachion dicros* Loeblich & Drugg 1968 has longer and more slender processes than *O. palidodigitatus* that taper to closed distal terminations.

Genus *Palacanthus* Wicander 1974.

Type species: *Palacanthus acutus* Wicander 1974.

Generic description: Wicander 1974, p.30.

Palacanthus tripus Martin 1984.

Plate 175, fig.7; pl.183, fig.1.

Description: Martin 1984b, p.27, pl.5, figs.6, 7 & 9.

Holotype: Martin 1984b, pl.5, figs.6. Age: Early Famennian.

Remarks: A comparable species is *Veryhachium trispininflatum* Cramer 1964 which has a similar vesicle shape. *Palacanthus tripus* however differs in possessing a microechinate ornamentation.

Genus *Peteinosphaeridium* Staplin, Jansonius & Pocock 1965 emend. Eisenack 1969.

Type species: *Peteinosphaeridium trifurcatum* Staplin, Jansonius & Pocock 1965.

Remarks: The genus *Peteinosphaeridium* is differentiated from the genus *Ordovicidium* by the presence of vela on the process shafts.

Peteinosphaeridium cruzianum Vavrdova 1990.

Plate 20, figs.4 & 5.

Description: Vavrdova 1990, p.246-247, pl.IV, fig.6; text-fig.7.

Holotype: Vavrdova 1990, pl.IV, fig.6. Age: Late Arenig.

Remarks: Specimens recorded here are fragmentary but the distinctive short vellate processes present enable the assignment to this species.

Peteinosphaeridium sp.

Plate 20, figs.6-11; pl.43, fig.2.

Remarks: Eight poorly preserved specimens of this taxon have been recorded. Specimens have a subspherical central body of approximately 40-50um. The processes are upto 18um in length with branched distal terminations. Vela are present on the shafts of the processes, which are approximately 2um wide and runs the entire length of process shaft.

Genus *Pirea* Vavrdova 1972.

Type species: *Pirea dubia* Vavrdova 1972.

Generic description: Vavrdova 1972, p.82.

Pirea colliformis complex.

Plate 21, figs.1 & 2.

Remarks: Burmann (1970) described nine species in the genus *Deunffia* which have subsequently been transferred to the genus *Pirea* by Eisenack, Cramer & Diez 1976. This group of morphotypes appear to have been 'over-split' at species level resulting in there being considerable scope for synonomy. There are four easily recognisable morphological groups of the published species within the genus that are as follows:

1. *Pirea colliformis* complex. This complex includes forms with a more or less smooth wall and a prominent horn (or process) with a blunt termination. The horn occupies greater than 1\5 the length of the body.

The published species included in this complex are *Pirea colliformis* (Burmann) Eisenack, Cramer & Diez 1976, *P. lagenaria* (Burmann) Eisenack, Cramer & Diez 1976, *P. inflata* (Burmann) Eisenack, Cramer & Diez 1976 and *P. transitoria* (Burmann) Eisenack, Cramer & Diez 1976.

2. *Pirea capitata* complex. This complex includes forms with a more or less smooth wall and a short, stubby apical horn that occupies less than 1\5 the length of the body.

The published species included in this complex are *Pirea capitata* (Burmann) Eisenack, Cramer & Diez 1976 and *P. capitulifera* (Burmann) Eisenack, Cramer & Diez 1976.

3. *Pirea ornata* (Burmann) Eisenack, Cramer & Diez 1976. This species includes forms with an apiculate ornament.

4. *Pirea nervata* (Burmann) Eisenack, Cramer & Diez 1976. This species has a horn of moderate length (approximately 1\5 the length the central body) with fine parallel ribs oriented longitudinally at the base of the process. Burmann (1970) illustrated *P. inflata* as having ribs at the base of the neck but they are not mentioned in the description (p.321).

Genus *Polyedryxium* Deunff 1954 emend. Deunff 1971.

Type species: *Polyedryxium deflandrei* Deunff 1954 *ex* Deunff 1971.

Generic description: Deunff 1971, p.17.

Polyedryxium evolutum Deunff 1955.

Plate 155, figs.5, 8 & 11; pl.167, figs.1, 2 & 3.

Description: Deunff 1955, p.147, pl.4, fig.7.

Holotype: Deunff 1955, pl.4, fig.7. Age: Middle Devonian.

Remarks: This distinctive species of *Polyedryxium* is distinguished by the numerous, short, denticulate processes.

Polyedryxium fragulosum Playford 1977.

Plate 155, fig.4; pl.175, figs.1, 2 & 3.

Description: Playford 1977, p.34, pl.16, figs.8-14.

Holotype: Playford 1977, pl.16, figs.8. Age: Emsian.

Remarks: This species of *Polyedryxium* can be distinguished by the three sided outline of the vesicle.

Polyedryxium pharoane Deunff 1954 *ex* Deunff 1961.

Plate 155, fig.7 & 9; pl.167, figs.4 & 5; pl.175, fig.3; pl.194, figs.1, 2 & 4.

Description: Deunff 1961, p.217.

Holotype: Deunff 1954, fig.13. Age: Couvinian (Devonian).

Remarks: *Eisenackidium martensianum* Stockmans & Williere 1969 and *Senziella incurvata* Stockmans & Williere 1969 are considered to be junior synonyms of this species (Lu Lichang & Wicander 1988).

Genus *Polygonium* Vavrdova 1966.

Type species: *Polygonium gracile* Vavrdova 1966.

Generic description: Vavrdova 1966b, p.412-413.

Remarks: Species included in the genus *Polygonium* have a polygonal, well defined central body, simple processes and a smooth or scabrate wall. *Micrhystridium* encompasses forms with a well defined, round to ovate central body. *Goniosphaeridium* has conical processes whose bases merge to form a poorly defined central body (i.e. the shape of the central body is dictated by the shape of the process bases). *Stellichinitum* and *Uncinisphaera* both have an ornament of echinae.

Polygonium gracile Vavrdova 1966.

Plate 6, figs.8, 9, 10 - 13; pl.21, figs.3-13; pl.32, fig.10.

Description: Vavrdova 1966b, p.413-414, pl.1, fig.3; pl.3, fig.1, text-figs.3b & 4b.

Holotype: Vavrdova 1966b, pl.1, fig.3, text fig.3b (non pl.2, fig.3). Age: Arenig.

Remarks: There is considerable variety in the morphology of the specimens that can be assigned to this rather broad species. Poor preservation of the specimens observed here prohibit the legitimate splitting of this species at the subspecies level.

Polygonium sp. 1.

Plate 6, figs.4 & 5.

Description: Acanthomorphic acritarchs which have a large subpolygonal central body. The body has a maximum diameter ranging between 57-65um. The processes are slender and rather flexible. The width at the process bases is approximately 2um tapering distally to accuminate tips. Process length ranges between 15-20um and the process length to central body diameter is approximately 1:3. The wall is relatively thick and black in colour in the material observed. No ornament is discernible on the vesicle and no regular form of opening is apparent.

Remarks: This species is conspicuous by its large size, flexible processes and subpolygonal central body.

Polygonium? sp. 2.

Plate 6, figs.6 & 7.

Description: Acanthomorphic acritarchs which have a polygonal-subpolygonal central body. The body has a maximum diameter ranging between 18-25um. There are approximately 60 processes present which are slender and rather flexible. The width at the process bases varies between 2-5um and they taper distally to swollen, rounded tips of upto 2um in diameter. The process length ranges between 6-11um and the process length to central body diameter is approximately 1:3. The wall is relatively thick. No ornament is discernible on the vesicle and no regular form of opening has been observed.

Remarks: The swollen tips of the processes are the most diagnostic feature of this taxon. It is questionably assigned to the genus *Polygonium* as the central body of some of the specimens are only slightly polygonal.

A morphologically similar form is the unpublished "*Archaeohistrichosphaeridium* sp.A" Rasul 1971 (unpublished Ph.D. thesis, University of Sheffield) which was described from the Tremadoc of Shropshire, England. *Baltisphaeridium clavicinctum* W. Wetzel 1967, *B. flagellicum* Kjellstrom 1971 and *B. perpaucispinum* Kjellstrom 1971 all have similarly swollen process tips. However, the wall relationship is different in these forms which is reflected by the more rounded central body of these species.

Genus *Pratulasphaera* Wicander & Playford 1985.

Type species: *Pratulasphaera novacula* Wicander & Playford 1985.

Generic description: Wicander & Playford 1985, p.114-115.

Pratulasphaera novacula Wicander & Playford 1985.

Plate 176, figs.1 & 2.

Description: Wicander & Playford 1985, p.115, pl.5, figs.8-13.

Holotype: Wicander & Playford 1985, pl.5, figs.8. Age: Frasnian.

Remarks: The blade-like processes protruding from the spherical central body are the distinguishing feature of this species.

Genus *Quadraditum* Cramer 1964.

Type species: *Quadraditum fantasticum* Cramer 1964.

Generic description: Cramer 1964, p.333.

Remarks: This genus includes species with a flattened, quadrate inner body enclosed by an outer membrane which is attached at the apices of the inner body. The outer membrane is rarely fully preserved. The genus *Duvernaysphaera* differs from *Quadraditum* in having a discoid, as opposed to a quadrate, central body.

Quadraditum fantasticum Cramer 1964.

Plate 87, fig.8; pl.130, figs.7, 9, 10 & 11; pl.141, fig. 8.

Synonomy: 1976, *Duvernaysphaera oa*, Loeblich & Wicander, p.28, pl.9, figs.10 & 11.

Description: Cramer 1964, p.334, pl.14, figs.3 & 4, text-fig.37, nos.1-3.

Holotype: Cramer 1964, pl.14, fig.3. Age: Ludlow-early Gedinnian.

Remarks: *Duvernaysphaera oa* Loeblich & Wicander 1976 appears to be identical to *Q. fantasticum* from the descriptions and illustrations given by the respective authors. *Quadraditum fantasticum* is the name used here as it is the senior.

Quadraditum incisum Cramer 1964 has an X-shaped central body as opposed to the quadrangular central body of *D. fantasticum*. *Quadraditum scutiferum* Deunff 1966 has shorter and broader processes at the apices of the central body.

Quadraditum scutiferum Deunff 1966.

Plate 109, fig.9; pl.122, figs.3 & 6.

Description: Deunff 1966, p.24, fig.3.

Holotype: Deunff 1966, fig.3,. Age: Devonian.

Remarks: This species of *Quadraditum* has capitate process terminations surmounted by 'umbrella-shaped' vela.

Genus *Quadrisporites* Henelly 1958, emend. Potonie & Lele 1961.

Generic description: Potonie & Lele 1961, p.33.

Quadrisporites cf. *acanthifer* Cramer & Diez 1976.

Plate 184, fig.9.

Holotype: Cramer & Diez 1976, pl.7, fig.77. Age: Emsian.

Remarks: Compare with Cramer & Diez 1976, p.92, pl.7, fig.77. The single specimen recorded in the present study is larger in size than *Q. acanthifer* (20-30um) measuring 47um in maximum length. The specimen observed here is otherwise identical in morphology to *Q. acanthifer.*

Genus *Quisquilites* Wilson & Urban 1963, emend Wilson & Urban 1971.

Type species: *Quisquilites buckhornensis* Wilson & Urban 1963.

Generic description: Wilson & Urban 1971, p.240..

Remarks: The genus *Navifusa* differs in having a linear long axis to the vesicle as opposed to the bean shaped vesicle of *Quisquilites.* The genus *Pseudolunulida* differs in possessing a sculptured vesicle wall.

Quisquilites buckhornensis Wilson & Urban 1963.

Plate 175, fig.1.

Synonomy: 1967, *Navifusa bacilla* forma *cresentis*, Combaz *et al*, p.299, pl.1, figs.G & M, text-fig.1.

Description: Wilson & Urban 1963, 18 & 19, pl.1, figs.1-12.

Holotype: Wilson & Urban 1963, 18 & 19, pl.1, fig.1. Age: Late Devonian.

Remarks: The single specimen of this taxon recorded here has a strongly curved vesicle. *Pseudulunulida imperatrizensis* Brito & Santos 1965 has a similarly shaped vesicle but differs in possessing a sculptures vesicle wall.

Genus *Salopidium* Dorning 1981.

Type species: *Salopidium granuliferum* (Downie) Dorning 1981.

Generic description: Dorning 1981, p.198.

Remarks: The species included in *Salopidium* have a subspherical, foveolate central body and simple processes that communicate freely with the central vesicle. The genera *Multiplicisphaeridium*, *Ammonidium* and *Percultisphaera* differ from *Salopidium* by possessing branched processes. *Baltisphaeridium* differs by possessing proximal plugs to the processes and *Micrhystridium* differs in having a smooth central body.

cf. *Salopidium woolhopensis* Dorning 1981.

Plate 64, figs.4 & 6.

Holotype: Dorning 1981, pl.1, fig.14. Age: Wenlock.

Remarks: Compare with Dorning 1981, p.199, pl.1, fig.14. The poorly preserved specimens included here have the same dimensions, number of processes and process distribution as the holotype but evidence of the sculptural detail on the central body is lacking.

Genus *Solisphaeridium* Staplin, Jansonius & Pocock 1965 emend. Sarjeant 1968.

Type species: *Solisphaeridium simuliferum* (Deflandre) Pocock 1972.

Generic description: Staplin, Jansonius & Pocock 1965, p.183-184; Sarjeant 1968, p.222.

Solisphaeridium solidispinosum Cramer & Diez 1977.

Plate 22, fig.1.

Description: Cramer & Diez 1977a, p.352, pl.2, figs.15, 17-19.

Holotype: Cramer & Diez 1977a, pl.2, fig.15. Age: Early Arenig.

Remarks: From the description and illustrations of Cramer & Diez (1977), it would appear that the morphology of *S. solidispinosum* grades into that of *S. solare* Cramer & Diez 1977, the former having shorter and broader processes. Specimens observed here have processes that are at the larger end of the 'process length spectrum' for the species *S. solidispinosum*.

Solisphaeridium sp. 1.

Plate 7, figs.1 & 2; pl.22, figs.2 & 3.

Description: Acanthomorphic acritarchs which have a spherical-subpolygonal central body. The body has a very thin wall (<1um) and measures between 26-33um in maximum diameter. Processes are solid and slender, tapering gradually to accuminate distal tips. They measure 1-2um wide at the base and 9-13um in length. The process to central body ratio is approximately 1:3. The processes are solid and the surface of the wall is smooth. No regular form of opening is apparent.

Remarks: Other species of *Solisphaeridium* described from the Ordovician include the following: *S. solidispinosum* Cramer & Diez 1977 which has shorter, broader processes; *S. solare* Cramer & Diez 1977 which has processes of similar length that are broader, and *S. lucidum* (Deunff) Turner 1985 which has a very similar process morphology but they are markedly fewer in number. *Solisphaeridium nanum* (Deflandre) Turner 1985 described from the Silurian is also similar but has slightly shorter processes which are described as being not completely solid. *Solisphaeridium* sp. 2 has fewer and shorter processes and is noticeably smaller in size.

Solisphaeridium sp. 2.

Plate 7, figs.3 & 4.

Description: Acanthomorphic acritarchs which have a spherical central body. The body has a very thin wall (<1um) and measures between 22-25um in maximum diameter. Processes are solid and relatively rigid. They measure 2-3um in width at the base and taper distally to accuminate tips. The length ranges between 8-10um. The process to central body ratio is approximately 1:2.5. The processes are solid and the surface of the wall is smooth. No regular form of opening is apparent.

Remarks: *Solisphaeridium* sp. 1 has longer and a greater number of processes and is noticeably larger in size. *Solisphaeridium nanun* (Deflandre) Turner 1984 is the most comparable species. Process length, size and distribution is very similar but the processes of *S. nanum* are described as having a degree of cavation in contrast to the solid processes of *Solisphaeridium* sp. 2.

Genus *Stellechinatum* Turner 1984.

Type species: *Stellechinatum celestum* (Martin) Turner 1984.

Generic description: Turner 1984, p.137.

Remarks: Comparable genera include *Uncinisphaera* Wicander 1974 and *Polygonium*. The former has a similar echinate ornamentation of the wall as *Stellichinatum* but differs in possessing a more rounded central body. *Polygonium* does possess a similarly shaped vesicle, however, this genus differs in having a smooth or granulate vesicle wall in contrast with the echinate wall of *Stellichinatum*.

Stellechinatum helosum Turner 1984.

Plate 22, figs.4, 5 & 6.

Description: Turner 1984, p.139, pl.14, figs.5 & 8.

Holotype: Turner 1984, pl.14, fig.5. Age: Caradoc.

Remarks: Specimens recorded in the present study accord well with the description and illustration of the type material.

Stellechinatum sp. 1.

Plate 7, figs.5 & 6.

Description: Acanthomorphic acritarchs with a polygonal-subpolygonal central body which measures 37-45um maximum diameter. The processes are of moderate length and are slender measuring upto 15um long and 4um wide at the base. The process terminations are simple. The ratio of process length to body width is approximately 1:3. The wall is composed of a single wall layer and the processes appear to communicate freely with the central body. The wall of the processes is ornamented with short (<3um), fine, hair-like echinae. There appears to be no ornamentation on the central body and no regular form of opening is apparent.

Remarks: *Stellichinitum helosum* has longer processes and coarser ornamentation than *Stellichinatum* sp. 1. *Stellichinatum* sp. 2 also has a more coarse ornamentation than this species.

Stellechinatum sp. 2.

Plate 7, figs.7 & 8.

Description: Acanthomorphic acritarchs with a subpolygonal central body which measures 39-47um maximum diameter. The processes are of moderate length, *ca.* 15um, slender and have simple distal terminations. The ratio of process length to body width is approximately 1:3. The wall is composed of a single wall layer and the processes communicate freely with the central body. The wall is ornamented with evenly spaced grana (*ca.* 1um diameter) and rare echinae. The ornament appears to be most prominent on the process stems and at the process bases. No regular opening is apparent.

Remarks: This form has an ornamentation of the wall dominated by grana with occasional echinae present. This contrasts with the dominance of the hair-like echinate ornamentation of *Stellichinatum* sp. 1 and *Stellichinatum* sp. 3 described herein.

Stellechinatum sp. 3.

Plate 7, fig.9.

Description: Acanthomorphic acritarchs which have a strongly polygonal central body of 26-37um maximum diameter. The processes are long and slender measuring upto 18um long and 4um wide at the base and they have simple terminations. The process to central body ratio is approximately 2:3. The wall is composed of a single layer and the processes appear to communicate freely with the central body. The wall of the processes is ornamented with short (<3um long) hair-like echinae but there appears to be no ornament on the central body. No regular form of opening is apparent.

Remarks: *Stellichinatum* sp. 3 has longer processes relative to the width of the central body than *Stellichinatum* sp. 1. In addition, the former differs in lacking ornamentation on the central body.

Genus *Stelliferidium* Deunff, Gorka & Rauscher 1974.

Type species: *Stelliferidium striatulum* (Vavrdova) Deunff, Gorka & Rauscher 1974.

Generic description: Deunff, Gorka & Rauscher 1974, p.13.

Remarks: The author follows the interpretation of Molyneux & Rushton 1988 of this genus (p.57, 4th paragraph).

Stelliferidium cortinulum (Deunff) Deunff, Gorka & Rauscher 1974.

Plate 8, figs.4, 7, 8 & 9; pl.22, fig.7.

Synonomy: 1988, *Stelliferidium barbarum*, Elaouad-Debbaj.

Description: Deunff 1961a, p.41, pl.1, figs.8 & 10; Deunff, Gorka & Rauscher 1974, p.14.

Holotype: Deunff 1961, pl.1, fig.8. Age: Tremadoc.

Remarks: This species of *Stelliferidium* is characterised by the relatively broad processes with multifurcate terminations.

Stelliferidium pseudoornatum Pittau 1985.

Plate 9, figs.1, 2 & 3.

Description: Pittau 1985, p.195-196, pl.8, figs.11-12, text-fig.24.

Holotype: Pittau 1985, pl.8, fig.11. Age: Tremadoc-Late Arenig.

Remarks: The contention of Tongiorgi *in* Bagnoli, Stouge & Tongiorgi 1988 (p.201), upheld by Fensome *et al.* 1990 (p.460) that this species is a junior synonym of *Caldariola* (then *Priscogalae*) *glabra* (Martin) Molyneux & Rushton 1988 is rejected here. The illustrations and description of the type material clearly indicates ornamentation at the base of the processes on the vesicle. The processes, with the associated radial ornamentation, are absent in *C. glabra*.

Stelliferidium simplex (Deunff) Deunff, Gorka & Rauscher 1974.

Plate 8, fig.3.

Description: Deunff 1961a, p.41, pl.1, fig.9.

Holotype: Deunff 1961a, pl.1, fig.9. Age: Tremadoc.

Remarks: Included here are forms with short processes (<5um in length) with accuminate and capitate distal terminations.

Stelliferidium cf. *simplex* (Deunff) Deunff, Gorka & Rauscher 1974.

Plate 8, fig.5.

Holotype: Deunff 1961a, pl.1, fig.9. Age: Tremadoc.

Remarks: Compare with Deunff 1961a, p.41, pl.1, fig.9. Specimens here have longer processes (8-10um) than in the type material (*ca.* 5um). Included here are forms with processes greater than 5um in length with accuminate and capitate distal terminations.

Stelliferidium striatulum (Vavrdova) Deunff, Gorka & Raucher 1974.

Plate 8, figs.1 & 2; pl.22, fig.8.

Description: Vavrdova 1966b, p.411-412, pl.1, fig.2; pl.2, fig.3, text-fig. 3a.

Holotype: Vavrdova 1966b, pl.2, fig.3. Age: Arenig.

Remarks: Processes in this species are multifurcate at the distal terminations as in *S. cortinulum* but the shafts are markedly thinner and generally shorter.

Stelliferidium trifidum (Rasul) Fensome *et al.* 1990.

Plate 7, figs.10-13; pl.22, figs.9, 10 & 11?

Synonomy: 1988, *Stelliferidium distincta*, Elaouad-Debbaj.

Description: Rasul 1974, p.60, pl.5, fig,7.

Holotype: Rasul 1974, pl.5, fig.7. Age: Tremadoc.

Remarks: *Stelliferidium trifidum* is morphologically similar to *S. timofeevii* (Deunff) Fensome *et al.* 1990. Illustrations and description of both species by these authors shows distinct similarity in shape of the central body and the size, number and distribution of processes. However, the process terminations are the critical feature. Rasul (1974, p.60) distinguishes his species by having trifid process tips in contrast to Deunff (1961a, p.39) who described his species as having simple or grooved (bifid) processes.

Genus *Stellinium* Jardine *et al.* 1972.

Type species: *Stellinium octoaster* (Staplin) Jardine *et al.* 1972.

Generic description: Jardine *et al.* 1972, p.298.

Remarks: These forms have a star-shaped outline composed of triangular expansions positioned in at least two planes. The expansions are commonly crested.

Stellinium comptum Wicander & Loeblich 1977.

Plate 176, figs.7 & 8; pl.183, fig. 7; pl.188, fig.5; pl.194, fig.9.

Description: Wicander & Loeblich 1977, p.151, pl.9, figs.1-6.

Holotype: Wicander & Loeblich 1977, pl.9, figs.1-4. Age: Late Devonian.

Remarks: This species is distinguished by having a quadrate, more or less square, vesicle outline.

Stellinium octoaster (Staplin) Jardine *et al.* 1972.

Plate 155, fig.10; pl.167, figs.6 & 8; pl.176, figs.5 & 6; pl.183, fig.8; pl.188, fig.7; pl.194, figs.3, 6, 7 & 8.

Description: Staplin 1961, p.413-414, pl.49, figs.3 & 4.

Holotype: Staplin 1961, pl.49, fig.3. Age: Late Devonian.

Remarks: *Stellinium micropolygonale* (Stockmans & Williere) Playford 1977 is considered to be a junior synonym of this species (Fensome *et al.* 1990). *Stellinium octoaster* incorporates forms with more than four processes in one plane (i.e. in outline) when compressed on a palynological slide. *Stellinium comptum* has only four processes forming the outline.

Genus *Striatotheca* Burmann 1970.

Type species: *Striatotheca principalis* Burmann 1970.

Generic description: Burmann 1970, p.299-300; for an English translation see Eisenack, Cramer & Diez 1979, p.755.

Striatotheca principalis Burmann 1970.

Plate 23, figs.1, 2 & 3; pl.34, fig.1; pl.43, figs.4 & 5.

Description: Burmann 1970, p.300, pl.11, fig.1.

Holotype: Burmann 1970, pl.11, fig.1. Age: Late Arenig-Early Llanvirn.

Remarks: Specimens assigned here have relatively fine striations on the central body that extend onto the process shafts.

Striatotheca principalis var. *parva* Burmann 1970.

Plate 34, figs.2 & 3.

Description: Burmann 1970, p.300, pl.8, fig.6.

Holotype: Burmann 1970, pl.8, fig.6. Age: Late Arenig-Early Llanvirn.

Remarks: This variety has thin processes with relatively few, coarse striations on the central body that do not extend onto the process shafts.

Striatotheca quieta (Martin) Rauscher 1973.

Plate 34, fig.4.

Description: Martin 1969, p.100, pl.5, fig.226; pl.6, fig.290; for an English translation see Eisenack, Cramer & Diez 1979, p.773-774.

Holotype: Martin 1969, pl.6, fig.290. Age: Middle-Early Ludlow, see remarks.

Remarks: The type material described from Belgium outcrop is believed to be reworked from the Ordovician (Eisenack, Cramer & Diez 1979, p.773). This species has shorter processes at the apices of the vesicle than *S. principalis*.

Genus *Tetraporina* (Naumova *ex* Bolkhovitina) Kar & Bose 1976

Synonomy: 1972, *Horologinella*, Jardine *et al*, p.296.

Type species: *Tetraporina pellucida* Naumova ex Bolkovitina 1953. (Lectotype designated by Jansonius & Hills 1981, card 3197.

Generic description: Kar & Bose 1976, p.79.

Remarks: The type species of the genus *Horologinella* Cookson & Eisenack 1962 is a dinoflagellate cyst. This genus should therefore be restricted to accommodate palynomorphs of that group. Acritarchs with a superficially similar morphology to *Horologinella* are best accommodated in the genus *Tetraporina*.

Tetraporina horologia Staplin 1960.

Plate 194, fig.12.

Synonomy: 1972, *Horologinella horologia*, Jardine *et al.*, p.296.

Description: Staplin 1960, p.6, pl.1, figs.4 & 6.

Holotype: Staplin 1960, pl.1, fig.4. Age: Carboniferous.

Remarks: This species has broad, descrete lobes at the apices of the four-sided vesicle. *Tetraporina quadrispina* has a more angular aspect to the vesicle with longer expansions at the apices.

Tetraporina quadrispina (Jardine *et al.*) comb nov.

Plate 194, figs.10 & 11.

Synonomy: 1972, *Horologinella quadrispina*, Jardine *et al.*, p.296, pl.1, figs.5 & 6.

Description: Jardine *et al.* 1972, p.296, pl.1, figs. 5 & 6.

Holotype: Jardine *et al.* 1972, pl.1, figs 5. Age: Upper Devonian, probably Famennian.

Remarks: This species is recombined with the genus *Tetraporina* as *Horologinella* is a dinoflagellate cyst genus.

The species is distinguished by the extended lobes at the apices of the four sided vesicle. The inter-lobe areas are highly concave.

Genus *Thysanoprobolus* Loeblich & Tappan 1970.

Type species: *Thysanoprobolus polykion* Loeblich & Tappan 1970.

Generic description: Loeblich & Tappan 1970, p.261.

Thysanoprobolus polykion Loeblich & Tappan 1970.

Plate 109, figs.10 & 11; pl.141, fig.3.

Synonomy: 1970 *Multiplicisphaeridium bonitum* Cramer, p.150-152, pl.15, figs.207-209 & 213, text-fig.55a.

Description: Loeblich & Tappan 1970, p.262-266, figs.1-12.

Holotype: Loeblich & Tappan 1970, figs.10-12. Age: Early Gedinnian.

Remarks: From the descriptions and illustrations of the type material, *Multiplicisphaeridium bonitum* Cramer 1970 *ex* Eisenack, Cramer & Diez 1973, described from the late Silurian-early Devonian of NW Spain, appears to be synonymous with *T. polykion.*

Genus *Tongzia* Li Jun 1987.

Type Species: *Tongzia meitana* Li Jun 1987.

Generic description: Li Jun 1987, p.626.

Tongzia meitana Li Jun 1987.

Plate 9, figs.12 & 13; pl.23, figs.4, 8, 9 & 10.

Description: Li Jun 1987, p.626, 628, pl.69, figs.1-3.

Holotype: Li Jun 1987, pl.69, fig.1. Age: Arenig.

Remarks: Specimens recorded here are generally poorly preserved. The species is distinguished by its spherical central body and the palmate, first order branching of the distal terminations of the hollow processes.

Vavrdova (1990) recorded this species from the Late Arenig of Czechoslovakia.

Genus *Trematophora* Eisenack 1965.

Type species: *Trematophora radiata* Eisenack 1965.

Generic description: Eisenack 1965, p.270.

Remarks: In his erection of the species *T. radiata*, Eisenack (1965, p.270) neglected to diagnose the new genus, *Trematophora*, into which he had placed his new species. As the genus is, to the present authors knowledge, monospecific, the diagnosis given for the species *T. radiata* also stands as the generic diagnosis.

Trematophora radiata Eisenack 1965.

Plate 79, figs.1, 2 & 3; pl.87, fig.4.

Description: Eisenack 1965, p.270, pl.23, figs.4 & 5.

Holotype: Eisenack 1965, pl.23, figs.4. Age: Wenlock.

Remarks: Specimens recorded here are the same size and have the same general morphology as the holotype.

Genus *Triangulina* Cramer 1964.

Type species: *Triangulina alargada* Cramer 1964.

Generic description: Cramer 1964, p.334.

Remarks: These triangular veryhachid-shaped forms are distinguished by having a two-layered wall structure in which there are cavations present between the wall layers at the apices of the vesicle.

Triangulina sanpetrensis (Cramer) Fensome *et al.* 1990.

Plate 110, fig.1?; pl.116, fig.5?; pl.123, fig.1; pl.156, fig.1?

Description: Cramer 1966, p.88, pl.2, figs. 14 & 15, text-fig.2, no.14.

Holotype: Cramer 1966, pl.2, fig.14. Age: Ludlow- Early Gedinnian?

Remarks: *Triangulina alargada* Cramer 1964 has a very similar morphology to *T. sanpetrensis*. It differs in the shape of the central body, the former having a rounded-triangular shape, the latter having a triangular shape with a more angular aspect.

Triangulina alargada Cramer 1964.

Plate 141, figs.4, 7 & 10; pl.150, figs.6 & 8.

Description: Cramer 1964, p.334-335, pl.6, figs.1 & 4, text-fig.39.

Holotype: Cramer 1964, pl.6, fig.4. Age: Emsian.

Remarks: This species is distinguished by the rounded inner body. Forms transitional between *T. alargada* and *T. sanpetrensis* have been recorded in the present study.

Genus *Trichosphaeridium* Timofeev 1966.

Type species: *Trichosphaeridium annolovaense* Timofeev 1966.

Generic description: Timofeev 1966, p.37.

Trichosphaeridium annolovaense Timofeev 1966.

Description: Timofeev 1966, p.37-38, pl.8, fig.5.

Holotype: Timofeev 1966, pl.8, fig.5. Age: Middle Cambrian.

Remarks: Two varieties of this relatively simple morphotype are recorded here. The varieties of this species are distinguished on the size of the central body and minor differences in the thickness of the wall.

Trichosphaeridium annolovaense var. A.

Plate 9, figs.4 & 8.

Remarks: Included here are relatively small forms (50-70um in maximum diameter) with a moderately thick wall.

Trichosphaeridium annolovaense var. B.

Plate 9, figs.7.

Remarks: These are relatively large forms (70-100um in maximum diameter) with a thin wall.

Genus *Tunisphaeridium* Deunff & Evitt 1968.

Type species: *Tunisphaeridium tentaculiferum* (Martin) Cramer 1970.

Generic description: Deunff & Evitt 1968, p.2.

Remarks: Species included in this genus have a spherical central body with thin, solid processes supporting a thin outer membrane.

Tunisphaeridium tentaculiferum (Martin) Cramer 1970.

Plate 116, fig.6.

Description: Martin 1967, p.312, pl.1, fig.23, text-fig.3.

Holotype: Martin 1967, pl.1, fig.23. Age: Silurian.

Remarks: A single damaged specimen is recorded here. However, the spherical central body, the slender capitate processes and the membrane are all discernible on the specimen. *Tunisphaeridium parvum* Deunff & Evitt 1968 has shorter processes than *O. tentaculaferum*.

cf. *Tunisphaeridium* sp.

Plate 156, fig.4; pl.167, figs.7 & 9.

Remarks: Specimens included here have an identical central body and process shaft morphology to *T. tentaculiferum*. However, these specimens have a pad shaped distal termination to the processes and they lack the outer membranous wall layer that characterises species of the genus *Tunisphaeridium*. The lack of outer wall layer may be a function of the preservation.

Genus *Tylotopalla* Loeblich 1970.

Type species: *Tylotopalla digitifera* Loeblich 1970.

Generic description: Loeblich 1970.

Tylotopalla astrifera Kiryanov 1978.

Plate 74, figs.1 & 2.

Description: Kiryanov 1978, p.86, pl.13, figs.5a-b.

Holotype: Kiryanov 1978, pl.13, figs.5a-b. Age: Wenlock.

Remarks: A morphologically similar species is *T. deerlijkianum* (Martin) Le Herisse 1989 which also possesses striate ornamentation that is best developed at the process bases. This species differs from *A. astrifera* in having a lower density of processes on the central body. Specimens recorded here are 59-64um in diameter which is towards the larger end of the rather broad size range for the species (39-72um) given by Kiryanov.

Tylotopalla cf. *deerlijkianum* (Martin) Le Herisse 1989.

Plate 64, fig.1.

Holotype: Martin 1973, pl.5, fig.167. Age: Ashgill-Early Llandovery.

Remarks: Compare with Martin 1973, p.23, pl.5, figs.167, 173. The poorly preserved specimens observed show the same morphology and density of processes on the central body as the type material. The size of the specimens here, 100-111um in diameter, is markedly greater.

Tylotopalla cf. *wenlockia* Dorning 1981.

Plate 74, figs.3, 4 & 7.

Holotype: Dorning 1981, pl.2, fig.4. Age: Wenlock.

Remarks: Compare with Dorning 1981, p.200, pl.2, fig.4. The poorly preserved specimens recorded here have approximately the same number and distribution of processes as the holotype but differs in the processes being of a shorter length.

Genus *Umbellasphaeridium* Jardine *et al.* 1972.

Type species: *Umbellasphaeridium saharicum* Jardine *et al.* 1972.

Generic description: Jardine *et al.* 1972, p.302-303.

Remarks: Species in this genus possess processes that have open and flared distal terminations.

Umbellasphaeridium deflandrei Moreau-Benoit 1967 *ex* Jardine *et al.* 1972.

Plate 176, figs.3 & 4; pl.183, figs.6, 9, 10 & 11; pl.195, figs.4 & 5.

Description: Moreau-Benoit 1967, p.203, pl.1, figs.22-23.

Holotype: Moreau-Benoit 1967, pl.1, figs.22-23. Age: Emsian.

Remarks: This species is distinguished from *U. saharicum* by the greater number of processes present on the vesicle, more than 10, which are shorter in length.

Umbellasphaeridium saharicum Jardine *et al.* 1972.

Plate 193, fig.9; fig.195, figs.1 & 2.

Description: Jardine *et al.*, p.303, pl.2, figs.11 & 12, pl.3, fig.1.

Holotype: Jardine *et al.* 1972, pl.2, fig.12: Age: Famennian.

Remarks: This species has relatively few, between four and 10 in number, trumpet-shaped processes. *Umbellasphaeridium deflandrei* has shorter and a greater number of processes (more than 10) that are generally shorter in length.

Genus *Uncinisphaera* Wicander 1974.

Type species *Uncinisphaera lappa* Wicander 1974.

Remarks: The genus *Stellichinitum* differs from *Uncinisphaera* in having a polygonal aspect to the central body.

Uncinisphaera? sp. 1.

Plate 23, figs.11, 12 & 13; pl.34, fig.10.

Description: Acanthomorphic acritarchs with a spherical central body of 35-40um maximum diameter. The processes are long and slender (upto 22um long and 2-3um wide at the base) and have simple distal terminations. The ratio of process length to body width is approximately 2:3. The wall is ornamented with short (<2um) hair-like echinae and no regular form of opening is apparent.

Remarks: This taxon is questionably assigned to the genus *Uncinisphaera* as the communication between processes and central body is not discernible in the carbonised specimens observed.

The only formally described species in this genus from the Ordovician is *U. protea* Playford & Wicander 1988. This species would appear to be better placed in the genus *Stellechinatum* as it possesses a polygonal central body. Molyneux (1987) published six forms that were questionably assigned to *Uncinisphaera* in open nomenclature from the Arenig of South Wales. *Uncinisphaera*? sp. 1 described in the present study has longer processes than any of those forms described by Molyneux.

Genus *Veliferites* Brito 1967a.

Type species: *Veliferites tunuimarginatus* Brito 1967a.

Remarks: Species included in this genus have a four, five or six sided flattened veryhachid-type vesicle. There is a thin transparent membrane at the equator of the vesicle which is supported by short processes at the apices. The genus *Duvernaysphaera* differs by possessing a discoid-shaped central body.

Veliferites? sp.

Plate 65, figs.1 & 2.

Remarks: Specimens included here have a five-sided flattened central body, 32-37um in diameter, with five short processes (4-7um long) at the apices. The membrane or velum is not fully preserved in the specimens observed, however, remnants of the membrane are evident in the viscinity of the processes.

Genus *Veryhachium* Deunff emend. Turner 1984.

Type species: *Veryhachium trisulcum* Deunff 1951 *ex* Deunff 1959.

Generic description: Turner 1984, p.139-140.

Remarks: The emendation of the genus by Turner 1984 states that the wall may be smooth or ornamented with grana. Forms with short spines or echinae are included in the genus *Villosacapsula* Loeblich & Tappan 1976.

Veryhachium cf. *arcarium* Wicander & Loeblich 1977.

Plate 156, fig.7; pl.168, fig.1-4.

Holotype: Wicander & Loeblich 1977, pl.10, figs.1 & 2. Age: Late Devonian.

Remarks: Compare with Wicander & Loeblich 1977, p.154, pl.10, figs.1 & 2. The specimens included here have a larger central body and longer, more slender processes than *V. arcarium*. The specimens here are almost identical in morphology to the thesis taxon *V. polyaster* subsp. *acutum* Deunff 1966 which is nomen nudum. The species *V. pentaster* Staplin 1961 has more concave vesicle sides than *V.* cf. *arcarium*.

Veryhachium cf. *cymosum* Wicander & Loeblich 1977.

Plate 168, figs.6 & 7.

Holotype: Wicander & Loeblich 1977, pl.10, figs.7 & 8. Age: Late Devonian.

Remarks: Compare with Wicander & Loeblich 1977, p.155, pl.10, figs.5-10. The specimens included here have the same arrangement of processes and the same size dimensions as *V. cymosum* but differ slightly in the nature of the distal terminations of the processes. The terminations in this taxon are more blunt with rounded tips than the sharply accuminate tips of the processes of the type specimens. *Veryhachium europaeum* Stockmans & Williere 1960 has a similar process number and arrangement as *V.* cf. *cymosum* but has more slender processes with sharply accuminate tips.

Veryhachium downiei Stockmans & Williere 1962.

Plate 150, fig.7; pl.195, fig.9?

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Description: Stockmans & Williere 1962a, p.47-48, pl.2, figs.20-22, text-fig.2; for an English translation see Eisenack, Cramer & Diez 1979, p.394.

Holotype: Stockmans & Williere 1962a, pl.2, fig.21. Age: Devonian.

Remarks: Specimens included here are generally poorly preserved.

Veryhachium downiei var. *downiei* Stockmans & Williere 1962.

Plate 177, fig.1; pl.184, fig.1; pl.188, fig.8; pl.195, figs.6, 7 & 8.

Description: Stockmans & Williere 1962a, p.47-48, pl.2, figs.20-22, text-fig.2; for an English translation see Eisenack, Cramer & Diez 1979, p.394.

Holotype: Stockmans & Williere 1962a, pl.2, fig.21. Age: Devonian.

Remarks: Specimens included here are those closely resembling the holotype of the species.

Veryhachium europaeum Stockmans & Williere 1960.

Plate 131, fig.2; pl.168, fig.5; pl.177, fig.2.

Description: Stockmans & Williere 1960, p.3, pl.2, fig.25.

Holotype: Stockmans & Williere 1960, pl.2, fig.25. Age: Frasnian.

Remarks: This relatively simple species of *Veryhachium* has four processes, three at the apices of the three sided vesicle and one protruding from the interapical region. The vesicle wall is smooth.

Veryhachium cf. *europaeum* Stockmans & Williere 1960.

Plate 87, figs.9 & 10; pl.123, fig.2.

Holotype: Stockmans & Williere 1960, pl.2, fig.25. Age: Frasnian.

Remarks: Compare with Stockmans & Williere 1960, p.3, pl.2, fig.25. Specimens assigned here have the same arrangement of the four processes that are present as in the type specimen but differ in having a more convex vesicle. Specimens assigned to *V. europaeum* by Cramer 1964 are very similar in morphology to the specimens assigned here.

Veryhachium lairdii Deflandre 1946 *ex* Loeblich 1970.

Plate 9, fig.9; pl.34, fig.6; pl.116, fig7.

Description: Deunff 1959, p.28, pl.8, figs. 75-79.

Holotype: Deunff 1959, pl.8, fig.75. Age: Middle Silurian.

Remarks: *Veryhachium lairdii* was considered to be a junior synonym of *V. valiente* Cramer 1964 by Martin 1969, p.95, Turner 1984, p.141-142 and Fensome *et al.* 1990, p.517. However, Cramer (1964) states in his remarks (under the sub-heading 'Similar forms', p.311) that *V. valiente* differs by having a more straight sided vesicle between the processes. This morphological differentiation is retained here as the specimens observed are more similar to the holotype *V. lairdii* with concave sides than that of *V. valiente* which is more straight sided.

Veryhachium longispinosum? Jardine *et al.* 1974.

Plate 24, fig.6; pl.51, figs.4, 6 & 7.

Description: Jardine *et al.* 1974, p.116, pl.1, fig.1; for an English translation see Eisenack, Cramer & Diez, 1979, p.449.

Holotype: Jardine *et al.* 1974, pl.1, fig.1. Age: Late Ordovician.

Remarks: Specimens are questionably assigned to *V. longispinosum* because the processes of the specimens recovered are broken. The central body and proximal parts of the processes are morphologically identical to the holotype.

Veryhachium minutum Downie 1958 emend.

Plate 141, fig.6; pl.51, figs.4, 6 & 7.

Holotype: Downie 1958, pl.17, fig.4. Age: Tremadoc.

Description: Downie 1958, p.344, pl.17. fig.4.

Emended description: A small species of *Veryhachium* with between four and six processes. Four processes are positioned at the apices of the equidimensional to slightly elongate central body, minor accessory processes may be present between the apical processes. The flattened central body has sides that are straight to slightly concave and it measures 10-30um in length and 10-25um in width. The processes are simple with accuminate distal terminations and they have a rather rigid, firm appearance. The processes measure between 8-30um in length. The wall of the vesicle is smooth or may have a scabrate surface. Opening of the vesicle is by epityche.

Remarks: The original description given by Downie (1958) states size dimensions for the vesicle of 3-15um. The species is broadened here to include larger forms of upto 30um vesicle width. *Veryhachium lairdii* Deflandre 1946 *ex* Loeblich is larger and has more concave sides. *Veryhachium valiente* Cramer 1964 has a similarly straight sided vesicle but is also larger in size.

From the specimens observed, three morphological varieties of this species can be recognised based on the length and number of the processes:

Veryhachium minutum var. A.

Plate 24, fig.11; pl.43, figs.7 & 8.

Remarks: Specimens here have processes that are shorter than the vesicle length. This variety is relatively common.

Veryhachium minutum var. B.

Plate 24, fig.10; pl.43, fig.9.

Remarks: Specimens here have processes that are longer than the vesicle length. This variety is relatively rare.

Veryhachium minutum var. C.

Plate 43, figs.10 & 11.

Remarks: Specimens here have a fifth and occasionally sixth process present which alters the simple four-sided outline of the vesicle. This variety is relatively rare.

Veryhachium reductum (Deunff) Downie & Sarjeant 1965.

Plate 12, fig.1; pl.35, figs.4 & 5; pl.44, figs.1, 5 & 6; pl.52, figs.2, 4 & 6; pl.65, fig.4.

Description: Deunff 1959, p.27-28, pl.1, figs.1, 3, 8, 10-12, 14, 16-17, 22-23.

Holotype: Deunff 1959, pl.1, fig.10. Age: Caradoc.

Remarks: The intraspecific variety illustrated by Deunff (1959, pl.1) is a good reflection of forms observed here. The central body has a maximum diameter ranging between 20-40um and the process length ranges between 10-30um. *Veryhachium trisulcum* Deunff 1951 *ex* Deunff 1959 has longer processes. *Villosacapsula setosapellicula* (Loeblich) Loeblich & Tappan 1976 has a similar body shape, spine length and overall size dimensions to *V. reductum* but differs in possessing an ornament of short spines or echinae.

Veryhachium subglobosum Jardine *et al.* 1974.

Plate 44, figs.8, 10, 11 & 12; pl.52, figs.1, 3 & 5.

Description: Jardine *et al.* 1974, p.115-116, pl.1, fig.2.

Holotype: Jardine *et al.* 1974, pl.1, fig.2. Age: Late Ordovician.

Remarks: This relatively large species of *Veryhachium* (central body 40-60um in maximum diameter; processes 30-100um in length) is characterised by the globose central body and long slender processes. Specimens recorded here have processes at the lower end of the size spectrum for the species that was given in the original diagnosis. Processes of the specimens observed here are commonly 30-35um in length. Breakage is common due to poor preservation.

A morphologically similar form is *V. trisulcum* var. *venutum* Deunff 1959, but this form has a more angular central body.

Veryhachium trapezionarion Loeblich 1970.

Plate 87, fig.7.

Description: Loeblich 1970, p.743 & 744, figs.38A-C.

Holotype: Loeblich 1970, fig 38B. Age: Middle Silurian.

Remarks: *Veryhachium rhomboidium* Downie 1959 is smaller in size and has a thinner wall than *V. trapezionarion*. The contention made by Turner (1984, p.145) that the former is a senior synonym of the latter is rejected here. *Veryhachium valiente* has fewer and shorter processes and is generally smaller in size than *V. trapezionarion*. *Veryhachium pertonense* Dorning 1981 is similar in terms of shape, size and number and distribution of processes but differs in having a granular as opposed to a smooth wall.

Veryhachium cf. *trapezionarion* Loeblich 1970.

Plate 73, fig.8.

Holotype: Loeblich 1970, fig 38B. Age: Middle Silurian.

Remarks: Compare with Loeblich 1970, p.743 & 744, figs.38A-C. The four specimens included here have the same number and distribution of processes and the same general shape as *V. trapezionarion* but differ in the process to central body ratio. The ratio is approximately 1:1 in *V. trapezionarion* in contrast with a ratio of approximately 2:1 in *V.* cf. *trapezionarion*.

Veryhachium trisulcum Deunff 1951 *ex* Deunff 1951.

Description: Deunff 1959, p.27-28, pl.1, figs.1-4, 8, 10, 12-14, 16, 17, 20, 22 & 23.

Holotype: Deunff 1959, pl.1, fig.4. Age: Middle Ordovician.

Remarks: Two varieties of this species have been recorded in the present study.

Veryhachium trisulcum var. *trisulcum* (Deunff) Fensome *et al.* 1990.

Plate 24, figs.2 & 3.

Description: Deunff 1959, p.27-28, pl.1, fig.4.

Holotype: Deunff 1959, pl.1, fig.4. Age: Middle Ordovician.

Remarks: The specimens observed here are rather poorly preserved. The small central body distinguishes this variety from *V. trisulcum* var. *venutum* Deunff 1959.

Veryhachium trisulcum var. *venutum* Deunff 1959.

Plate 43, fig.12; pl.44, fig.2.

Description: Deunff 1959, p.27-28, pl.1, figs.2 & 20.

Holotype: Deunff 1959, pl.1, fig.2. Age: Ordovician.

Remarks: *Veryhachium subglobosum* Jardine *et al.* 1974 differs by having a more globose central body.

Veryhachium valiente Cramer 1964.

Plate 87, fig.5.

Description: Cramer 1964, p.311, pl.12, figs.3, 4 & 6.

Holotype: Cramer 1964, pl.12, fig.3. Age: Late Ludlow-Emsian.

Remarks: *Veryhachium lairdii* differs from *V. valiente* in having concave as opposed straight sided inter-apical outline.

Veryhachium wenlockianum (Downie *ex* Wall & Downie) Downie & Sarjeant 1965.

Plate 65, fig. 3; pl.110, figs.2, 3, 5 & 6; pl.116, figs.8 & 9; pl.131, fig.1; pl.141, fig.5.

Description: Downie 1959, pl.12, figs.9 & 11.

Holotype: Downie 1959, pl.12, fig.9. Age: Wenlock.

Remarks: This species is distinguished by the small three-sided central body and the three long needle-like processes. The processes are commonly broken in the material observed.

Veryhachium sp. 1.

Plate 45, fig.1 & 2.

Description: A species of *Veryhachium* with three processes and a concave or straight sided central body, rarely with slightly convex sides. The central body measures between 30-41um in maximum diameter. Processes are simple and measure upto 18um in length and are commonly broken.

Remarks: The angularity of the central body distinguishes this species from other tri-processed forms described from the Ordovician. *Veryhachium reductum* (Deunff) Downie & Sarjeant 1965 is of similar size and process morphology but has a more convex central body.

Veryhachium sp. 3.

Plate 45, fig.3.

Description: A three sided species of *Veryhachium* with three short (<5um in length) accuminate processes at the apices of the vesicle. The wall has a finely granulate ornament giving it a scabrate appearance. The vesicle is 30-40um in maximum diameter. Opening is by epityche.

Remarks: *Villosacapsula entrichos* (Loeblich) comb nov. has a similar central body and process shape but differs by being covered in short conical spines of upto 2um in length.

Veryhachium sp. 4.

Plate 44, figs.3, 4, 7 & 9.

Description: A species of *Veryhachium* with three sides and three short (<5um in length) truncated processes at the apices of the central body. The central body has convex sides and has a maximum diameter of 30-40um. The wall is relatively thick, 1-2um, and has a smooth distinctive porcelain-like texture. The truncated tips of the processes bare slight thickenings of the wall in some specimens.

Remarks: This species is distinguished by the short truncated processes, the convex central body and the thick porcelain-like wall.

Veryhachium sp. 5.

Plate 45, fig.5.

Description: A species of *Veryhachium* with three sides and three short (<5um in length) truncated processes at the apices of the central body. The central body has concave-straight sides and has a maximum diameter of 28-37um. The wall is relatively thick, 1-2um, has a porcelain-like textured and is smooth. The truncated tips of the processes bare slight thickenings of the wall in some specimens.

Remarks: This species is distinguished by its short truncated processes, concave-straight sided central body and thick 'porcelain-like' textured wall. This form is distinguished from *Veryhachium* sp. 4 by the straight sided as opposed to convex sided vesicle.

Veryhachium sp. 7.

Plate 10, figs.1-4.

Description: A species of *Veryhachium* with four sides and four processes positioned at the apices of the central body. The central body is square to slightly rectangular in outline and has slightly convex sides. The maximum diameter of the vesicle measures between 30-35um. The processes are broad at the bases (<1um) and taper distally to truncated tips. Their length varies between 5-15um. The wall of the vesicle is very thick (>1um) and no ornamentation is visible. Opening of the vesicle is by epityche.

Remarks: This species is distinguished by its truncated processes and thick walled robust vesicle.

Veryhachium sp. 8.

Plate 9, fig.10.

Description: A species of *Veryhachium* with four sides and four long slender processes at the apices of the central body. The central body is rectangular in outline and measures between 28-32um in length and 18-21um in width. The processes are 3-4um wide at the bases and taper distally to accuminate tips. Process length ranges between 20-29um. At the junctions of the processes and the central body the wall is punctured with pores of approximately 1um in diameter. Opening of the vesicle is by epityche.

Remarks This species is distinguished by the rectangular central body, the long slender processes and the punctured vesicle wall.

Veryhachium? sp. 9.

Plate 65, figs.7, 8 & 9.

Description: A veryhachid-shaped species with three sides and three processes positioned at the apices of the vesicle. The central body has convex sides and is 40-65um in maximum diameter. The processes are plugged at the bases and hollow distally. The processes on all the specimens recorded here are broken. The vesicle wall is thick (*ca.* 1um), smooth and dark in colour which contrasts with the lighter coloured hollow processes.

Remarks: The distal terminations of the processes have not been observed due to the poor preservation of specimens, hence the questioned assignment of these forms to the genus *Veryhachium*. *Veryhachium checkleyensis* Dorning 1981 has a similarly thick vesicle wall and thinner walled processes, however, *Veryhachium* sp. 9 has a larger central vesicle. Poor preservation of specimens recorded does not permit comparison of the processes between these two species.

Veryhachium? sp. 10.

Plate 65, figs.10 & 11.

Description: A veryhachid-shaped species with three sides and three processes at the apices of the vesicle. The central body has slightly convex sides and measures between 32-38um in maximum diameter. The processes are plugged at the bases and are hollow distally. The processes on all the specimens recorded here are broken. The vesicle wall is very thick (*ca.* 2um) and has a granulate ornament. The processes are thin walled and smooth.

Remarks: The distal terminations of the processes have not been observed due to the poor preservation of specimens, hence the questioned assignment of these forms to the genus *Veryhachium*. *Veryhachium*? sp. 10 has similar morphology to *Veryhachium*? sp. 9 (herein) but differs in having a thicker, granular wall.

Genus *Villosacapsula* Loeblich & Tappan 1976.

Type species: *Villosacapsula setosapellicula* (Loeblich) Loeblich & Tappan 1976.

Generic description: Loeblich & Tappan 1976, p.307-308.

Remarks: Veryhachid forms with short spines or echinae are included here.

Villosacapsula fakirum (Martin) comb. nov.

Plate 24, fig.9?

Synonomy: 1968, *Veryhachium fakirum*, Martin, p.93-94, pl.2, figs.109 & 110; pl.6, fig.256, text-figs. 42 & 43.

Description: Martin 1968, p.93-94, pl.2, figs.109 & 110; pl.6, fig.256, text-figs. 42 & 43.

Holotype: Martin 1968, text-fig. 42. Age: Ordovician-Silurian. The holotype is believed to be reworked from the Ordovician (Eisenack, Cramer & Diez 1979, p.411).

Remarks: The morphological limits of *Veryhachium* and *Villosacapsula* outlined in the generic remarks above necessitate the transfer of *Veryhachium fakirum* Martin 1968 to the genus *Villosacapsula*.

The few poorly preserved specimens of *V. fakirum* observed have a scabrate wall with rare echinae. The lack of echinae is believed to be the result of the poor preservation.

Villosacapsula horridum (Paris & Deunff) comb. nov.

Plate 45, fig.5.

Synonomy: 1970, *Veryhachium horridum*, Paris & Deunff, p.27, pl.1, fig.8; pl.3, fig.3.

Description: Paris & Deunff 1970, p.27, pl.1, fig.8; pl.3, fig.3.

Holotype: Paris & Deunff 1970, pl.1, fig.8. Age: Llanvirn.

Remarks: The morphological limits of *Veryhachium* and *Villosacapsula* outlined in the generic remarks above necessitates the transfer of *Veryhachium horridum* Paris & Deunff 1970 to the genus *Villosacapsula.*

Villosacapsula setosapellicula (Loeblich) Loeblich & Tappan 1976.

Plate 45, figs.7,8,10-12.

Description: Loeblich 1970, p.743, figs.36A-B, 37A-B.

Holotype: Loeblich 1970, fig.36A. Age: Ashgill.

Remarks: In the poorly preserved material observed here, the echinae are commonly abraded giving a granular appearance to the vesicle wall.

Villosacapsula sp. 2.

Plate 66, figs.1 & 2.

Remarks: Included here are two poorly preserved specimens, both with a four-sided central body and with four processes positioned at the apices. The sides of the central body are straight to slightly convex. The central body is approximately 25um in diameter and the processes vary between 10-28um in length. The vesicle and processes are ornamented with echinae. *Villosacapsula fakirum* has a larger central body than *Villosacapsula* sp. 2.

Genus *Virgatasporites* Combaz 1967.

Type species: *Virgatasporites rudii* Combaz 1967.

Generic description: Combaz 1967a, p.14.

Remarks: *Abacum* Fombella 1978 is a junior synonym of this genus (Fensome *et al.* 1990, p.23).

Virgatasporites rudii Combaz 1967.

Plate 10, figs.5 & 6.

Description: Combaz 1967a, p.12, pl.1, figs.27 & 28.

Holotype: Combaz 1967a, pl.1, fig.27. Age: Tremadoc.

Genus *Visbysphaera* Lister 1970.

Type species: *Visbysphaera dilatispinosa* (Downie) Lister 1970.

Generic description: Lister 1970, p. 98.

Visbysphaera microspinosa (Eisenack) Lister 1970.

Plate 88, fig.2; pl.141, fig.9.

Description: Eisenack 1954, 209-210, pl.1, fig.8.

Holotype: Eisenack 1954, pl.1, fig.8. Age: Wenlock.

Remarks: The intraspecific variation within this taxon recorded by Le Herisse (1989) is similar to that observed here. Within this spectra of morphotypes that have been observed here, three consistent varieties can be recognised which are defined as follows:

Visbysphaera microspinosa var. A.

Plate 66, figs.5 & 6; pl.74, figs.5, 6, 8 & 9; pl.81, fig.1

Remarks: The specimen recorded here have short (<2um) broad (1-2um) conate or baculate processes. The elements are of relatively low spatial density on the central body with >2um between each. The diameter of the vesicle varies considerably in this form, measuring between 35-70um.

This variety closely resembles some species of *Lophosphaeridium* but can be distinguished by the thick vesicle wall.

Visbysphaera microspinosa? var. B.

Plate 123, fig.7 & 8.

Remarks: Specimens included here have short (<3um long) broad (approximately 2um wide) baculate processes. The elements are densely spaced on the central body with <2um between each. The diameter of the vesicle measures between 45-60um. This variety is questionably included in this species as the wall is relatively thin in comparison with the other varieties.

Visbysphaera microspinosa var. C.

Plate 110, figs.7-10; pl.116, figs.10 & 11; pl.123, figs.4 & 5.

Remarks: Specimens included here have short (<3um) echinate processes. The elements are densely spaced on the central body with <2um between each. The diameter of the vesicle measures between 42-60um.

Visbysphaera cf. *oligofurcatum* (Eisenack) Lister 1970.

Plate 110, fig.4; pl.123, fig.3.

Holotype: Eisenack 1954, pl.1, fig.8. Age: Late Llandovery.

Remarks: Compare with Eisenack 1954, p.209-210, pl.1, fig.8. Specimens here have processes which have a more sparse distribution on the central body than *V. oligofurcatum.*

Visbysphaera pirifera (Eisenack) Kiryanov 1978.

Plate 66, fig.4.

Description: Eisenack 1954, p.206-207, pl.1, figs.1a-b; text-fig.1.

Holotype: Eisenack 1954, pl.1, figs.1a-b. Age: Late Llandovery.

Remarks: A morphologically comparable species is *V. dilatispinosa* (Downie) Lister 1970. Both *V. pirifera* and *V. dilatispinosa* have thin balloon-shaped processes protruding from the thick-walled, spherical central body. However, the processes on V. *dilatispinosum* are ornamented with echinae in contrast with the smooth processes of *V. pirifera.*

Visbysphaera sp. 1.

Plate 66, figs.7-11.

Description: Acanthomorphic acritarchs which have a robust, thick-walled, spherical central body ranging between 21-25um in maximum diameter. The processes are conical or clavate in shape. The processes length ranges in size from 5-9um in length and the processes number approximately 15-25 on each specimen. The process length to maximum body width ratio is approximately 1:4. The wall of the central body is composed of two wall layers giving it a relatively dark appearance. The wall of the processes is composed of a single layer and consequently appears relatively light in colour. The wall of the central body and the processes is smooth. No regular opening is apparent.

Remarks: This species of *Visbysphaera* is distinguished by the small, robust central body and the prominent processes. The variability in the nature of the processes which has been observed here is probably a function of poor preservation. The author would expect the clavate process form to predominate in better preserved material.

Visbysphaera pirifera has a very similar morphology to *Visbysphaera* sp. 1 in terms of body and process form. However, they differ in size, the former being approximately three times larger than the latter, and also in the degree of inflation of the processes. *Visbysphaera piriferum* has more distinctly club-shaped processes. *Visbysphaera dilatispinosa* is also larger in size and has an echinate ornamentation on the processes.

Visbysphaera sp. 3.

Plate 67, fig.1.

Remarks: The single specimens recorded here has a central body diameter of 85um. The processes are short (<10um) and have accuminate terminations. The specimen observed is rather poorly preserved and the processes are commonly damaged. *Visbysphaera oligofurcatum* has a smaller central body and longer processes relative to the central body diameter than *Visbysphaera* sp. 1. *Visbysphaera microspinosa* differs in having very short (<5um long) processes.

Genus *Vogtlandia* Burmann 1970.

Type species: *Vogtlandia ramifurcata* Burmann 1970.

Generic description: Burmann 1970, p.292.

Remarks: The genus *Vulcanisphaera* differs from *Vogtlandia* in possessing clusters of processes that radiate out from the same points on the central body.

Vogtlandia sp. 1.

Plate 10, figs.7-11.

Synonomy:
1988, *Vogtlandia coalita*, Molyneux & Rushton, fig.7d, e & f.
1989, *Vogtlandia coalita*, Cooper & Molyneux, fig.4e.

Description: Acanthomorphic acritarchs which have a polygonal central body ranging between 25-42um in maximum diameter. The processes shafts are conical or cylindrical in shape and have ramusculose distal terminations. The terminations may branch upto the 4th order. The processes length ranges in size from 25-30um in length and they number between 15-20 on each specimen. The process length to maximum body width ratio is approximately 1:1. In some specimens, there appears to be a grouping of processes at each pole with a girdle present. The wall is composed of a single wall layer and the processes communicate freely with the central body. The wall is smooth and no regular form of opening is apparent.

Remarks: Molyneux & Rushton (1988, fig. 7d, e, f) and Cooper & Molyneux (1989, fig. 4e) illustrate the same species as described here. They assigned it to *Vogtlandia coalita* Martin *in* Martin & Dean 1978. However, *V. coalita* is not a legitimate name as it was placed into synonomy with *V. flosmaris* (Deunff) Molyneux 1987 by Martin in the paper in which it was described, this was done as an addendum to that paper (Martin 1978, p. 19). *Vogtlandia coalita* is therefore considered to be a junior synonym of *V. flosmaris*. Specimens observed here have far more complex distal process terminations than the holotype of *V. flosmaris* and are therefore informally assigned to a new species.

Genus *Vulcanisphaera* Deunff 1961 emend. Rasul 1976.

Type species: *Vulcanisphaera africana* Deunff 1961.

Description: Rasul 1976, p.479.

Vulcanisphaera nebulosa Deunff 1961.

Plate 11, figs.1 & 2.

Synonomy: 1988, *Vulcanisphaera africana*, Elaouad-Debbaj, pl.4, figs.9, 10, 11, 13 & 14; pl.6, fig.2.

Description: Deunff 1961a, p.42, pl.2, fig.3

Holotype: Deunff 1961a, pl.2, fig.3. Age: Tremadoc.

Remarks: A morphologically similar species is *V. africana* Deunff 1961 but this form has less elaborate processes than *V. nebulosa*.

Vulcanisphaera simplex Jardine *et al.* 1974.

Plate 24, fig.6.

Description: Jardine *et al.* 1974, p.119, pl.2, fig.7.

Holotype: Jardine *et al.* 1974, pl.2, fig. 7. Age: Lower Tremadoc.

Remarks: This species is distinguished from others in the genus *Vulcanisphaera* by having an almost polygonal central body. This is due to broadening of the vesicle at the base of the processes. This species is also distinguished by having relatively simple furcations at the distal ends of the processes.

Genus *Winwaloeusia* Deunff 1977.

Type species: *Winwaloeusia distracta* (Deunff) Deunff 1977.

Generic description: Deunff 1977b, p.466.

Remarks: This genus is superficially similar to *Veryhachium*. It differs in the presence of crests on the vesicle wall forming a "pseudo-trilete mark". The vesicle opens by splitting into two parts which quite distinct from the epityche style of opening in *Veryhachium* species.

Winwaloeusia distracta (Deunff) Deunff 1977.

Plate 150, fig.5; pl.177, fig.5.

Description: Deunff 1966, p.22, fig.2.

Holotype: Deunff 1966, fig.2. Age: Middle-late Devonian.

Remarks: *Winwaloeusia ranulaeforma* Martin 1984 has an identical vesicle shape to *W. distracta* but differs in having an vesicle ornamented with grana. *Winwaloeusia tumida* Deunff 1977 has processes which have more constricted proximal terminations than the processes of *W. distracta*. These three species are closely similar in morphology.

Acritarch Form A.

Plate 11, figs.6, 7, 9 & 10.

Remarks: Acanthomorphic acritarchs which have a spherical to subspherical central body measuring 30-37um in diameter. The processes are short, 5-7m in length, with slightly tapering shafts in a distal direction. The ramusculose distal branching of the processes is to the 2nd or 3rd order. The central body to process ratio is approximately 5:1. The wall is composed of a single layer and the nature of the communication between the processes and the central body is not discernible in the specimens observed. No regular form of opening is apparent.

Species of the genus *Timofeevia* differs by having the central body divided into fields. *Vulcanisphaera* species have clusters of processes sprouting from the same point on the central body. *Vogtlandia* species differ in possessing a polygonal central body.

Acritarch Form B.

Plate 11, figs.3, 4 & 5.

Remarks: Acanthomorphic acritarchs which have a polygonal central body. The central body has a maximum diameter ranging between 25-32um (two specimens measured). There are approximately 15-20 processes which are 2-3um wide at the base and taper gradually to accuminate tips. They support a fine trabeculum running along the shaft. The processes are 13-15um in length. The central body to process ratio is approximately 2:1. The nature of the wall structure is indeterminate from the dark specimens observed. No regular form of opening is apparent.

This species is distinguished by the *Polygonium*-type central body, the process arrangement and the trabeculae running along the shafts of the processes. Only two specimens have been recorded.

Acritarch Form C.

Plate 45, fig.6.

Remarks: Acanthomorphic acritarchs which have a subspherical to ovate central body. The body is 25-34um in length and 21-24um wide. The processes are rigid, they have solid 'pin-like' shafts and bifurcating or trifurcating pinnae at the distal extremities. They range between 10-15um in length, number approximately 50 and are evenly distributed. The process to central body ratio is approximately 1:2. The wall is thin, smooth and appears to be composed of a single layer. Opening is by means of a pylome.

The wall of this form is very thin and has a very distinct hyaline appearance. The bifurcating pin-like processes are also diagnostic but they are commonly broken in this poorly preserved material.

Acritarch Form D.

Plate 25, figs.1-5.

Remarks: Acanthomorphic acritarchs which have a rigid spherical central body measuring between 39-48um in diameter. The processes appear to have hollow tubular shafts with fine branching pinnae sprouting from the distal ends. The processes are closely spaced and are approximately 100-150 in number. They measure between 9-13um in length, 2-4um wide at the base and they flare distally. The process to central body ratio is approximately 1:4. The wall appears to be composed of two layers, the outer layer forming the processes. There is no communication between the processes and the central body. The occasional openings that have been observed are pylomes.

These forms occur in high numbers in sample JW 5. Superficially they appear similar to *Lua erduapuziana* Martin & Yin Leiming 1988, however this species is reported as having an apical tabular extension with a circular opening which was not evident here. In addition, the processes are generally shorter and more robust distally.

Acritarch Form E.

Plate 67, figs.2 & 4.

Remarks: Spheromorphic acritarchs measuring between 60-92um in maximum diameter. The wall is composed of two layers that show variable degrees of separation. The vesicle is ornamented with low irregular verrucae and rugulae. The only method of opening observed is by medium split.

Species of *Dictyotidium* show a more regularly ordered polygonal pattern of ornamentation on the vesicle.

Acritarch Form F.

Plate 81, figs.1 & 4.

Remarks: Acanthomorphic acritarchs which have a rigid, spherical central body measuring between 40-48um in maximum diameter. The processes appear to have hollow tubular shafts with capitate or bifid distal terminations. The processes are closely spaced and are approximately 100 in number. They measure between 10-20um in length and 2-4um in width. The process to central body ratio is approximately 1:3.5. The wall is thin and is composed of a single layer. No regular form of opening is apparent.

Four specimens of this form are recorded from the Late Telychian (Llandovery) samples analysed here. The relationship between the processes and the central body, and the detail of the morphology of the process tips is not discernible from the specimens observed.

Acritarch Form G.

Plate 88, figs.4, 5, 7 & 8; pl.110, figs.11 & 12; pl. 117, fig.1; pl.123, figs.6 & 9; pl.141, fig.11.

Remarks: Forms included here are single walled acritarchs that when compressed have a circular outline. The outer margin of the circular vesicle (i.e. the outermost quarter of the radius of the vesicle) is always folded. The central part of the vesicle is generally not folded. The surface of the vesicle may be smooth or ornamented with ridges. No regular form of opening is apparent.

The regularity in the arrangement and distribution of the folds distinguishes Acritarch Form G from the genus *Leiosphaeridia*. The genus *Saharidia* has a similar tendency to possess peripheral folds but can be distinguished by having a smooth or finely granulate surface with a central pylome present.

Acritarch Form H.

Plate 88, fig.6.

Remarks: The single well preserved specimen included here is a spheromorphic acritarch with a subspherical vesicle of 45um in maximum diameter. The wall is single layered and thin. There appears to be a pore or pylome present from which an ornament of linear striations radiate. The striations extend approximately half way around the subspherical vesicle. The other half of the vesicle is smooth.

Acritarch Form I.

Plate 88, fig.3; fig.117, fig.6.

Remarks: Included here are spheromorph acritarchs measuring between 35-45um in diameter. The wall of the vesicle is thin, less than 1um, and ornamented with an open reticulum. The elements are closely spaced (< 1mm apart) vermiculae and rugulae. The ornament is less than 1um in height. No regular form of opening is apparent.

Species of *Lophosphaeridium* differ from Form I in possessing equidimensional ornamental elements.

Acritarch Form J.

Plate 117, 2-5.

Remarks: Four specimens of this form are recorded from the *Monograptus uniformis* (graptolite) Zone (Gedinnian) in the present study. They are flattened or pad-shaped acritarchs with four or five sides. The maximum diameter of the vesicle ranges between 55-65um. A slight thickening at the peripheral margin of the vesicle is apparent. In addition, irregular thickenings of the wall on the upper and lower faces of the vesicle are present. No regular form of opening has been observed in the specimens studied.

Acritarch Form K.

Plate 53, fig.1, 2 & 3?

Remarks: Five specimens of this form have been recorded from a single sample, DJ 10, of Ashgill age. They are acanthomorphic acritarchs with a subspherical central body which measures between 60-75um in diameter. The processes are between 25-35um in length but are commonly damaged in the material observed. The processes are narrow, less than 5um wide, and are of a consistent width along the entire length of the shaft. The process terminations furcate upto the first order at the distal extremity. The wall appears to be composed of two wall layers, the outer wall layer forming the very thin transparent processes. The central body is thick walled relative to the wall of the processes. The wall is ornamented with grana and echinae. No regular form of opening is apparent in the specimens observed.

These thin processed acanthomorphs are comparable with *Actipilion druggii* Loeblich 1970 which was also described from Late Ordovician sediments. The thin walled processes are a characteristic feature of this species. However, *A. druggii* has simple processes in contrast to the branching processes of Acritarch Form K.

Acritarch Form L.

Plate 67, figs.3-7; pl.88, figs.9, 10 & 11; pl.111, fig.1; pl.117, fig.9; pl.123, fig.14.

Remarks: Included here are very large acanthomorphic acritarchs with a spherical central body and sturdy, evenly distributed processes. The central body measures between 130-200um in maximum diameter. The processes have simple distal terminations and appear to solid. They measure upto 90um in length. In the material studied, this form commonly occurs as fragmentary pieces. No regular form of opening is apparent.

This acanthomorphic form is conspicuous by its very large size.

Acritarch Form M.

plate 11, figs. 8 & 11.

Remarks: Acanthomorphic acritarchs which have a spherical-subspherical central body measuring between 32-42um in diameter. The processes have narrow (2-3um wide) straight sided shafts of between 12-20um in length. The process terminations branch in a ramusculose manner. Processes may branch upto the 5th order, the higher order branches forming a fine mesh of pinnae. The central body to process ratio is approximately 2:1. The nature of the wall structure is indeterminate from the dark specimens observed. No ornament is evident on the central body and no regular form of opening is apparent.

Acritarch Form N.

Plate 25, figs.6-9; pl.35, fig.1

Remarks: Acanthomorphic acritarchs which have a rigid, spherical central body measuring between 45-56um in maximum diameter. The processes appear to have hollow tubular shafts with simple open distal terminations. The processes are closely spaced and are approximately 100-150 in number. They measure between 18-25um in length and 2-4um wide at the base. The process to central body ratio is approximately 1:2.5. The wall appears to be composed of two layers, the outer layer forming the processes. There is no communication between the processes and the central body. No regular form of opening is apparent.

Acritarch Form D, described above, differs by having branching pinnae at the distal terminations of the processes. It also has a smaller central body and the processes are shorter.

Acritarch Form P.

Plate 184, figs.2-8.

Remarks: Included here are acanthomorphic forms with a subspherical central body and short, hollow, distally open processes. The central body is thick walled and measures between 30-65um in maximum diameter. The processes vary considerably in number and size in the population studied. They number between 10 and 60 and measure upto 10um in length. The width of the processes is also variable measuring upto 12um wide at the base. The processes commonly taper distally, however specimens with straight sided processes also occur. The processes are always open distally. No regular form of opening is apparent.

A comparable genus is *Dilatisphaera* which also includes forms with open ended processes, however species included in *Dilatisphaera* have a thinner walled central body generally have longer processes.

Acritarch Form R.

Plate 184, fig.10.

Remarks: The single specimen included here is a coenobial form composed of four cylindro-conical shaped cells radiating from a central point. Each cell measures approximately 30um in length and has an open distal termination which is circular in outline.

Acritarch Form S.

Plate 184, fig.11.

Remarks: The single specimen included here is triangular in outline and measures 47um in maximum diameter. The apices of the vesicle are echinate with spines less than 2um in length. The interapical areas are smooth and their outline is concave. No opening is apparent.

Acritarch Form T.

Plate 111, figs.2, 3 & 4.

Remarks The two specimens included here are spherical in shape and measure 55um and 59um in diameter. The vesicle is divided into numerous polygonal fields by low ridges, as in species of *Dictyotidium*. Within each field, what appear to be pores, 3-6 in number, are present. The pores are arranged in a regular manner within each field.

This form is of similar morphology to species within the genus *Orygmahapsis*. *Orygmahapsis* species differ by having just a single pore at the centre of each field.

Acritarch Form U.

Plate 123, figs.10, 11.

Remarks: Included here are thick walled (approximately 2um thick) spheromorphic acritarchs with a coarsely scabrate or rugulate ornamentation. The vesicle is spherical and measures between 40-65um in maximum diameter. No regular form of opening is apparent.

This form was recorded in large numbers in graptolite dated samples of late Siegenian age.

Acanthomorphic acritarchs indet.

Remarks: This category includes acanthomorphic acritarchs which are poorly preserved and which can not be allocated to a published genus.

Spheromorphic acritarchs indet.

Remarks: Included here are spherical or subspherical forms which are too poorly preserved to be assigned to a genus.

Chapter 5. The Prasinophyta Round 1971.

Introduction.

The Prasinophyta are a division of the green algae. There appears to be no definition of the group in the literature that is satisfactory for use by palynologists who are concerned only with the fossilised phycoma stage of the life cycle. However, Tappan (1980, p.818) provided the following definition: "Motile stage with ultramicroscopic body scales, and two to four scaly flagella arising from the apical pit that is surrounded by four apical projections; large axial plastid; may have colonial, coccoid, palmelloid, or branching stage; cysts or phycoma enlarge vegetatively. Planktonic and benthic; marine and freshwater; *Platymonas* may be symbiotic with the marine worm *Convoluta*. Precambrian to Holocene."

The prasinophyte fossil record is not fully representative of the geological history of the group as only a small proportion of the group produce a fossilisable phycoma as part of their life cycle (Tappan 1980). However, fossil prasinophytes commonly form significant proportions of palynological assemblages throughout the Phanerozoic. They appear to be 'disaster species' (Tappan 1980) surviving and flourishing, in the middle and late Palaeozoic for example, when other phytoplankton groups underwent decline.

Fossil prasinophyte morphology.

In the literature, it is common to see the same set of morphological descriptors used to describe the fossilised prasinophytes as those used to describe the acritarchs. This is all well and good for the description of the detail of morphology, e.g. the ornamentation, however, confusion could arise from the use of terms which have functional connertations.

This problem was addressed by Colbath (1983) who warned against the use of the term 'cyst' when describing the fossilised body of prasinophytes. "The term 'cyst'" he said, "is best used to describe the resting stage of an organism, but because the acid resistant bodies are formed by prasinophyceans during a stage of active growth and division, they are better referred to by the term 'phycoma' (plural: phycomata)."

In the present study, terms used for the detailed ornamentation are those used for the acritarchs. However, it is necessary to define the following terms which are particularly applicable to the prasinophytes.

Ala: Flange like extension from the equator of the central body.

Central body: The phycoma minus the ala or membranous outgrowths.

Crest: Flange like, membranous outgrowth from the central body.

Phycoma: The fossilised organic body of the prasinophyte as a whole.

Phycoma development in the Prasinophyta.

Our Knowledge of the prasinophycean life cycle is based on numerous field and laboratory investigations of modern day species (Ostenfeld 1910; Parke & Hartog-Adams 1965; Parke 1966; Parke *et al.* 1978).

A brief summary of the life cycle of the modern day prasinophyte *Pterosperma* is given in fig. 12. The stages that are potentially fossilisable are those from the beginning of the phycoma phase, phase 3 on the diagram, through to phase 8, which shows the empty phycoma having released the inner wall containing the motile cells. The phycomata produced by modern species are closely comparable with some of the organic walled microfossils recorded from palynological preparations from rocks. It is based on these comparisons that several fossil microplankton genera have been classified under the Prasinophyta. For a comprehensive review of the biology of the Prasinophyta, a subject which falls outside the realms of the present study, the reader is referred to Tappan 1980, p.806-812.

Classification of the Prasinophyta.

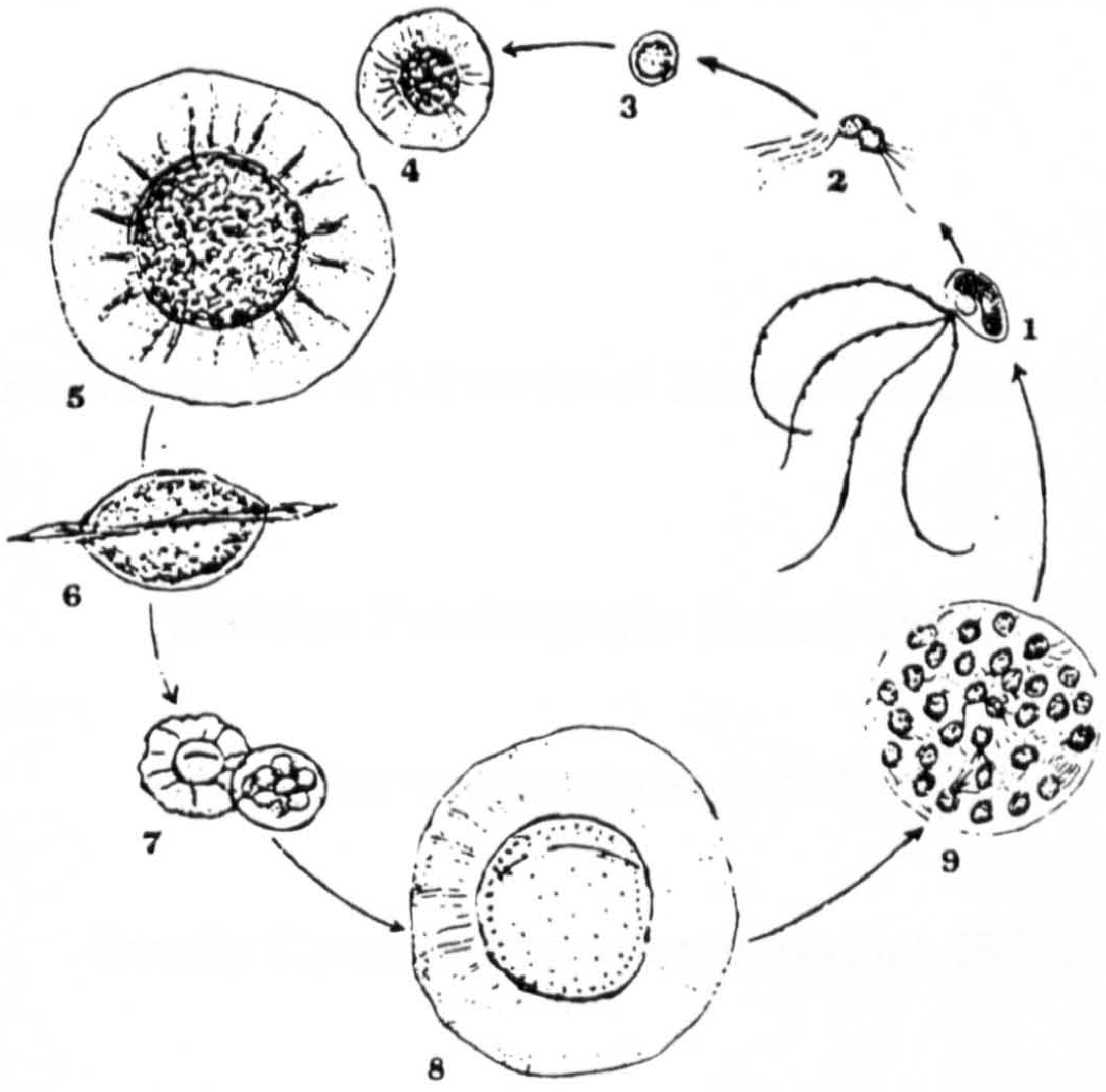
The classification of the Divison Prasinophyta was addressed by Tappan (1980) who proposed a system incorporating both present day and fossil forms.

Several palynomorph genera included in the Prasinophyta by Tappan show only superficial similarity to the phycomata of modern day species. For example, *Leiosphaeridia*, which shows superficial similarity to the phycomata produced by the modern day *Halosphaera* has been demonstrated to have a dissimilar wall ultrastructure (Jux 1969). There is also the distinct possibility that the great variety of *Leiosphaeridia* species recorded in the literature are multi-sourced, possibly by animal and plant. For this reason, it is dangerous to include this genus, as it is presently diagnosed, in the Prasinophyta.

In the present study, only the genera which are now indisputably considered to be prasinophytes (Fensome *et al.* 1990) are included in this division. These are *Tasmanites* Newton 1875, which is produced at the present day by *Pachysphaera pelagica* Ostenfeld, *Pterospermella* which is produced by *Pterosperma moebii* (Jorgensen) Ostenfeld, and *Cymatiosphaera* which is produced by *Pterosperma marginatum* Gaarder.

The suprageneric scheme of Tappan (1980, Table 10.1) is here used in part. The position of the Leiosphaeridiaceae Timofeev 1956 in the Prasinophyta is rejected until further evidence is available

Figure 12. The life cycle of *Pterosperma*.



Life cycle of *Pterosperma*. **1.** Motile phase, a scale-covered cell with excentric nucleus, large saucer-shaped plastid lying against the convex side of the body, and starch-enclosed pyrenoid; four long excentrically inserted scale- and hair-covered flagella. Motile phase may reproduce independently and repeatedly by fission. **2.** Dividing motile cells. **3.** Beginning of phycoma phase as motile cell loses flagella, rounds off, and develops thickened wall and a flangelike ala. Phycoma increases rapidly in volume, plastid divides into many smaller ones that surround a central lipid globule; size increase continues to maturity, requiring from two weeks to three-and-a-half months in culture. **4,5.** Mature phycomata of varied size, with thickened inner wall, just prior to division of cell contents. **6.** Phycoma in edge view. **7.** Thickened inner wall of phycoma and contained cell material has escaped through the release suture, a slit in the outer phycoma wall; after escape, the former inner wall enlarges to double the previous diameter and the contents divide into two, four, or eight uninucleate masses that develop flagella. **8.** Empty phycoma, showing release suture (compare fossil prasinophytes of Figure 10.17 part 1 and Figure 10.5), peripheral ala, and ring of alaband pores, as well as other scattered pores. **9.** Phycoma inner wall, each of the early 8 quadriflagellate cells having divided twice to produce 32 motile cells; inner wall increases in diameter up to 16 times that prior to release from outer wall, accompanied by decrease in wall thickness and continued division of motile cells that finally burst the wall and escape. Based on various species, data from Parke et al., 1978. 1, ×1000; others, ×150.

regarding their prasinophycean affinity. The families Tasminaceae Sommer 1956, Cymatiosphaeraceae Madler 1963 and Pterospermellaceae Eisenack 1972 are utilised to accommodate the genera *Tasmanites*, *Cymatiosphaera* and *Pterospermella* respectively. However, the inclusion of other palynomorph genera in these families by Tappan (see Table 10.1) is rejected, again pending further evidence.

Prasinophyte systematics.

The synonomy of the taxa in this section follows that of Fensome *et al* 1990 unless otherwise stated.

Division Prasinophyta Round 1971.

Order Pterospermatales Schiller 1925

Family Cymatiosphaeraceae Madler 1963.

Genus *Cymatiosphaera* O. Wetzel 1933 *ex* Deflandre 1954 emend. Deflandre & Cookson 1955.

Type species: *Cymatiosphaera radiata* O. Wetzel 1933.

Generic description: Deflandre and Cookson 1955, p.288.

Remarks: The genus is included in the division Prasinophyta as phycomata of identical morphology are produced by the modern day prasinophyte species *Pterosperma marginatum*. The acritarch genus *Dictyotidium* differs from *Cymatiosphaera* in possessing low solid ridges defining the boundaries between the fields on the vesicle as opposed to the membranous septa in species of *Cymatiosphaera*.

Cymatiosphaera carminae Cramer 1964.

Plate 156, figs.2, 3 & 5; pl.168, figs 8 & 9.

Description: Cramer 1964, p.325-326, pl.6, fig.9, pl.14, fig.10.

Holotype: Cramer 1964, pl.14, fig.10. Age: Emsian.

Remarks: This distinctive species of *Cymatiosphaera* has striations present on the outer membranous wall layer. *Cymatiosphaera peligrosa* Cramer 1964 has a similar over-all shape to *C. carminae* but lacks the striations on the outer wall. A pictorial comparison of these two species is given by Cramer 1964, p.325.

Cymatiosphaera gorstia Dorning 1981.

Plate 74, fig.10.

Description: Dorning 1981, p.185, pl.2, fig.7.

Holotype: Dorning 1981, pl.2, fig.7. Age: Ludlow.

Remarks: *Cymatiosphaera octoplana* Downie 1959 is smaller, has fewer fields and has higher flanges.

Cymatiosphaera Kiryanovii (Kiryanov) Fensome *et al.* 1990.

Plate 68, figs.6 & 7.

Description: Kiryanov 1978, p.32-33, pl.7, fig.6.

Holotype: Kiryanov 1978, pl.7, fig.6. Age: Late Silurian.

Remarks: Colbath (1983) observed this taxon in his study of the microfloras from the Silurian Bainbridge Formation, Missouri, USA. As a consequence he transferred this species, then named *Cymatiosphaeropsis reticulosa*, to the genus *Cymatiosphaera*. In doing so, Colbath created a junior homonym of *Cymatiosphaera reticulosa* Takahashi 1964. Fensome *et al.* 1990 subsequently proposed the present name.

The species is distinguished by the thick vesicle wall (4-8um thick) and a two-tier reticulum. The first-order reticulum is broad, fields commonly between 10-15um wide, with a second order microreticulum within these fields.

Cymatiosphaera cf. *ledburica* Dorning 1981.

Plate 89, figs.1, 2 & 3.

Holotype: Dorning 1981, pl.2, figs.13 & 14. Age: Ludlow.

Remarks: Compare with Dorning 1981, p.185, pl.2, figs.13-14. Specimens here have a similarly thick, smooth wall, and a similar number of fields on the vesicle as the holotype. They are also of a similar size. The type material differs in possessing higher flanges.

Cymatiosphaera leonensis Cramer & Diez 1976.

Plate 185, figs.1, 2 & 3; pl.196, fig.1.

Description: Cramer & Diez 1976, p.80, pl.4, fig.35.

Holotype: Cramer & Diez 1976, pl.4, fig.35. Age: Late Emsian.

Remarks: Specimens recorded appear to be identical to the type material described by Cramer and Diez (1976) from Iberia.

Cymatiosphaera nebulosa (Deunff) Deflandre 1954.

Plate 142, figs.3, 4 & 5; pl.177, figs.8 & 9.

Description: Deunff 1954, p.214, fig.8.

Holotype: Deunff 1954, fig.8. Age: Devonian.

Remarks: This relatively small species of *Cymatiosphaera* is characterised by the thick walled, dark coloured central body.

Cymatiosphaera octoplana? Downie 1959.

Plate 79, figs.7, 8 & 9.

Description: Downie 1959, p.63, pl.11, fig.2.

Holotype: Downie 1959, pl.11, fig.2. Age: Wenlock.

Remarks: The proposed synonomy of *C. wenlockia* Downie 1959 with *C. octoplana* by Dorning (1981, p.186) allows for greater variation in the number of fields present on the vesicle within this species. The specimens here, which are questionably assigned to the species, show variation in the number of fields present. The high flanges dividing the fields are commonly damaged due to poor preservation.

Cymatiosphaera peligrosa Cramer 1964.

Plate 168, fig.10.

Description: Cramer 1964, p.326, pl.17, figs.4-8.

Holotype: Cramer 1964, pl.17, fig.6. Age: Emsian.

Remarks: This species is morphologically similar to *C. nebulosa* but differs in possessing short spines at the distal extremities of the crest junctions. *Cymatiosphaera carminae* differs in possessing striations on the crests of the outer wall layer.

Cymatiosphaera sp. 1.

Plate 111, figs.5, 6 & 7; pl.117, figs.7 & 8; pl.131, pl.5; pl.142, fig.1.

Description: A species of *Cymatiosphaera* with a subspherical, transparent, thin walled central body which measures between 28-35um in diameter. The central body is divided into approximately 10-15 indistinct fields by tall (upto 12um high) membranous septa which are composed of the outer wall layer. The septa are smooth.

Remarks: *Cymatiosphaera velata* Deunff 1966, described from the Devonian of Canada has similarly tall septa relative to the diameter of the central body. However, this species is considerably smaller in size, the central body measuring between 11-15um, than *Cymatiosphaera* sp.1. *Cymatiosphaera* *pterophora* (Deflandre & Courteville) Downie & Sarjeant 1965, which was described from the Cretaceous of France has almost identical flange morphology to *Cymatiosphaera* sp. 1 but differs in having a thicker, granulate central body.

Family Pterospermellaceae Eisenack 1972.

Genus *Pterospermella* Eisenack 1972.

Type species: *Pterospermella aureolata* (Cookson & Eisenack) Eisenack 1972.

Generic description: Eisenack 1972, p.597.

Remarks: The genus *Pterospermella* is included in the Prasinophyta as phycoma of identical morphology have been observed to be produced by the modern day species *Pterosperma moebii.*

Pterospermella circumstriata (Combaz *et al.*) Eisenack, Cramer & Diez 1973.

Plate 142, figs.6, 7, 8? & 9.

Description: Combaz *et al.* 1972, p.304, pl.3, figs.13 & 14a-b.

Holotype: Combaz *et al.* 1972, pl.3, figs.14a-b. Age: Emsian.

Remarks: This species can be distinguished by the presence of concentric striations on the central body of the phycoma.

Pterospermella eruptio Martin 1984.

Plate 185, fig.12; pl.196, fig 5?.

Description: Martin 1984, p.29-30, pl.9, figs.5, 7, 11 & 12.

Holotype: Martin 1984, p.29-30, pl.9, figs.12. Age: Early Famennian

Remarks: This species is morphologically similar to *P. onondagaensis* (Deunff) Eisenack, Cramer & Diez 1973 but differs in having a broader, more rigid ala.

Pterospermella onondagaensis (Deunff) Eisenack, Cramer & Diez 1973.

Plate 131, figs.6, 7 & 8; pl.142, fig.10; pl.150, fig.11?

Description: Deunff 1955, p.148, text-fig.27.

Holotype: Deunff 1955, text-fig.27. Age: Middle Devonian.

Remarks: A closely comparable species is *O. eruptio* Martin 1984, which was described from the early Fammenian of Belgium. This species is here taken to differs from *O. onondagaensis* in possessing more ribs supporting the ala which is relatively broad.

Family Tasmanitaceae Sommer 1956 ex Tappan 1980.

Genus *Tasmanites* Newton 1875.

Type species: *Tasmanites punctatus* Newton 1875.

Generic description: Newton 1875, p.341.

Remarks: Phycomata of identical morphology to *Tasmanites* are produced by the modern day prasinophyte *Pachysphaera*. It is for this reason that the fossil genus *Tasmanites* is included in the division Prasinophyta.

Tasmanites martinssonii Eisenack 1958.

Plate 34, figs.9 & 12; pl.43, figs.3 & 6.

Description: Eisenack 1958a, p.6, pl.1, figs.10-13.

Holotype: Eisenack 1958a, pl.1, fig.10. Age: Ordovician (based on material from an erratic).

Tasmanites medius Eisenack 1931.

Plate 68, figs.2, 3 & 5.

Description: Eisenack 1931, p.109, pl.5, fig.1.

Holotype: Eisenack 1931, pl.5, fig.1. Age: Silurian.

Neotype: Eisenack 1955, pl.5, fig.13. Age: Silurian.

Remarks: Specimens observed here are smaller in size than the type material, measuring 35-62um in diameter compared to 120um of the type specimen, the neotype is 114um in diameter. As discussed above, the phycoma of the prasinophyte grows during ontogeny, therefor size is maturity dependant as opposed to species dependant. For this reason the small forms of this morphotype, falling outside the stated size measurements for the species, are included.

Chapter 6. The Chitinozoa Eisenack 1931.

Introduction.

The term chitinozoa was introduced by Eisenack (1931) for the pseudochitinous, capsulate, acid resistant fossils that he recorded from the Baltic Silurian. In that publication (p.80) he defined the group as follows: "Axially symmetrical animals of small rod, club, flask or bubble shape, structureless, chitinous cuticle which is always open at the oral end and the aboral end is probably closed or at best furnished with a very narrow opening. In the majority of cases this end is indented. Size from 70um-1500um. Often the test bears characteristic spines. (etc. The open oral end becomes oriented downwards in the genus *Desmochitina*)."

Since the early records of the chitinozoa, which relied primarily on the shape of the blackened outline of the vesicle for their recognition, chitinozoan studies have progressed greatly, notably with the introduction of scanning electron microscopy, to provide refined biostratigraphic resolution in lower Ordovician-Devonian sequences.

Chitinozoan morphology.

The morphological terms used for the chitinozoa in this study are mainly those published by Combaz *et al.* 1967. Subsequent to this publication several contributions to the dictionary of morphological terms for this group have been made, notably those of Cramer 1967, Taugourdeau *et al.* 1967, Jansonius 1970, Jenkins 1970, Eisenack 1968b, 1972a & 1972b, Legault 1972a, & 1972b, Laufeld 1974, Wrona 1980 and Paris 1981.

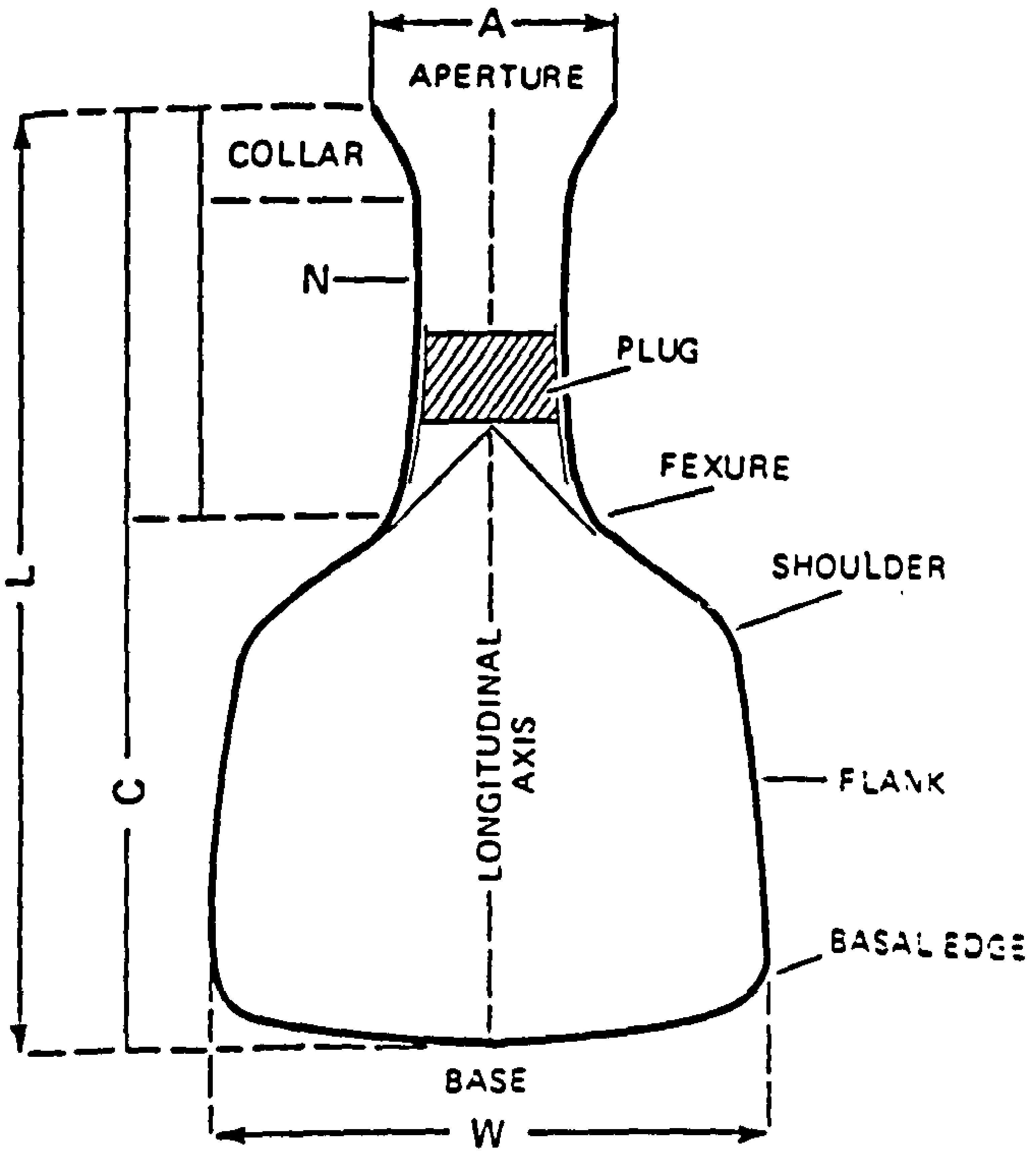
A glossary of alphabetically ordered descriptive terms is given below which is largely after Laufeld 1974 (p.37) with some minor alterations and additions made. A pictorial representation of some of the terms used is presented (fig. 13).

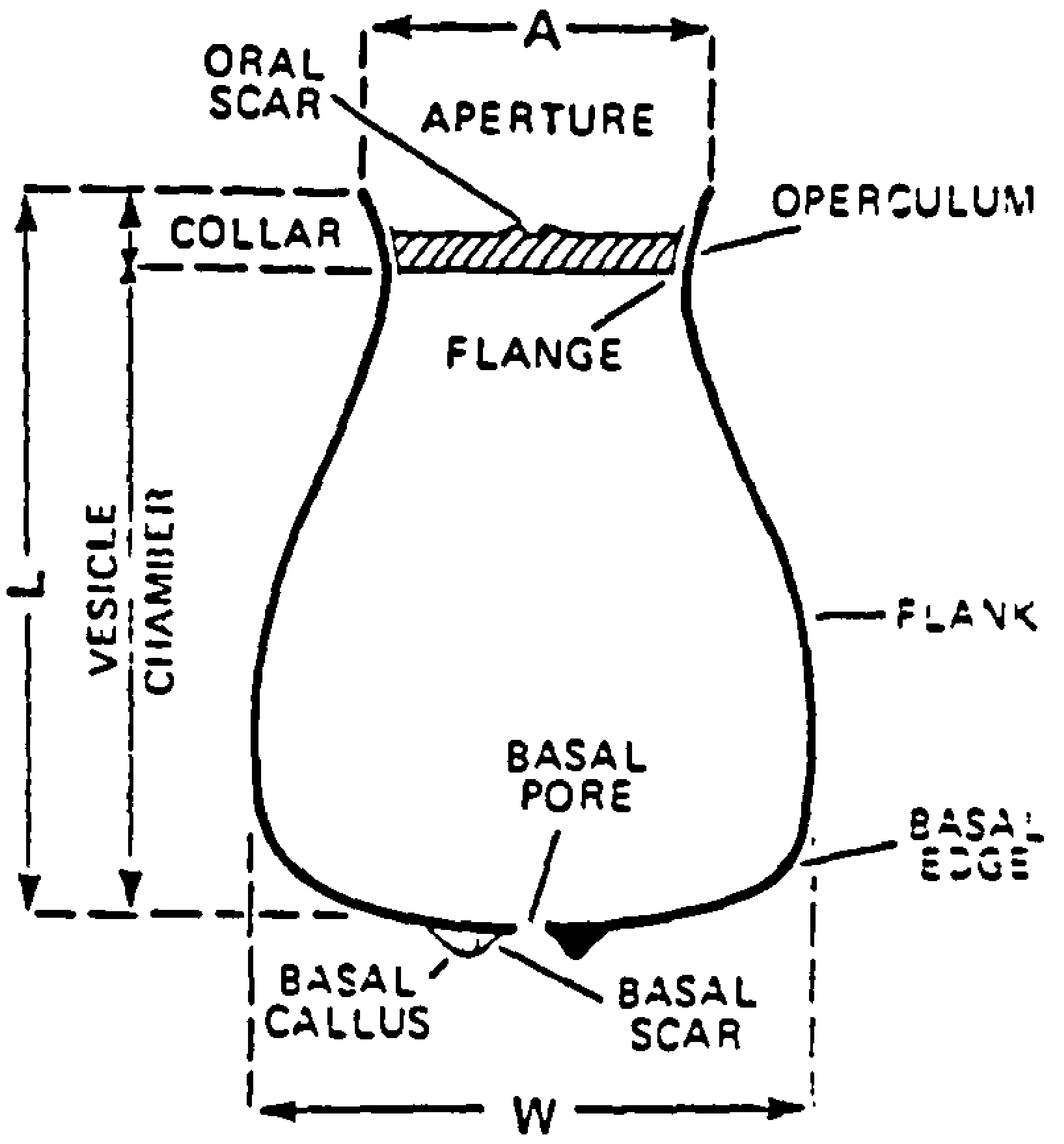
Aboral: The closed part of the vesicle opposite to the aperture.

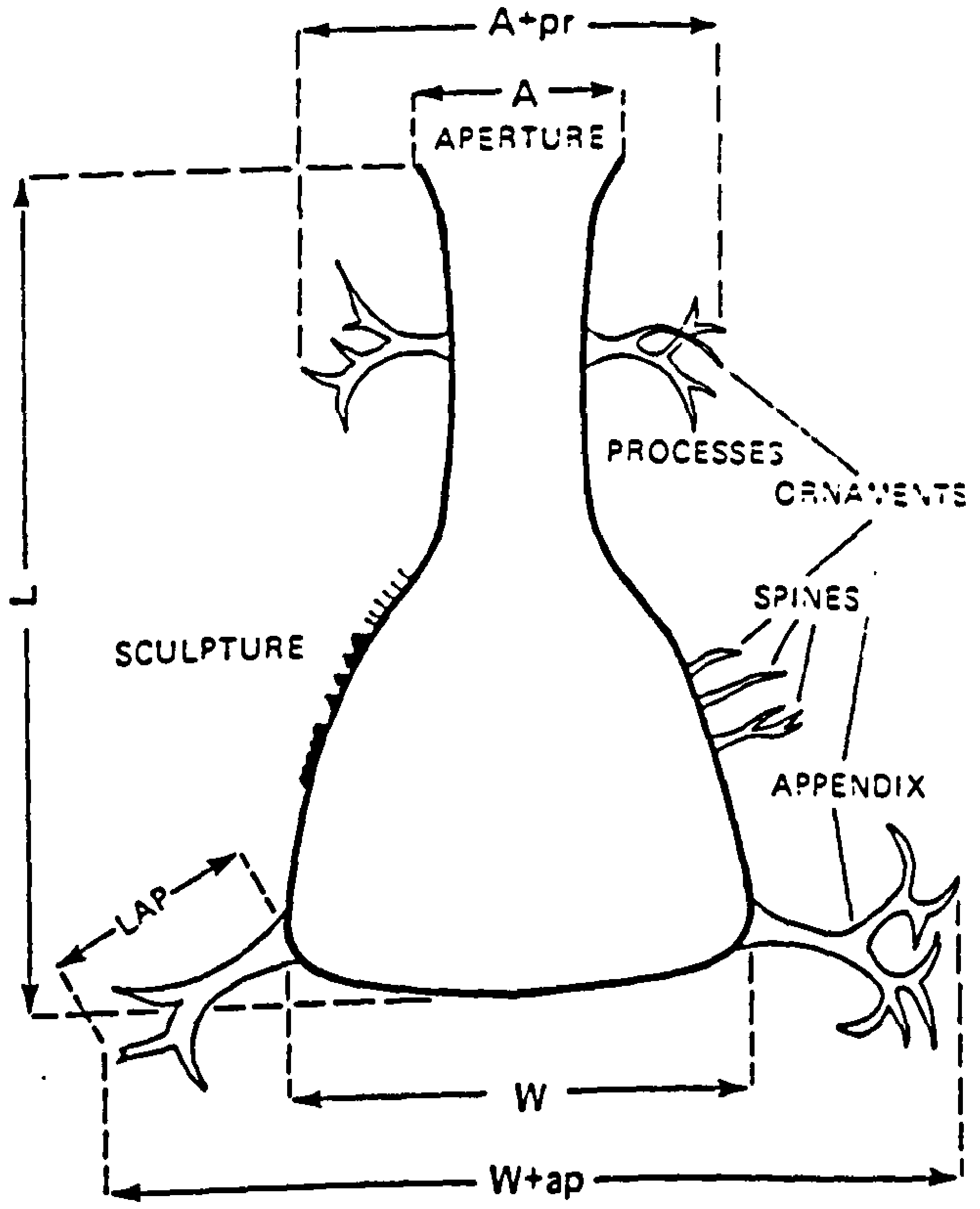
Aboral scar: Thin walled, central part of the base. Synonymous with the basal scar.

Aperture: The main opening by which the vesicle communicates with the exterior.

Figure 13. Chitinozoan morphology.







A	— Width (diameter) of aperture
C	— Length of the chamber
L	— Total length of the vesicle
N	— Minimum width of neck
W	— Maximum width of the vesicle
A+pr	— Joint width of the aperture and the length of the neck processes
W+ap	— Joint width of the vesicle and the length of the appendices
Lap	— Length of the appendices

Appendages: Processes extending from the basal edge. They may be reduced, elongated, simple, branching, coalescent or rhizoid, see Combaz *et al.* 1967, fig.4.

Basal callus: The thickened central part of the base.

Basal edge: The convex part of the vesicle constituting the transition from the chamber to the base.

Basal process: A process protruding aborally from the central part of the base.

Base: The part of the chamber aborally of the basal edge.

Body: Synonymous with chamber, sometimes referred to as the body chamber.

Carina: A flange or membrane positioned at the basal edge of the chamber. It may be reduced, extended, perforate, reticulate or digitate, see Combaz *et al.* 1967, fig.4.

Chain: Three or more vesicles connected along their longitudinal axis.

Chamber: The part of the vesicle between the base and the flexure, or where the latter is lacking, the collar or lip.

Collar: The subcylindrical or orally widened part of the vesicle between the aperture and the chamber in forms lacking a neck.

Distal: In an outward direction from the longitudinal axis.

Flank: The part of the chamber between the shoulder and the basal edge.

Flexure: The concave part of the vesicle constituting the transition between the chamber and the neck.

Longitudinal axis: The geometrical axis that runs from the aboral pole through the centre of the of the aperture.

Mucron: The small teat or thickening that extends from the aboral pole, synonymous with basal callus.

Neck: The part of the vesicle between the flexure and the lip, or where the latter is lacking, the aperture.

Operculum: A thin disc closing the vesicle. This is positioned between the chamber and the collar, or where the latter is lacking, the aperture.

Oral: The part of the vesicle where the aperture is located.

Ornamentation: External morphological elements and sculpture of the vesicle wall. The following descriptive terms are used here: scabrate, granulate, echinate (slender simple elements <5um in length) and spinose (elements >5um in length). Spinose ornamentation maybe simple or branching.

Prosome: A thick plug-like element closing the vesicle. This is positioned between the chamber and the collar, or where the latter is lacking, the aperture.

Proximal: In an inward direction towards the longitudinal axis.

Shoulder: The convex part of the chamber positioned aborally of the flexure in forms with subcylindrical flanks.

Twin: Two specimens connected along their longitudinal axis.

Vesicle: The organic test as a whole.

Vesicle shape: The terms used to describe the vesicle shape are: cylindrical, cylindro-spheroidal, spheroidal, conical, cylindro-conical, ovoidal or discoidal, see Combaz *et al.* 1967, fig.2.

Vesicle wall: The organic wall of the test enclosing the central cavity and consisting of one or more layers. The interior and exterior part of the vesicle wall may be smooth or ornamented.

The biological affinity of the chitinozoa: A brief review.

The biological affinity of the chitinozoa has been a point of much debate since the group was given its name by Eisenack (1931). The one, and probably only, aspect of their affinity that is agreed upon is their placement in the animal kingdom (Eisenack 1931; Laufeld 1974).

The problems of understanding the group biologically are much enhanced by the absence of modern day representatives. This, subsequently, leads to a lack of knowledge of the other stages of their life cycle. However, several speculative ideas have been made as to their affinity based upon observation of the morphology of the fossilised stage of the life cycle which is what we observe in palynological preparations. Observations of the detail in morphology took a major step foreword with the introduction of scanning electon microscopy. The availability of such detail has brought about a surge in interest in solving the chitinozoan affinity problem.

The mode of occurrence, as individuals, chains or cocoons, and their spatial distribution, chitinozoans having only been recovered from sedimentary rocks deposited in the marine realm, is additional information available to us. The group is also apparently stratigraphically restricted to the early Ordovician through late Devonian with records of chitinozoan like microfossils reported from the earlier Precambrian and Cambrian (Bloeser *et al.* 1977, Bokhari 1980) and the later Mississippian (Wilson & Clarke 1960).

Initial observations using light microscopy by Eisenack (1931) led to the suggestion that they may be related to testacean rhizopods (Rhyzopodae=protozoans with root like pseudopodia). The fact that testacean rhizopods are fresh water dwellers, coupled with their susceptibility to dissolution when subjected to palynological oxidation agents, e.g. KOH, indicates that they are not related to this group (Eisenack 1931; Jansonius 1970 & Jenkins 1978).

A number of theories concerning chitinozoan affinity are in debate at the present time. The suggestion that they were some kind of ciliate protists was first suggested by Eisenack (1932) and has received subsequent support from Deflandre (1942) and Reid & John (1981). The contention that the chitinozoa may be related to the allogromiid foraminifera was first proposed by Collinson & Schwalb (1955) and has been recently reintroduced, amongst considerable controversy, by Cashman (1991). Cashman (1990; 1991) observed microstructures, including micropores, a laminated wall structure and what he interprets to be juvenile chitinozoans positioned on the adult vesicle wall, which has led him to proposed that the chitinozoans were a monophyletic group of rhizopods. He also proposes an evolutionary pathway along which the chitinozoa evolved into the allogromiid foraminifera.

A common interpretation of the chitinozoan test has been that it serves the purpose of an egg case. Various groups of fossils have been considered for the source of the eggs, the groups proposed having a similar spatial distribution and stratigraphic occurrence as that of the chitinozoa. The groups considered to be potential producers of the eggs include metazoans of unknown affinity (Kozlowsky 1963), graptolites (Jenkins 1970), scolecodonts and gastropods (Laufeld 1974, Paris 1981). Recent study of Late Silurian teratologic chitinozoan morphotypes by Jaglin & Paris (1992) led them to conclude that it is far more likely that the chitinozoa where eggs of marine organisms as opposed to a vegetative reproductive organ.

Other less favourable interpretations include that of Obut (1973) who proposed the chitinozoa could be related to the dinoflagellates and Loquin (1981) who proposed a fungal affinity. Finally, there is the option that the chitinozoa may form an entirely unknown group of organisms (Bockelie 1981) with no fossil or modern day representatives.

The broad nature of the present study does not allow time for detailed SEM analysis of the chitinozoa assemblages. It is primarily for this reason, coupled with the general poor state of preservation of the assemblages that no further light can be shed on the chitinozoan affinity debate from this research.

Chitinozoan classification.

The chitinozoa areconsidered undoubtedly to belong to the animal kingdom (Laufeld 1974). For this reason, their classification is subject to the rules of the International Code of Zoological Nomenclature (ICZN).

The earlier publications regarding the suprageneric classification of the chitinozoa are largely based upon the original suprageneric structure proposed by Eisenack (1931). The three families proposed by Eisenack (1931) were the Lagenochitinidae, containing flask shaped forms, the Conochitinidae, including forms with a conical shaped vesicle and the Desmochitinidae which includes species with a more globular vesicle which commonly form chains of individuals. Over the following 35 years, these families were emended and supplemented with additional families (Van Oyen & Calandra 1963; Wilson & Dolly 1964; Jansonius 1964; Taugourdeau 1966; Tappan 1966) as researchers felt the need for a more extensive suprageneric structure to cope with the, by then, rapidly expanding 'pool' of chitinozoan taxa.

The only diversion from this trend was by the French school (Taugourdeau 1965; Combaz ed. 1965) who proposed an elaborate key to genera based on the presence or absence and the general nature of the copula, which they considered to be a critical feature of the chitinozoa. Descriptive terms rather than formal family names were utilised initially, however, Taugourdeau (1966) replaced his earlier descriptive terms by emending the original families of Eisenack (1931) and he, in addition, introduced the family Ancyrochitinidae.

Eisenack (1968b) divided the chitinozoans into two groups above the family level which he called the operculida and the prosomida, the former possessing an operculum, the latter a prosome. In 1972 he renamed the groups the Operculatifera and the prosomatifera.

In his Ph.D. thesis, Paris (1981) produced a comprehensive suprageneric scheme based on the broad framework introduced by Eisenack (1931). A phylogenetic model for the chitinozoa (fig.67) is also provided which lends considerable weight to his ideas. The scheme utilises the two groupings of Eisenack (1968; 1972), the Operculatifera and the Prosomatifera at the order level, and the three families of Eisenack (1931); the Desmochitinidae, which is emended; the Conochitinidae which is restricted; and the Lagenochitinidae at the family level. Twelve subfamilies were also introduced with genera listed alphabetically within them. In the 11 years since its publication, the scheme has commonly been adopted by chitinozoan workers dispite the prior warnings of Laufeld (1974) and Bockolie (1978).

Laufeld (1974, p.37) gives two substantial reasons for discarding any suprageneric scheme for the chitinozoa, both of which are still significant at the present time. He stated that a systematic scheme at the family level of a group of extinct fossils of uncertain affinity is far from convincing. His second criticism, which follows on from the first, is the potential of difficulty of access to a particular taxon positioned in an outdated scheme for future workers.

Bockolie (1978) observed specimens of *Lagenochitina* from the Arenig of Spitsburgen which show the presence of an operculum and a prosome in a single specimen. The fact that both an operculum and a prosome can occur in the same specimen raises doubts as to the groupings of he chitinozoa into the Operculatifera and the Prosomatifera.

For the reasons of i. the questionable features of chitinozoan morphology (Bockolie 1978), ii. the inherent instability of any suprageneric scheme involving biota of unknown biological affinity and iii. the ease of access to taxa for future workers, the chitinozoa are listed here in alphabetical order.

Chitinozoan systematics.

Chitinozoan taxa are listed in alphabetical order for the reasons given in the previous chapter. All measurements given are based on five specimens unless stated otherwise.

Synonomy for the chitinozoa here largely follows that of Paris 1981. A synonymy list is provided where the present author is in disagreement with Paris (1981) or where the taxon was published post 1981.

The ages stated here for the holotypes of the species are those sited by their authors.

Genus *Ancyrochitina* Eisenack 1955.

Type species: *Ancyrochitina ancyrea* Eisenack 1931.

Generic description: Eisenack 1955, p.163.

Ancyrochitina ancyrea (Eisenack) Eisenack 1955.

Plate 46, figs.1, 2 & 3; pl.90, figs.1, 3 & 5; pl.124, figs.1 & 2?

Description: Eisenack 1931, p.88-89, pl.2, fig.8-11, pl.4, fig.4.

Holotype: Eisenack 1931, pl.4, fig.4. Age: Indeterminate, holotype recovered from drift sediments.

Remarks: The morphological limits of *A. ancyrea* as outlined by Laufeld 1974, p.39 are adhered to here. The most diagnostic feature of this taxon are the appendages arising from the basal edge of the vesicle that branch in an antler-like fashion. *Ancyrochitina primativa* Eisenack 1964 and *A. pachyderma* Laufeld 1974 both possess simple appendages. *Ancyrochitina merga* Jenkins 1970 differs in possessing a greater number of appendages that are generally shorter in their length than those on *A. ancyrea*. *Ancyrochitina fragilis* Eisenack 1955 has slender, more fragile appendages.

Ancyrochitina ancyrea? var. A.

Plate 157, figs.1-4; pl.169, fig.1.

Remarks: Specimens included here are questionably assigned to the species *A. ancyrea* due to the thick shafts of the appendages and the limited branching of the appendage distal extremities. However, this variety is characterised by this appendage morphology and by the spinose ornamentation on the vesicle neck.

Comparable forms are *A. frankeli* Wright 1976 and *A. morzadeci* sensu Boumenjel *et al* 1988. The former differs in possessing larger and more prominent ornamentation on the neck. The latter has the same style and distribution of ornamentation on the vesicle as but differs from *A ancyrea*? var. A. in possessing shorter appendages.

Ancyrochitina fragilis Eisenack 1955.

Plate 92, figs.5, 6 & 7.

Description: Eisenack 1955, p.175, pl.2, figs.1-6.

Holotype: Eisenack 1955, pl.2, fig.1. Age: Silurian.

Remarks: *Ancyrochitina fragilis* differs from *A. ancyrea* in possessing longer and more slender appendages that generally branch in a less complex manner. Several varieties of this species have been recorded in the present study.

Ancyrochitina fragilis var. *brevis* Taugourdeau & Jekhowsky 1960.

Plate 90, figs.2, 4 & 6.

Description: Taugourdeau & Jekhowsky 1960, p.1219, pl.I, figs.12 & 13.

Holotype: Taugourdeau & Jekhowsky 1960, pl.I, fig.12. Age: Gothlandien-Lower Devonian.

Remarks: This variety is distinguished by the presence of slender appendages that furcate at the distal quarter of the appendage length. The furcating spines reunite at the distal extremity of the appendage to give a hollow, subspherical structure.

Ancyrochitina fragilis var. *regularis* Taugourdeau & Jekhowsky 1960.

Plate 91, figs.1 & 3.

Description: Taugourdeau & Jekhowsky 1960, p.1219, pl.I, figs.15.

Holotype: Taugourdeau & Jekhowsky 1960, pl.I, fig.15. Age: Lower Devonian.

Remarks: This variety has simple appendages and a much shorter neck than the holotype of the species.

Ancyrochitina fragilis var. A

Plate 91, figs.2, 4 & 5; pl.92, figs.1-4; pl.124, figs.4 & 5.

Remarks: This variety of *A. fragilis* has relatively long and slender appendages protruding from the basal edge of the vesicle. The appendages furcate in the distal half of the process, usually in the distal third, to form flexible slender pinnae. Branching of the appendages is upto the third order. The slender nature of the appendages and the branching pinnae at the appendage terminations distinguish this variety.

Ancyrochitina pachyderma Laufeld 1974.

Plate 93, figs.1-5.

Description: Laufeld 1974, p.45-46, fig.10A-F.

Holotype: Laufeld 1974, fig.10F. Age: Silurian.

Remarks: *Ancyrochitina pachyderma* closely resembles *A. primativa* Eisenack 1964 in possessing simple appendages. However, *A. pachyderma* has appendages which are generally longer with much broader bases.

Ancyrochitina pilosa Taugourdeau & Jekhowsky 1960.

Plate 94, figs.1, 2 & 3.

Description: Taugourdeau & Jekhowsky 1960, p.1220, pl.II, figs.23 & 24.

Holotype: Taugourdeau & Jekhowsky 1960, pl.II, figs.23. Age: Silurian.

Ancyrochitina primativa Eisenack 1964.

Plate 69, figs.1 & 2; pl.75, fig.1-5.

Description: Eisenack 1964, p.323-324, pl.27, figs.1-6 & 8-14, pl.28, figs.1-5.

Holotype: Eisenack 1964. Age: Silurian.

Remarks. All specimens recorded here are from Telychian (upper Llandovery) to Sheinwoodian (lower Wenlock) aged sediments. The species is characterised by relatively short, simple appendages. *Ancyrochitina pachyderma* generally has longer simple appendages that have broader bases.

Ancyrochitina tormentosa Taugourdeau & Jekhowsky 1960.

Plate 143, 1?; pl.124, figs.6 & 7?

Description: Taugourdeau & Jekhowsky 1960, p.1220-1221, pl.II, figs.27, 28 & 27.

Holotype: Taugourdeau & Jekhowsky 1960, pl.II, fig.27. Age: Gothlandian.

Remarks: This species is characterised by the presence of short, sturdy appendages arising from the basal edge that start branching adjacent to the vesicle. Spines are also apparent on the neck of the vesicle in this taxon, in contrast with the otherwise similar species *Ancyrochitina asterigis* Paris 1981 which has a smooth neck.

Ancyrochitina tumida Taugourdeau & Jekhowsky 1960.

Plate 124, fig.8; pl.143, fig.2.

Description: Taugourdeau & Jekhowsky 1960, p.1221, pl.II, fig.30 & 31.

Holotype: Taugourdeau & Jekhowsky 1960, pl.II, fig.30. Age: Lower Devonian.

Remarks: This species has a similarly shaped body chamber and form of basal edge appendages as *A. ancyrea* but differs in possessing a much shorter neck. *Ancyrochitina tomentosa* has more robust appendages that start to branch adjacent to the vesicle.

Ancyrochitina sp. 1.

Plate 53, figs.4, 5 & 6; pl.54, figs.1-4.

Description: A species of *Ancyrochitina* with a cylindro-conical shaped vesicle. The length of the vesicle ranges between 135-175um. The chamber width ranges between 70-85um and the width of the neck is between 30-40um. The neck is slightly flaring towards the oral opening. The chamber occupies between 1/2 to 3/4 the total length of the vesicle. Long slender appendages protrude from the basal edge. The appendages are upto 40um in total length and less than 7um wide. They branch upto the second order in the distal half of their length. The appendages appear to have a rhyzoid (sponge-like) texture. The wall of the vesicle has a scabrate surface.

Remarks: This species is distinguished by the cylindro-conical shaped vesicle and the rhyzoid textured, slender branching processes. A closely comparable species, which was recorded from a similar stratigraphic level, is *Plectochochitina spongiosa* (Achab 1977) which has a similar vesicle shape and rhyzoid textured appendages. The appendages of this species, however, join distally to form a trabeculum. *Ancyrochitina merga* Jenkins 1970 possesses a greater number of appendages that are shorter in their length than those of *Ancyrochitina* sp. 1.

Specimens recorded here are commonly without appendages due to mechanical breakage. However, the proximal stubs of the broken appendages are apparent when observed under high magnification.

Ancyrochitina sp. 2.

Plate 70, figs.1 & 2.

Remarks: The six poorly preserved specimens included here are all fragmented. For this reason a full description of this taxon is not possible. However, there are several features apparent that may enable this form to be identified by future workers. The chamber is ovoidal in shape and surmounted by a cylindrical neck of moderate length (neck length is approximately equal to chamber length). The entire vesicle length is approximately 150-200m (4 specimens measured). The surface of the vesicle is scabrate or micro-echinate. Several appendages protrude from the basal edge, the number and morphology of which is not clear from these fractured specimens. A diagnostic feature is the rhyzoid texture of the appendages.

Ancyrochitina sp. 2 is only recorded from Telychian (late Llandovery) sediments in the present study.

Genus *Angochitina* Eisenack 1931.

Type species: *Angochitina echinata* Eisenack 1931.

Generic description: Eisenack 1931, p.82.

Angochitina ceratophora? Eisenack 1964.

Plate 125, figs.1 & 2.

Description: Eisenack 1964, p.320-321, pl.30, figs.7-9.

Holotype: Eisenack 1964, pl.30, fig.7. Age: Silurian.

Remarks: Three poorly preserved specimens are questionably assigned to this taxon. These specimens are distinguished from *Ancyrochitina* species by the subspherical body chamber indicating the absence of a basal edge.

Angochitina chlupachi Paris & Laufeld 1981.

Plate 132, figs.2, 3 & 6.

Description: Paris & Laufeld 1981, p.14, pl.3, figs.9, 10, 13, 14, 16, 18, 20 & 22.

Holotype: Paris & Laufeld 1981, pl.3, figs.9. Age: Lochkovian.

Remarks: This species has a more ovoidal shaped body chamber and less dense ornamentation than *A. echinata* Eisenack 1931.

Angochitina crassispina Eisenack 1964.

Pl.118, fig.1, 2, 3 & 4?

Description: Eisenack 1974, p.320, pl.30, figs.3 & 4.

Holotype: Eisenack 1974, pl.30, fig.3. Age: Silurian.

Remarks: This species has a very sparse ornament of prominent spines. *Angochitina echinata* Eisenack 1931 has a more dense ornamentation. *Angochitina chlupachi* has a more elongate, ovoidal shaped vesicle.

Angochitina echinata Eisenack 1931.

Plate 94, figs.4, 5 & 6.

Description: Eisenack, p.82, pl.1, figs.6 & 7.

Holotype: Eisenack 1931, pl.1, fig.7. Age: Silurian.

Remarks: A complex of *Angochitina* species of similar morphology occur in the Silurian samples studied here. Laufeld (1974) reported a similar range of morphotypes from the Silurian of Gotland and it is essentially his parameters for the species that have been utilised here.

Angochitina echinata has a more globose body chamber than both *A. elongata* Eisenack 1931 and *A. longicollis* Eisenack 1959. These three species all possess simple ornamental spines. *Angochitina* *devonica* Eisenack 1955 has longer, robust, furcating spines and a shorter neck than the three species mentioned above.

Angochitina elongata Eisenack 1931.

Plate 95, figs.1 & 2.

Description: Eisenack 1931, p.82, pl.1, figs.8 & 9.

Holotype: Eisenack 1931, pl.1, fig.8. Age: Silurian.

Remarks: *Angochitina echinata* has a more globose body chamber and *A. longicollis* has a longer neck than *A. elongata*.

Angochitina milanese Collinson & Scott 1958.

Plate 169, fig.5.

Description: Collinson & Scott 1958, p.11-13, pl.1, figs.1-5, 7, 8, 19 & 26.

Holotype: Collinson Y Scott 1958, pl.1, fig.2. Age: Middle Devonian.

Angochitina philippoti Complex.

Plate 157, figs.5 & 6; pl.158, figs.1-5; pl.169, figs.3 & 4.

Remarks: Included here are a range of morphotypes from the Lower and Middle Devonian that without the use of scanning electron microscopy are not practically distinguishable. The vesicle shape is cylidro-spheroidal and is ornamented with numerous branching processes positioned on the body chamber and on the neck. In the darkened material studied here, the distribution of processes, be it in vertical rows as in *Gothlandochitina*, or in horizontal rows as in *Alpenachitina* or randomly distributed as in *Angochitina*, is not apparent using the light microscope. At the present time, this group of forms are of little value for high resolution biostratigraphy because of the numerous misidentifications of these morphotypes in the literature (Paris 1988). As a result of both the observation technique used in the present study (light microscopy only) and the state of preservation, this situation can not be improved upon here.

Species included in this complex of forms are *Angochitina philippoti* Paris 1976, *A. caeciliae* Paris 1976, *A. devonica* Eisenack 1955, *Gothlandochitina jouannensis* Paris 1976, *G. illiziensis* Boumenjel 1985, *G. marettensis* Paris 1981, *G. racheboefi* Paris 1981 and *Gothlandochitina* sp. A Paris 1985.

Angochitina? cf. *seurati* Paris 1988.

Plate 70, figs.4, 5 & 6.

Holotype: Paris 1988, pl.12, fig.2. Age: Rhuddanian (early Llandovery).

Remarks: Compare with Paris 1988, p.77-78, pl.12, figs.1a-b, 2 & 3. The four specimens assigned to this taxon, all recorded from Telychian (late Llandovery) aged sediments, have the same slender shaped vesicle as *A. seurati*. These specimens also have a pilose ornamentation which is a diagnostic feature of *A. seurati*, the detail of which is not apparent from the light microscopy analysis undertaken. It appears that the specimens observed in the present study have shorter pila than those of the type specimens. This brings about the questionable assignation of this species (i.e. cf. *seurati*) to the genus *Angochitina*. It may be argued that this species be best accommodated in the genus *Sphaerochitina* Eisenack 1955 because of the presence of shorter ornamental spines.

Angochitina sp. 1.

Plate 76, figs.1-7.

Description: A species of *Angochitina* with a cylindro-spherical shaped vesicle. The vesicle is relatively small ranging in length from 90-110um. The chamber width ranges between 65-80um and the width of the neck is between 25-30um. The neck flares towards the oral opening. The chamber occupies approximately 1/2 of the total length of the vesicle. Short slender appendages are present on the chamber and on the neck. They tend to be better developed on the body chamber towards the aboral surface where they commonly bifurcate at the distal extremity. The appendages are upto 8um in total length and are no more than 3um wide at their base. The wall of the vesicle has a smooth or scabrate.

Remarks: Appendages are commonly broken in the poorly preserved assemblage observed here. However, this species is distinct by way of its vesicle shape and its delicate bifid spines. *Angochitina devonica* has a similar shaped vesicle but differs in possessing more robust appendages.

Genus *Armoricochitina* Paris 1981.

Type species: *Armoricochitina ceneratiensis* (Paris) Paris 1981.

Generic description: Paris 1981, p.175-176.

Armoricochitina nigerica (Bouche) Molyneux & Paris 1985.

Plate 55, figs.1-5.

Description: Bouche 1965, p.157-158, pl.2, figs.8, 12 & 13.

Holotype: Bouche 1965, pl.2, fig.8. Age: Upper Ordovician.

Remarks: The specimens recorded here show a considerable variation in the overall size of the vesicle.

Genus *Belonechitina* Jansonius 1964.

Type species: *Belonechitina micracantha* (Eisenack) Paris 1981.

Generic description: Jansonius 1964, p.906.

Belonechitina capitata (Eisenack) Paris 1981.

Plate 47, figs.1-4; pl.56, fig.4 & 5.

Description: Eisenack 1962, p.310-311, pl.15, figs.6-8.

Holotype: Eisenack 1962, pl.15, fig.6. Age: Indeterminate as the holotype was recovered from drift sediments.

Remarks. This species of *Belonechitina* has a low apiculate ornamentation and a rather bulbous aboral margin.

Belonechitina micracantha (Eisenack 1931)

Plate 35, figs.6 & 9; pl.47, fig.5; pl.48, fig.1 & 6.

Description: Eisenack 1931, p.84-85, pl.1, figs.19-21, pl.2, figs.20-22, pl.4, fig.15.

Holotype: Eisenack 1931, pl.1, fig.19. Age: Ordovician.

Remarks: Specimens included here are generally too poorly preserved to be assigned to a subspecies of *B. micracantha*. *Belonechitina robardeti* Paris 1981 has a more sparse distribution of spines over the vesicle than *B. micracantha*.

Belonechitina micracantha subsp. *micracantha* (Eisenack 1959).

Plate 26, figs.2 & 3; pl.35, figs.7 & 8; pl.47, figs.6, 7 & 8.

Description: Eisenack 1959, pl.1, fig.5, pl.3, fig.12.

Holotype: Eisenack 1959, pl.1, fig.5. Age:

Remarks: This subspecies is distinguished by the short ornamental spines and the angular nature of the vesicle between the aboral margin and the side of the body chamber.

Belonechitina micracantha subsp. *pellifera* (Eisenack 1959).

Plate 36, figs.1, 4 & 5.

Description: Eisenack 1959, pl.1, fig.5-7.

Holotype: Eisenack 1959, pl.1, fig.7. Age:

Remarks: This subspecies is distinguished by the relatively long spines and the convex aboral vesicle margin.

Belonechitina micracantha subsp. *robusta* (Eisenack 1959).

Plate 26, pl.1; pl.36, figs.2 & 3.

Description: Eisenack 1959, pl.1, fig.5, pl.3, fig.12.

Holotype: Eisenack 1959, pl.1, fig.5. Age:

Remarks: This subspecies is distinguished by the relatively long and rigid ornamental spines. It differs from *B. micracantha* subsp. *pellifera* in the shape of the aboral margin. The junction between the aboral margin and the side of the body chamber is noticeably more angular in *B. micracantha* subsp. *robusta* than in the subsp. *pellifera*.

Genus *Bursachitina* Taugourdeau 1966.

Type species: *Bursachitina bursa* (Taugourdeau & Jekhowsky) Taugourdeau 1966.

Generic description: Taugourdeau 1966, p.34.

Bursachitina bursa (Taugourdeau & Jekhowsky) Taugourdeau 1966.

Plate 159, figs 3 & 4; pl.169, fig.6

Description: Taugourdeau & Jekhowsky 1960, p.1225, pl.VII, figs.89 & 90.

Holotype: Taugourdeau & Jekhowsky 1960, pl.VII, figs.89. Age: Lower Devonian.

Remarks: A similar species morphologically is *Bulbochitina bulbosa* Paris 1981 which differs in possessing a narrower aperture and a more inflated aboral part of the chamber.

Genus *Calpichitina* Wilson & Hedlund 1964.

Type species: *Calpichitina scabiosa* Wilson & Hedlund 1964.

Generic description: Wilson & Hedlund 1964.

Calpichitina lenticularis (Bouche) Paris 1981.

Plate 56, figs.1 & 2.

Description: Bouche 1965, p.160, pl.2, figs.14 & 15.

Holotype: Bouche, 1965, pl.2, fig.14. Age: Silurian.

Remarks: Specimens observed here are almost identical in morphology to those recorded from the Ashgill of the Anti Atlas by Elaouad-Debbaj (1984a).

Calpichitina sphaerica (Taugourdeau & Jekhowsky) Paris 1981.

Plate 132, figs.4 & 5; pl.144, fig.1.

Description: Taugourdeau & Jekhowsky 1960, p.1227, pl.7, fig.103.

Holotype: Taugourdeau & Jekhowsky 1960, pl.7, fig.103.

Remarks: Specimens recorded here are of closely comparable morphology with those illustrated by Paris 1981 from the Gedinnian of Armorica.

Calpichitina sp. 1.

Plate 100, fig.1.

Description: Vesicle subspherical with a thickened rim bordering the spherical aperture. The vesicle is ornamented with densely packed echinae of <3um in height. The diameter of the vesicle ranges between 50-75um (two specimens measured).

Remarks: Only two specimens of this taxon have been recorded in the present study. It can be distinguished by the presence of fine echinae on the chamber wall.

Calpichitina sp. 2.

Plate 80, figs.8 & 9; pl.100, fig.2; pl.134, figs.3, 5 & 6.

Description: Vesicle subspherical with a thickened rim bordering the spherical aperture. The vesicle is ornamented with densely packed grana <2um in height and <2um in diameter. The diameter of the vesicle ranges between 60-75um.

Remarks: This species of *Calpichitina* is distinguished by the presence of grana on the vesicle wall. *Calpichitina* sp. 1 differs in possessing an echinate ornamentation.

Genus *Cingulochitina* Paris 1981.

Type species: *Cingulochitina cingulata* Eisenack 1937.

Generic description: Paris 1981, p.164-165.

Remarks: The author has endeavoured to use the species in this genus that were utilised by Paris 1981, (p.165) to maximise the comparability of the assemblages studied here with those from south-west Europe

Cingulochitina convexa (Laufeld) Paris 1981

Plate 95, fig.3 & 6; pl.133, figs.1, 2 & 3; pl.144, fig.5.

Description: Laufeld 1974, p.97, fig.58.

Holotype: Laufeld 1974, fig.58D.

Remarks: Specimens recorded here accord well with the type material.

Cingulochitina cf. *convexa* (Laufeld) Paris 1981

Plate 95, figs.4 & 5; pl.96, figs.1-7; pl.112, figs.5 & 6; pl.125, figs.3-7; pl. 133, figs.4-8; pl.144, figs.2 & 3.

Holotype: Laufeld 1974, fig.58D.

Remarks: Compare with Laufeld 1974, p.97, fig.58. *Cingulochitina* cf. *convexa* here has a more elongate vesicle than type specimens of the species. Laufeld described the type material as having uncommon twins and chains which also differs from the present material as many chains of specimens have been recorded. *Cingulochitina* cf. *convexa* is synonymous with C. sp. aff. *convexa* of Paris 1981, p.165.

Cingulochitina ervensis (Paris) Paris 1981.

Plate 144, figs.7, 8 & 9; pl.112, figs.3 & 4?; pl.118, fig.6.

Description: Paris 1979, p.59-61, pl.1, fig.1-8.

Holotype: Paris 1979, pl.1, fig.1. Age: Emsian.

Remarks: The interpretation of this species by Paris 1981 (p.167, text-fig.78) is followed here.

Cingulochitina plusquelleci Paris 1981.

Plate 144, fig.6.

Description: Paris 1981, p.171-174, pl.32, figs.1-5, 10 & 21, text-fig.78.

Holotype: Paris 1981, pl.32, figs.3. Age: Gedinnian.

Remarks: The interpretation of this species by Paris 1981 (p.167, text-fig.78) is followed here.

Cingulochitina serrata (Taugourdeau & Jekhowsky) Paris 1981.

Plate 96, fig.1-7; pl.112, fig.2; pl.126, fig.1; pl.134, fig.1; pl.144, fig.5; pl.151, figs.4 & 5.

Description: Taugourdeau & Jekhowsky 1960, p.1226, pl.6, figs.76-79 & 81 (not 80, [Paris, 1981]).

Holotype: Taugourdeau & Jekhowsky 1960, pl.6, fig.76. Age Gotlandian.

Remarks: *Cingulochitina serrata* has a short neck and an almost equidimensional vesicle (i.e. the length is equal or slightly greater than the width). This species is shorter in length than the other species of *Cingulochitina* recorded in the present study.

Cingulochitina cf. *serrata* (Taugourdeau & Jekhowsky) Paris 1981.

Plate 97, figs.8, 9 & 10; pl.126, figs.2, 3, 4 & 6; pl.134, figs.4 & 7.

Holotype: Taugourdeau & Jekhowsky 1960, pl.6, fig.76. Age Gotlandian.

Remarks: Compare with Taugourdeau & Jekhowsky 1960, p.1226, pl.6, figs.76-79 & 81 (not 80, [Paris, 1981]). Specimens included here are essentially transitional forms between *C. serrata* and *Cingulochitina* sp. A (herein). Specimens are slightly longer than they are broad, in a similar manner to C. serrata, but they are rather larger in size (> 100um in length). *Cingulochitina* sp. 1 is a more slender form than C. cf. *serrata*.

Cingulochitina sp. 1.

Plate 79, figs.10 & 11; pl.98, figs.1-8; pl.126, figs.5 & 7.

Description: A species of Cingulochitina with an almost straight sided, conical vesicle. The length of the vesicle ranges between 115-145um. The vesicle width ranges between 50-65um at the aboral margin and tapers towards the oral opening. The vesicle width at the oral margin ranges between 27-45um. The vesicle flares orally from the position of the prosome. A reduced carina is present at the basal edge. The vesicle wall is smooth.

Remarks: The shape of the specimens included in *Cingulochitina* sp. 1 are comparable with the illustration of *C. cingulata* by Laufeld 1974, fig.57D, but they tend to be slightly more elongated. An additional difference is that *Cingulochitina* sp. 1 encompasses forms with broad and narrow carina. This taxon includes this variation as it is commonly not possible to decipher the carina width using light microscopy. *Cingulochitina* sp. 1 is also larger than *C. cingulata*, having a vesicle length greater than 115um. These forms are very similar in shape and size to *Cingulachitina* sp. A of Paris 1981 (p.174, fig.78).

An unusual variety of this rather broad taxon has been recorded from Ludlow aged sediments.

Cingulochitina sp. 1 var. A.

Plate 99, figs.1, 2 & 3.

Remarks: This variety is only recorded from latest Gorstian (Ludlow) aged sediments in this study. It is distinguished by the presence of striations running perpendicular to the longitudinal axis of the vesicle.

Genus *Conochitina* Eisenack 1931 emend. Paris 1981.

Type species: *Conochitina claviformis* Eisenack 1931.

Generic description: Paris 1981, p. 178.

Conochitina armilata Taugourdeau & Jekhowsky 1960.

Plate 80, fig.3.

Description: Taugourdeau & Jekhowsky 1960, p.1222, pl.3, figs.44, 45 & 46.

Holotype: Taugourdeau & Jekhowsky 1960, pl.3, fig.44. Age: Silurian.

Conochitina brevis Taugourdeau & Jekhowsky 1960.

Plate 12, figs.1-8; pl.26, figs.4, 5 & 6; pl.70, fig.3; pl.80, fig.2.

Description: Taugourdeau & Jekhowsky 1960, p.1222, pl.3, figs.47, 48 & 49.

Holotype: Taugourdeau & Jekhowsky 1960, pl.3, fig.47. Age: Silurian.

Conochitina chydaea Jenkins 1967.

Plate 37, fig.4-7.

Description: Jenkins 1967, p.453, pl.70, figs.4-8.

Holotype: Jenkins 1967, pl.70, fig.4. Age: Llanvirn.

Remarks: *Conochitina simplex* Eisenack 1931 has a broader chamber than *C. chydaea*. *Conochitina intermedia* Eisenack 1955 has a simple conical chamber.

Conochitina cf. *chydaea* Jenkins 1967.

Plate 37, figs.2 & 3.

Holotype: Jenkins 1967, pl.70, fig.4. Age: Llanvirn.

Remarks: Compare with Jenkins 1967, p.453, pl.70, figs.4-8. Specimens included here have a more rounded aboral margin than does *C. chydaea*. The sides of the vesicle are also more parallel in these forms compared to the orally tapering sides of the type specimens. A comparable form is one described in open nomenclature by Paris 1981. His *Conochitina* sp. D (p.189, pl.9, fig.4) is almost identical to the specimens included in C. cf. *chydaea* here.

Conochitina cf. *lepida* Jenkins 1967.

Plate 26, fig.9; pl.48, fig.5.

Holotype: Jenkins 1967, pl.70, fig.2. Age: Caradoc.

Remarks: Compare with Jenkins 1967, p.452-453, pl.70, figs.2 & 3. Specimens included here have a less pronounced flexure between the body chamber and the neck of the vesicle than in the type material.

Genus *Cyathochitina* Eisenack 1955 emend. Paris 1981.

Type species: *Cyathochitina campanulaeformis* (Eisenack) Eisenack 1955.

Generic description: Paris 1981, p.287.

Cyathochitina calix (Eisenack) Eisenack 1958.

Plate 37, fig.1.

Description: Eisenack 1931, p.87, pl.2, fig.3, pl.4, fig.14, text-fig.1.

Holotype: Eisenack 1931, pl.2, fig.3. Age: Indeterminate as the holotype was recovered from Baltic drift sediments.

Remarks: *Cyathochitina campanulaeformis* (Eisenack) Eisenack 1955 has a broader and more stout test than *C. calix*. The former also differs in possessing a conical chamber that tapers rapidly orally.

Cyathochitina campanulaeformis (Eisenack) Eisenack 1955.

Plate 27, fig.1; pl.36, fig.6; pl.49, figs.2 & 5; pl.74, fig.4.

Description: Eisenack 1931, p.86, pl.2, figs.1 & 2, pl.4, figs.1 & 11-13.

Holotype: Eisenack 1931, pl.2, fig.2. Age: Indeterminate as the holotype was recovered from Baltic drift sediments.

Remarks: *Cyathochitina kuckersiana* (Eisenack) Eisenack 1962 and *C. calix* are morphologically similar to *C. campanulaeformis*. The former has a wide, membranous skirt-like carina compared with the more narrow and rigid carina of *C. campanulaeformis*. *Cyathochitina calix* has a barrel-shaped body chamber as opposed to the orally tapering conical shaped chamber of *C. campanulaeformis*.

Cyathochitina dispar Benoit & Taugourdeau 1961.

Plate 48, fig.7; pl.49, fig.1.

Description: Benoit & Taugourdeau 1961, pl.3, figs.22-28.

Holotype: Benoit & Taugourdeau 1961, pl.3, figs.28. Age: Ordovician.

Remarks: Specimens included here are almost identical to the type specimen.

Cyathochitina cf. *elenitae* Cramer 1964.

Plate 77, figs.1, 2 & 3.

Holotype: Cramer 1964, pl.XXIII, fig.9. Age: Ludlow.

Remarks: Compare with Cramer 1964, p.345, pl.XXIII, figs.9 & 10. The three specimens included here have a similar shaped vesicle to the type specimens of *C. elenitae*. However, specimens here have a greater constriction of the neck in the viscinity of the prosome which is positioned further from the oral opening than in the type material.

Cyathochitina cf. *fistulosa* Taugourdeau & Jekhowsky 1960.

Plate 27, fig.2.

Holotype: Taugourdeau & Jekhowsky 1960, p.1224 pl.V, fig.67. Age: Ordovician.

Remarks: Compare with Taugourdeau & Jekhowsky 1960, p.1224, pl.V, figs.67 & 68. The three specimens recorded here have the characteristic straight sided vesicle of this species, however they have a more stout vesicle than the type specimens.

Cyathochitina sp. 1.

Plate 71, figs.1, 2 & 3.

Description: A species of *Cyathochitina* with a long cylindrical neck and a conical body chamber. The length of the vesicle ranges between 140-190um. The chamber width ranges between 76-90um and the width of the neck is between 25-33um. The chamber occupies between 1/3 and 1\2 the length of the vesicle. A reduced carina is present at the basal edge. The vesicle wall is covered with a granulate and microechinate ornamentation.

Remarks: The distinctive cylindro-conical vesicle shape, the reduced carina and the ornamentation distinguish this species of *Cyathochitina*. *Cyathochitina kuckersiana* has the same general vesicle shape but this species has an extended carina and a smooth vesicle wall. *Fungochitina* species have the same vesicle shape and they also possess ornamentation. However, the presence of a reduced carina distinguishes *Cyathochitina* sp. 1 from these forms.

Genus *Desmochitina* Eisenack 1931 emend. Eisenack 1962.

Type species: *Desmochitina nodosa* Eisenack 1931.

Generic description: Eisenack 1931, p.91-92.

Desmochitina minor Eisenack 1931.

Plate 13, fig.4?; pl.26, fig.8; pl.38, figs.3 & 4; pl.49, fig.4.

Description: Eisenack 1931, p.93, pl.3, figs.9-11.

Holotype: Eisenack 1931, pl.3, fig.9. Age: Ordovician.

Remarks: Eisenack (1962) united the four previously named species of *Desmochitina*, *D. minor* Eisenack 1931, *D. erinacea* Eisenack 1931, *D. cocca* Eisenack 1931, and *D. amphorea* Eisenack 1931 under the name *D. minor*. The variation that is apparent is now considered to be intraspecific. Several of the original species names are presently in use as *forma* names within the species *D. minor*.

Desmochitina minor forma *cocca* Eisenack 1931.

Plate 26, fig.7; pl.38, figs.2 & 5; pl.49, fig.3.

Description: Eisenack 1931, p.94, pl.3, figs.14 & 15.

Holotype: Eisenack 1931, pl.3, fig.14. Age: Ordovician.

Remarks: This forma has a subspherical shaped vesicle. A pictorial comparison with some of the other published formae (e.g. forma *typica*, forma *ovulum*) within the species *D. minor* is given by Paris 1981, p.119, fig.68.

Desmochitina piriformis Laufeld 1967.

Plate 38, fig.1; pl.49, fig.6.

Description: Laufeld 1967, p.332-333, fig.27A-E.

Holotype: Laufeld 1967, fig.27A. Age: Caradoc.

Remarks: This species is distinguished by having the widest part of the body chamber positioned towards the oral opening, as opposed to the widest part being mid-way between the aboral and oral poles of the chamber, as in *D. minor*.

Genus *Eisenackitina* Jansonius 1964.

Type species: Eisenackitina castor Jansonius 1964.

Generic description: Jansonius 1964, p.912

Eisenackitina castor Jansonius 1964.

Plate 159, fig.6.

Description: Jansonius 1964, p.912-913, pl.2, figs.15-17.

Holotype: Jansonius 1964, pl.2, figs.16. Age: Givetian.

Eisenackitina raucheri Paris 1976.

Plate 145, fig.8.

Description: Paris 1976, p.103, pl.17, figs.13, 14, 19 & 23; pl.18, fig.18 & 22; pl.21, figs.6, 8 & 14.

Holotype: Paris 1976, pl.76, fig.17. Age: Lochkovian.

Eisenackitina taugourdeaui (Rauscher & Doubinger) Paris 1981.

Plate 145, figs.1, 2, 4 & 5.

Description: Rauscher & Doubinger 1967, p.319-320, pl.4, fig.6.

Holotype: Rauscher & Doubinger 1967, pl.4, fig.6. Age: Devonian.

Genus *Eremochitina* Taugourdeau & Jekhowsky 1960.

Type species: *Eremochitina baculata* Taugourdeau & Jekhowsky 1960.

Generic description: Taugourdeau & Jekhowsky 1960, p.122.

Eremochitina cf. *baculata* Taugourdeau & Jekhowsky 1960.

Plate 28, figs.1 & 2.

Holotype: Taugourdeau & Jekhowsky 1960, pl.VIII, fig.107.

Remarks: Compare with Taugourdeau & Jekhowsky 1960, p.1228, pl.VIII, figs.107 & 108. Forms included here are transitional morphotypes between the species *E. baculata* and *Eremochitina brevis* (Benoit & Taugourdeau) Paris 1990.

Eremochitina brevis (Benoit & Taugourdeau) Paris 1990.

Plate 27, figs.3, 4 & 5; pl.28, fig.5 & 6.

Description: Benoit & Taugourdeau 1961, p.1410, pl.4, figs.44-46.

Holotype: Benoit & Taugourdeau 1961, pl.4, fig.44. Age: Ordovician.

Remarks: *Eremochitina baculata* has a longer and more slender vesicle.

Genus *Fungochitina* Taugourdeau 1966.

Type species: *Fungochitina fungiformis* (Eisenack) Taugourdeau 1966.

Generic description: Taugourdeau 1966.

Fungochitina pistilliformis (Eisenack) Taugourdeau 1966.

Plate 169, fig. 2?

Description: Eisenack 1931, p.88, p.88, pl.2, figs.6 & 7, pl.4, figs.2 & 3.

Holotype: Eisenack 1931, pl.4, fig.2. Age: Silurian.

Remarks: Two varieties of this species have been recorded in the present study.

Fungochitina pistilliformis var. *lata* (Taugourdeau & Jekhowsky) Taugourdeau 1966.

Plate 127, fig.4; 145, figs.3, 6 & 7.

Description: Taugourdeau & Jekhowsky 1960, p.1232, pl.XI, figs.156 & 157.

Holotype: Taugourdeau & Jekhowsky 1960, pl.XI, figs.156. Age: Lower Devonian.

Remarks: This variety possesses a relatively dense ornament of cones and short spines.

Fungochitina pistilliformis var. A

Plate 127, figs.1 & 2.

Remarks: Only two specimens of this taxon have been recorded in the present study. This variety has a relatively sparse distribution of ornamentation compared to *Fungochitina pistilliformis* var. *lata* which are in the form of broad based, rather rigid spines.

Genus *Gotlandochitina* Laufeld 1974.

Type species: *Gotlandochitina martinssoni* Laufeld 1974.

Generic description: Laufeld 1974, p.83.

Gotlandochitina labdata Diez & Cramer 1978.

Plate 99, fig.4.

Description: Diez & Cramer 1978, p.207, pl.1, figs.37-39, 41 & 42.

Holotype: Diez & Cramer 1978, pl.1, fig.39. Age: Lower Devonian.

Remarks: The single specimen recorded here shows the diagnostic trabeculate ornamentation of this species.

Genus *Hoegisphaera* Staplin 1961.

Type species: *Hoegisphaera glabra* Staplin 1961.

Generic description: Staplin 1961, p.419.

Hoegisphaera cf. *glabra* Staplin 1961.

Plate 80, fig.4; pl.99, figs.5 & 6; pl.113, fig.7; pl.118, fig.7; pl.134, fig.2; pl.154, fig.5.

Holotype: Staplin 1961, pl.50, fig.5. Age: Upper Devonian.

Remarks: Compare with Staplin 1961, p.419-420, pl.50, figs.5-7. Specimens Included here are identical to the type specimens in all respects apart from size. The type specimens have a size range of 110-130um in contrast with a diameter of 60-90um in the present material.

Genus *Jenkinochitina* Paris 1981.

Type species: *Jenkinochitina oelandica* (Eisenack) Paris 1981.

Generic description: Paris 1981, p.190.

Jenkinochitina vulgaris Complex.

Plate 38, fig.6; pl.49, figs.8 & 9.

Remarks: The state of preservation of the material observed and the fact that time only permits the use of light microscopy and not SEM analysis in the present study makes it impractical to split this complex of morphotypes. Species included in this complex are *Jenkinochitina vulgaris*, *J. actonica* (Jenkins) Paris 1981, *J. communis* (Taugourdeau) Paris 1981 and *J. travillensis* (Paris) Paris 1981.

Genus *Lagenochitina* Eisenack 1931.

Type species: *Lagenochitina baltica* Eisenack 1931

Generic description: Eisenack 1931, p.80-81.

Lagenochitina baltica Eisenack 1931.

Plate 29, figs.1 & 2; pl.38, fig.8.

Description: Eisenack 1931, p.80-81, pl.1, figs.1-3.

Holotype: Eisenack 1931, pl.1, fig.1. Age: Ordovician.

Remarks: *Lagenochitina capax* Jenkins 1967 has a greater degree of flexure between the neck and the body chamber than *L. baltica*.

Lagenochitina capax Jenkins 1967.

Plate 38, fig.7.

Description: Jenkins 1967, p.465, pl.73, figs.2-3. (Fig. 2 is in fact a specimen of L. deunfii).

Holotype: Jenkins 1967, pl.73, fig. 3. Age: Caradoc.

Remarks: *Lagenochitina deunfii* Paris 1974 is smaller than *L. capax* and *L. baltica* differs from the former in having a lesser degree of flexure between the body chamber and neck.

Lagenochitina? *destombesi* Elaouad-Debbaj 1988.

Plate 13, figs.1 & 2.

Description: Elaouad-Debbaj 1988, p.91-92, pl.7, fig.1, 4-6, 10-12, 15, 17 & 20.

Holotype: Elaouad-Debbaj 1988, pl.7, fig.6. Age: Tremadoc.

Remarks: The assignment of this species to the genus *Lagenochitina* is questioned as the flexure between body chamber and neck is not at all clear on the illustrations of the type specimens by Elaouad-Debbaj.

Lagenochitina deunffi Paris 1974.

Plate 50, figs.1, 2, 5 & 6; pl.100, fig.3.

Description: Paris 1974, 322-323, pl.1, figs.1-3, pl.3, figs.1, 2 & 4, pl.4, figs.7 & 10.

Holotype: Paris 1974, pl.3, fig.1. Age: Lower Caradoc.

Remarks: *Lagenochitina capax* Jenkins 1967 is considered to be a larger species than *L. deunffi*. Two specimens of *L. capax* are illustrated by Jenkins (pl.73, figs.2 & 3) with the holotype, fig.3, measuring 209um in length. This contrasts with the vesicle length range for the species *L. deunffi* of 73-140um. Interestingly, given the range of the length of the vesicle in *L. deunffi*, the other specimen illustrated by Jenkins, fig.2, falls within this range, and is therefore a specimen of *L. deunffi*.

Lagenochitina cf. *deunffi* Paris 1974.

Plate 49, figs.7 & 8.

Holotype: Paris 1974, pl.3, fig.1. Age: Lower Caradoc.

Remarks: Compare with Paris 1974, 322-323, pl.1, figs.1-3, pl.3, figs.1, 2 & 4, pl.4, figs.7 & 10. Specimens included here have a similarly narrow aperture and are of a similar size to *L. deunffi*. However, these forms have a more elongated vesicle.

Lagenochitina cf. *navicula* Taugourdeau & Jekhowsky 1960.

Plate 135, fig.1.

Holotype: Taugourdeau & Jekhowsky 1960, pl.IX, fig.119. Age: Silurian.

Remarks: Compare with Taugourdeau & Jekhowsky 1960, p.1229-1230, pl.IX, figs.119 & 120. Specimens observed here have the same vesicle shape as *Lagenochitina navicula* but do not show evidence of the scar on the vesicle wall which occurs as a result of the unusual method of chain formation in this species. No chains of this taxon were observed.

Lagenochitina ventriosa (Achab) Elaouad-Debbaj 1988.

Plate 13, fig.3.

Description: Achab 1980, p.232, pl.IV, figs.5-7.

Holotype: Achab 1980, pl.IV, figs.5. Age: Arenig.

Remarks: Specimens recorded here are closely comparable to the type specimens.

Genus *Margachitina* Eisenack 1968

Type species: *Margachitina margaritana* (Eisenack) Eisenack 1968.

Generic description: Eisenack 1968, p.182.

Margachitina catenaria catenaria Obut 1973.

Plate 151, fig.7?

Description: Obut 1973, p. pl.15, fig.11

Holotype: Obut 1973, pl.15, fig.11.

Margachitina catenaria crassipes Paris 1981.

Plate 146, figs.2? & 3?

Description: Paris 1981, p.143-145, pl.25, figs.13-16.

Holotype: Paris 1981, pl.25, fig.16. Age: Lochkovian.

Margachitina catenaria tenuipes Paris 1981.

Plate 146, fig.5.

Description: Paris 1981, p.145-147, pl.32, fig.13?; pl.33, figs.12, 16 & 18; pl.34, figs.4 & 6; pl.37, figs.13, 14 & 16.

Holotype: Paris 1981, pl.34, fig.4. Age: Pragian.

Genus *Muscochitina* Paris 1981.

Type species: *Muscochitina muscosa* Paris 1981.

Generic description: Paris 1981, p.268.

Muscochitina muscosa Paris 1981.

Plate 113, figs.2? & 3?; pl.146, figs.6, 7 & 8.

Description: Paris 1981, p.269-270, pl.30, figs.7, 8, 13-15 & 17-20; pl.41, figs.13 & 14.

Holotype: Paris 1981, p.269-270, pl.30, fig.17. Age: Gedinnian.

Genus *Plectochitina* Cramer 1964.

Type species: *Plectochitina carminae* Cramer 1964.

Generic description: Cramer 1964, p.346.

Plectochitina carminae? Cramer 1964.

Plate 100, figs.5-8; pl.101, figs.1-4.

Description: Cramer 1964, p.346-347, pl.XX, figs. 19 & 21, text-fig.49.

Holotype: Cramer 1964, pl.XX, fig. 21. Age: Ludlow.

Remarks: The specimens recorded here are poorly preserved, hence the elaborate and delicate appendages of this species are commonly broken. For this reason, the specimens recorded are questionably assigned to *P. carminae*. The rhizoid (sponge-like) texture of the appendages of the specimens recovered here appears identical to that of the appendages on the type specimens. *P. carminae*? is recorded only from the *Saetograptus incipiens* graptolite zone (latest Gorstian, lower Ludlow) in the present study.

Plectochitina sp. 1.

Plate 113, figs.1, 4, 5 & 6.

Remarks: Only one reasonably well preserved specimen and several damaged specimens have been recorded. The vesicle is cylindro-spheroidal in shape and approximately 150um in length. There are trabeculate aboral appendages arising from the basal edge measuring upto approximately 40um in length. The appendages branch distally to join up with adjacent appendages. They appear to be solid and are commonly broken in the material observed. The wall of the chamber and the neck appears to be smooth.

This form of *Plectochitina* is recorded from the *Monograptus transgrediens* graptolite zone (latest Pridoli) in the present study.

Genus *Pogonochitina* Taugourdeau 1961.

Type species: *Pogonochitina simplex* Taugourdeau 1961.

Generic description: Taugourdeau 1961, p.147-148.

Pogonochitina? *secunda* (Schallreuter) Paris 1981.

Plate 39, fig.4.

Description: Schallreuter 1963, p.394, pl.1, fig.1.

Holotype: Schallreuter 1963, pl.1, fig.1. Age: Middle Ordovician.

Remarks: *Pogonochitina grandis* Taugourdeau 1961, *P. simplex* Taugourdeau 1961 and *P. spinifera* Taugourdeau 1961 all possess a more conical test than P? *secunda*. *Pogonochitina*? *secunda* has a distinct flexure between the body chamber and the neck.

Genus *Pseudoclathrochitina* Cramer 1967.

Type species: *Pseudoclathrochitina carmenchuae* (Cramer) Cramer 1967.

Generic description: Cramer 1967, p.46.

Pseudoclathrochitina cf. *carmenchuae* (Cramer) Cramer 1967.

Plate 71, figs.6-9.

Holotype: Cramer 1964, pl.XXIV, fig.18. Age: Lower Devonian.

Remarks: Compare with Cramer 1964, p.346, pl.XXII, figs.8, 9 & 10, pl.XXIV, fig.18. The specimens recorded here have the same general vesicle shape and dimensions as *P. carmenchuae*. However the ornamentation is more elaborate in the present material. Of the three specimens recorded, only one is very well preserved. This specimen shows appendages protruding from the vesicle which branch in an anastomosing fashion distally to form a dense mesh. The two less well preserved specimens have a damaged mesh as can be seen in the plate illustrations. *Pseudoclathrochitina* cf.

carmenchuae is recorded from the Telychian (late Llandovery) aged sediments here, contrasting with the Upper Ludlow-Lower Gedinnian stratigraphic records of *P. carmenchuae* by Cramer (1964). Another species with a closely comparable morphology to P. cf. *carmenchuae* is *Acanthochitina*? *rashidi* Jenkins 1970, a form probably better placed in the genus *Pseudoclathrochitina*. This species, described from the late Ordovician of Oklahoma, has a similarly structured ornamentation which tends to be better developed on the flanks of the vesicle in the type specimens. *Pseudoclathrochitina* cf. *carmenchuae* has ornamentation better developed at the aboral margin.

Genus *Pterochitina* Eisenack 1955.

Type species: *Pterochitina perivelata* (Eisenack) Eisenack 1955.

Generic description: Eisenack 1955, p.177.

Pterochitina perivelata (Eisenack) Eisenack 1955.

Plate 127, fig.6; pl.134, fig.8; pl.135, fig.2; pl.147, figs.1, 2 & 3.

Description: Eisenack 1937, p.229-230, pl.16, fig.4, text-fig.7.

Holotype: Eisenack 1937, pl.16, fig.4. Age: Silurian

Genus *Rhabdochitina* Eisenack 1931.

Type species: *Rhabdochitina magna* Eisenack 1931.

Generic description: Eisenack 1931, p.90-91.

Rhabdochitina magna Complex.

Plate 29, figs.3 & 7; pl.56, fig.3; pl.71, fig.5; pl.77, fig.5; pl.102, figs.6 & 7

Remarks: This complex of forms have been commonly recorded in the literature from Ordovician and Silurian sediments, e.g. Eisenack 1931, 1939, Jenkins 1967, Benoit & Taugourdeau 1961, Lister & Downie 1967. The species of *Rhabdochitina* included in the complex are of very similar morphology and are not practically discernible from in the poorly preserved material observed here. For this reason, these species have been grouped into the *R.. magna* Complex. They are *Rhabdochitina magna* Eisenack 1931, *R.. concephala* Eisenack 1934, *R.. truncata* Taugourdeau 1961 & *R.. virgata* Taugourdeau 1961.

Genus *Sagenachitina* Jenkins 1970.

Type species: *Sagenachitina oblonga* (Benoit & Taugourdeau) Jenkins 1970.

Generic description: Jenkins 1970, p.270.

Sagenachitina oblonga (Benoit & Taugourdeau) Jenkins 1970.

Plate 30, fig.5; pl.39, fig.1.

Description: Benoit & Taugourdeau 1961, p.1406, pl.1, figs.1-6.

Holotype: Benoit & Taugourdeau 1961, pl.1, figs.1 & 2. Age: Arenig.

Remarks: *Sagenachitina retifera* (Taugourdeau & Jekhowsky) Jenkins 1970 has a longer neck relative to the body chamber than *S. oblonga*. The former has the more slender test of the two species. The mesh-work carinas of the specimens observed are generally poorly preserved.

Sagenachitina cf. *retifera* (Taugourdeau & Jekhowsky) Jenkins 1970.

Plate 30, figs.1-4.

Holotype: Taugourdeau & Jekhowsky 1960, pl.2, fig.25. Age: Arenig.

Remarks: Compare with Taugourdeau & Jekhowsky 1960, p.1222, pl.2, figs.25 & 26. The specimens recorded here have constricted necks as opposed to the parallel-sided necks of the type specimens. Specimens observed have an almost identical test form to specimens assigned to S. cf. retifera by Paris 1981 (p.303, pl.10, fig.18).

Genus *Sphaerochitina* Eisenack 1955.

Type species: *Sphaerochitina sphaerocephala* (Eisenack) Eisenack 1955.

Generic description: Eisenack 1955, p.162.

Sphaerochitina pilosa Collinson & Scott 1958.

Plate 178, figs.1-4; pl.196, fig.6.

Synonomy: 1985, *Fungochitina pilosa*, Paris *et al.*, pl.28, figs.3-6 & 10.
1988, *Fungochitina pilosa*, Paris *in* Streel *et al.*

Description: Collinson & Scott 1958, p.21-22, pl.3, figs.1-5.

Holotype: Collinson & Scott 1958, pl.3, fig.2. Age: Middle Devonian.

Remarks: The transfer of this species to the genus *Fungochitina* by Paris (1981) is rejected on the basis of the spheroidal body chamber of this species, as illustrated by Collinson & Scott (1958, text-fig.10, pl.3, figs.1-5). Specimens recorded here have a very similar morphology to the type specimens.

Sphaerochitina sphaerocephala (Eisenack) Eisenack 1955.

Plate 50, figs.3, 4 & 7; pl.102, fig.1?; pl.135, figs.3, 4 & 5; pl.151, fig.8?; pl.178, fig.5.

Description: Eisenack 1932, p.271-272, pl.12, figs.14 & 15.

Holotype: Eisenack 1932, pl.12, fig.15. Age: Silurian.

Remarks: *Sphaerochitina impia* Laufeld 1974 has a similar morphology but is smaller in size than *S. sphaerocephala*, ranging in length from 80-105m. Specimens with this relatively simple morphology that have a vesicle length greater than 105m are included in *S. sphaerocephala*.

Genus *Urnochitina* Paris 1981.

Type species: *Urnochitina urna* (Eisenack) Paris 1981.

Generic description: Paris 1981, p.153.

Urnochitina urna (Eisenack) Paris 1981.

Plate 136, figs.1 & 2.

Description: Eisenack 1934, p.69, pl.5, figs.7-13, text-fig.34.

Holotype: Eisenack 1934, pl.5, fig.7. Age: Silurian.

Genus *Velatachitina* Poumot 1968.

Type species: *Velatachitina nebulosa* Poumot 1968.

Generic description: Poumot 1968, p.49-51.

Remarks: Two genera to compare with *Velatachitina* are *Eremochitina* and *Siphonochitina* which both differ from the former in the structure of the aboral pole. The difference in these structures is well illustrated by Paris 1981, p.231, fig.100.

Velatachitina nebulosa Poumot 1968.

Plate 29, fig.4.

Description: Poumot 1968, p.52, pl.1, figs.9 & 10.

Holotype: Poumot 1968, pl.1 fig.9. Age: Llandeilo.

Remarks: *Velatachitina veligera* has a more elongate test and a shorter aboral velum than *V. nebulosa*.

Velatachitina veligera Poumot 1968.

Plate 39, figs.5, 6 & 7.

Description: Poumot 1968, p.50-51, pl.1, figs.7 & 8.

Holotype: Poumot 1968 pl.1, fig.7. Age: Arenig.

Remarks: *Velatachitina nebulosa* has a shorter, more stout test and a longer aboral velum than *V. veligera*.

Velatachitina sp.

Plate 29, figs.5? & 6?; pl.39, fig.3.

Remarks: The specimens recorded here have a similar test shape to that of *V. copulata* Poumot 1968. However, the specimens observed have a much shorter aboral *velum* (< 1/3 the total vesicle length) than in *V. copulata*.

Chitinozoan Form A.

Plate 50, figs.8 & 9.

Remarks: Fourteen poorly preserved specimens, which are all recorded from Caradoc aged sediments, are assigned to this taxon. The diagnostic feature is the oral aperture of the vesicle which is composed of a mesh-work type of wall structure. This type of structure is apparent in the species *Sphaerochitina fenestrata* Taugourdeau & Jekhowsky 1960 which was described from the Devonian of the Sahara. Analysis of the vesicle shape is not reliable if based on the poorly preserved specimens observed here. The variation in vesicle form can be seen in the photographic illustrations.

Chapter 7. Stratigraphic palynology.

The primary aim of the present study was to produce a complete palynological zonation for the Ordovician to Devonian interval of the Anti Atlas. However, it was evident from very early in the study that this would not be possible due to the limited number and stratigraphic spread of the samples made available and also due to the non productive nature of palynological preparations from certain intervals (e.g. the Llandeilo). As a consequence, the palynostratigraphy of the present study is presented in the form of a series of described palynological associations with stratigraphic gaps between, as seen in the accompanying figures.

The assemblages are considered in three sections; the first deals with the assemblages recorded from the Ordovician field samples, the second with the assemblages recovered from the Silurian to Lower Devonian field samples and the third deals with the assemblages recorded from the exploration well Oum Doul-1. Within each section, the assemblages, many of which are macrofossil dated, are described and compared with palynomorph assemblages of a similar age that have been reported in the literature.

A notable limitation of the present study is the difficulty in stratigraphically relating field samples collected from a single formation to each other. The field samples provided for the study were largely collected as single samples from roadside exposures. Although it has been possible to allocate all the samples utilised in the study to a particular formation, it is often not possible to say how samples from a single formation relate to each other in terms of their relative stratigraphic position.

An alternative method of ordering the samples is to have them in chronostratigraphic order by utilising the macrofossils present. This was found to solve the problem in part. Having the benefit of the abundant graptolitic faunas recorded from the Silurian-Lower Devonian field samples does allow these samples to be placed in a chronostratigraphic order. However, the Ordovician field samples, in which the shelly macrofossil biostratigraphic resolution is rather limited, this method of ordering samples within formations was not always found to be possible.

Where several assemblages are recorded from samples within a formation whose relative ages are not known from the macrofossil information, e.g. from the Fezouata (shale) Formation and from the Ktaoua (sandstone and shale) Formation, attempts have been made to place the samples in chronostratigraphic order using the palynomorph assemblages. This has been attempted by comparing the present assemblages with previous palynological studies. Where several assemblages have been recorded from samples within a formation which cannot be placed in relative stratigraphic order, these assemblages are only described and illustrated as having been reported from that particular formation.

In describing the assemblages, the terms rare, occasional, common and abundant are used when referring to the proportions of taxa recorded in an assemblage. These terms refer to the following percentages of taxa recorded:

Less than 1% - RARE
2-5% - OCCASIONAL
6-14% - COMMON
More than 15% - ABUNDANT

The assemblage compositions are illustrated on the enclosed Tilia graphs with the proportions of the major palynomorph groupings illustrated towards the right hand side of the graphs. The palynomorph groupings utilised are the acritarchs, the prasinophytes, the chitinozoa and the spores. As stated in the earlier chapter regarding the class Prasinophyceae, only the microplankton indisputably assignable to this class are included in this grouping. Within the acritarchs, a three fold subdivision of the group has been made, namely the 'acanthomorphic acritarchs', the 'spheromorphic acritarchs' and the 'other acritarchs'(i.e. non acanthomorphic and non spheromorphic acritarchs). The morphological scope of each of these three subdivisions of the Acritarcha is as defined by Cramer & Diez 1979, p.23-29. The acritarchs have been subdivided in such a manner in order to apply the environmental model of Dorning (1987) which relates the palaeoenvironment of deposition of the host sediments to the broad morphotypic composition of the acritarch assemblage.

The term '*association*' is used here as a characteristic assemblage or group of similar assemblages that possess a taxa composition and/or taxa abundances that are practically recognisable by future workers for biostratigraphical purposes.

In the vast majority of cases where more than one assemblage is allocated to an 'association', establishing the degree of similarity of the taxonomic composition of the assemblages is beneficial in establishing the 'association'. The degree of similarity is calculated with the aid of a cluster analysis of the assemblages which is run using the Tilia graph program, the results from which must then be interpreted manually. Assemblages falling within a cluster on the Tilia graph dendrogram which have a total sum of squares of approximately two or less is here considered to be a potential 'association' (D. W. Jolley pers. comm. 1992). However, this grouping by statistical analysis must be analysed manually to verify the practicability of the 'association' i.e. that it may be recognised by future workers. For example, relatively insignificant taxonomic categories in the data, e.g. Acanthomorphic acritarchs indet., may heavily influence the cluster which would make future recognition of an 'association' defined on such biostratigraphically insignificant groups impractical.

Under the sections headed 'relevant literature', a brief resume of the palynostratigraphic studies that have been utilised for comparison with the assemblages analysed is given. Comparisons are primarily made with northern Gondwanan studies which include those from Iberia (Cramer & Diez 1978, Diez & Cramer 1978, Paris 1981), North Africa (Taugourdeau & Jekhowsky 1960, Poumot & Van Oyen 1964,

Figure 14. A comparison of chitinozoan biozonations from Northern Gondwana published pre 1982, from Paris 1981.

	AGE		BIOZONES DE CHITINOZOAIRES	Taug. & Jehkow. 1960	Magloire 1967	Poumot & al. 1964	Cramer & Diez 1978
DEVONIEN	Emsien	38	B. *riclonensis*	8			18
		37	B. *riclo*. B. *bulbosa*		?		
		36	B. *bulbosa*				17
	Praguien= Siegenien	35	B. *maritima*				
		34	G. *jouann*.-A. *caeciliae*	?			
		33	M. *catenaria tenuipes*				
		32	A. *comosa*- M. *cat. tenuipes*		J	18	16
	Lochkovien= Gedinnien	31	C. *plusq*.- A. *cenzratiensis*		I_3	17	15
		30	C. *plusquelleci*	7	I_1	16	12
		29	C. *plusq*.- A. *tomentosa*	6	I		
		28	L. *navicula*	5			
		27	E. *bohemica*				11
		26	A. *fragilis*				
		25	E. *bohem*.- A. *chlupaci*				
SILURIEN	Pridolien	24	U. *urna*		H	15	10
		23	P. *perivelata*	4			9 ?
	Ludlow	22	A. cf. *echinata*				6
		21	A.? *thadeui*		G		?
	Wenlock	20	S. *lycoperdoides*				
	Llandovery	19	C. *proboscifera truncata*-	3		9 à 13 8	2+3,base
ORDOVICIEN	Ashgill	18	B. *micrac*. - B. sp. B		F		
	Caradoc	17	C. *homoclaviformis*				
		16	B. *robusta* -C. *homocla*.				
		15	R.? cf. *gallica*				
		14	J. *tanvillensis*				
		13	L. *dalbyensis*				
		12	L. *deunffi*				
	Llandeilo	11	L. *pissotensis*				
		10	L. *pissot*. - L. sp. aff. *pissot*.	?	?	?	
		9	L. sp. aff. *pissotensis*				
	sup.	8	C.? *armoricana*				
	Llanvirn inf.	7	S. *formosa*		E_2	5	
		6	C. *camp*. - L. *esthonica*	?	E_1		
		5	C. *calix*				
		4	C. *protocalix*			4	
	Arenig	3	B. *henryi*				
		2	D. (P.) *ornensis*- C. *pseudocar*.	2			
		1	E. *baculata brevis*		D_3		
					D2+ D3	2 + 3	

Tabl. 40 : Essai de corrélations entre la biozonation des Chitinozoaires proposée ici, et les zonations établies par d'autres auteurs [Sahara et Afrique du Nord s.l. : Taugourdeau et Jekhowsky (1960), Poumot et Van Oyen (1964), Magloire (1967), Jardiné et Japaudjan (1968) ; Espagne : Cramer et Diez (1978), Diez et Cramer (1978)].

Magloire 1967, Jardine & Japaudjian 1968, Jardine *et al.* 1974, Paris 1990) and the Middle East (Keegan, Rasul & Shaheen 1988). Many of the older publications regarding Northern Gondwanan palynostratigraphy have had their rather low resolution zonal schemes calibrated against the more comprehensive recent schemes e.g. Paris 1981 (fig. 14). In the present study, there is a tendency to compare the assemblages recorded to the more recent zonal schemes in which the data from the older publications has been considered. Comparisons are made with the UK, Baltica and N. America where appropriate.

The assemblages recorded from the Ordovician aged field samples.

Tremadoc-earliest Arenig.

The oldest samples analysed for palynology in the present study were taken from the Fezouata (shale) Formation of Tremadoc to earliest Arenig age. The five samples investigated from this interval, none of which have been dated by macrofossils, are assigned to one of three palynological associations described below.

Relevant literature: The earliest palynological studies of Tremadoc age were carried out by Deunff (1961a & 1964a) on material from the Algerian Sahara. More recently, Jardine *et al.* (1974) established four palynological zones through the Tremadoc of Algeria and Elaouad-Debbaj (1988) published six zones for the same stratigraphic interval in Morocco. Eight zones for the Tremadoc of the UK were erected by Rasul (1979) which were compared to the North African schemes by Elaouad-Debbaj (1988), fig.15. Assemblages recorded from the UK by Molyneux & Dorning 1989 and Molyneux & Rushton 1988 and by Mette 1989 from SW Spain are also comparable to those recorded here.

General composition of the Tremadoc-earliest Arenig assemblages.

The generic composition of the Tremadoc-earliest Arenig assemblages are dominated by *Acanthodiacrodium, Cymatiogalea, Polygonium* and *Stelliferidium*. Low diversity chitinozoan assemblages were only recorded in the latest Tremadoc-earliest Arenig assemblages studied, although, chitinozoans have been reported from the late early Tremadoc-early late Tremadoc in Morocco by Elaouad-Debbaj (1988).

Figure 15. A comparison of the Tremadoc aged acritarch zonation of a. Rasul 1979, b. Naumova 1950, c. Jardina *et al.* 1974 and d. Elaouad-Debbaj 1988, from Elaouad-Debbaj 1988.

Ages	a	ANGLETERRE	b	BALTIQUE	c	SAHARA ALGERIEN	d	MAROC
ARENIG							-?-	
TREMADOC	8	Arenaceous Beds (A)			?	Argiles d'El Gassi		Trémadoc inférieur
	7	*Shumardia pusilla* Beds (A)			C1		?	
	6	Brachiopod Beds (B)			?		6?	
	5						5	
	4	*Clonograptus tenellus* Beds (C)			B2		4	
	3						3	
	2				B1	Argiles d'El Louha	2	
		Trans. beds (T)						
	1	*Dictyonema flabelliforme* Beds (D)	XIII	*Dictyonema* Beds			1	
			XII X IX VIII	*Obolus* Beds	B0	Argilo-gréseux de l'Oued Mya		

Detail of the Tremadoc-earliest Arenig Assemblages.

Association 1 (see Tilia graph 1).

Association 1, recorded from samples DW 105 and DW 115 from the Fezouata Formation, is dominated by acanthomorphic acritarchs with the notable absence of chitinozoa. *Stelliferidium* spp. are abundant, notably *S. cortinulum* and *S. trifidum*, with common\abundant *Polygonium gracile* and *Acanthodiacrodium* spp. e.g. *A. uniforme, A. constrictum* and *A. amplium*. Other significant occurrences include *Vigatasporites rudii* and *Trichosphaeridium annolovaense*.

Discussion: The palynology of the Fezouata Formation has been studied previously by Elaouad-Debbaj (1988b), however, her study is difficult to compare to the present due to her speciation which is based on observations using electron microscopy. Comparison of stratigraphically important groups such as the *Stelliferidium* and *Cymatiogalea* species is difficult due to her adoption of taxa based on minute detail which is not apparent under the light microscope. Despite these problems, synonomy of the detailed SEM taxa utilised by Elaouad-Debbaj into morphologically broader light microscopy determinable taxa does enable the partial application of her zonal scheme. The presence of abundant *Stelliferidium cortinulum* (= *S. barbarum* of Elaouad-Debbaj [1988b]) indicates that the association in question is no younger than her Zone 3.

As mentioned by Elaouad-Debbaj (1988b), assemblages from Morocco are broadly comparable with those reported from the UK by Rasul (1974, 1979). Rasul (1979) proposed eight zones within the Tremadoc series of the UK based on 55 commonly occurring and relatively short ranging species. The association under discussion appears to resemble his Zone 2 based on the abundant occurrence of *Stelliferidium cortinulum* in association with presence of *S. simplex* and *Acanthodiacrodium amplium*. In addition, Jardine *et al.* (1974) recorded *Priscogalae cortinulum* (=*Stelliferidium cortinulum*) in their Zones B1-B2.

A tentative comparison of the three affore mentioned zonal schemes is suggested by Elaouad-Debbaj (1988b), fig. 15. This shows that Zone 2 of Rasul (1979) and the upper part of B1 of Jardine *et al.* (1974) to be approximately equivalent in age to Zone 2 of Elaouad-Debbaj (1988b). It would appear likely, therefore, given the presence of abundant *Stelliferidium cortinulum* in association with *S. simplex* and *Acanthodiacrodium amplium*, that Association 1 is assignable to Zones 2 of both Rasul (1979) and Elaouad-Debbaj (1988b) and probably the upper part of Zone B1 of Jardine *et al.* (1974).

Figure 16. A correlation of the standard graptolite zones and the Northern Gondwanan chitinozoan zones with the palynological associations defined herein from the Ordovician.

SYSTEM	SERIES	STAGES	GRAPTOLITE ZONES *From Paris 1990*	N. GONDWANA CHITINOZOAN ZONES *From Paris 1990*	PALYNOLOGICAL ASSOCIATION
ORDOVICIAN	ASHGILL	Hirnantian	G. persculptus C. extraordina	▨ ? T. elongata	▨
		Rawtheyan	D. anceps	A. merga	Association 12
		Cautleyan			
		Pusgillian	D. complanatus P. linearis	A. nigerica	▨ Association 11
	CARADOC	Onnian	D. clingani	▨	▨
		Actonian		B. robusta	
		Marshbrook			
		Longvillian		J. tanvillensis	
		Soudleyan	C. multidens	? ▨	
		Harnagian		L. dalbyensis	Association 10
		Costonian	N. gracilis	L. deunffi	Association 9
	LLAND.	Late		L. ponceti	▨
		Early	G. teretiusculus	L. pissotensis	
	LLANV.	Late	D. murchisoni	L. clavata A. armoricana ▨	
		Early	D. artus	S. formosa C. calix C. protocalix	Association 8
	ARENIG	Fennian	D. hirundo I. gibberulus	D. bulla ▨	▨
		Whitlandian	D. nitidus	B. henryi D. ornensis E. brevis	Association 7 Association 5 & 6 ▨ / Association 4
		Moridunian	D. deflexus P. approximatus	E. baculata C. symmetrica A. conifundus	Association 3
	TRE.	Late	R. flabelliforme	▨	▨ Association 2
		Early		L. destombesi ▨	▨ Association 1

Not sampled or barren ▨

Association 2 (see Tilia graph 1).

Association 2, recorded from sample DW 65 from the Fezouata Formation, is composed of a low diversity acritarch assemblage dominated by *Cymatiogalea messaoudii* which makes up approximately 65% of the assemblage. Other forms present include *Polygonium gracile*, *Goniosphaeridium* cf. *connectum*, *Caldariola glabra*, and *Acanthodiacrodium costatum*.

Discussion: This association of species was not recorded by Elaouad-Debbaj (1988b) in her study of the Moroccan Tremadoc. However, Jardine *et al.* (1974) recorded *Cymatiogalea messaoudii* from Algeria in their Zones B1 & B2. The presence of *Caldariola glabra* and *Goniosphaeridium* cf. *connectum* would suggest that this association is probably younger than this level if we compare the association with assemblages recorded from the UK e.g. Molyneux & Rushton 1988. The absence of chitinozoa in this association implies an older age relative to Association 3 described below.

Association 3 (see Tilia graph 1).

Association 3, recorded from samples DW 304 and DW 305 from the Fezouata Formation, incorporates assemblages with diverse acritarchs and low numbers of primitive chitinozoans. Notable taxa present are common\abundant *Acanthodiacrodium raia*, common\abundant *Cymatiogalea* sp. 1, common *Stelliferidium trifidum* and common *Vogtlandia* sp. 1. A significant occurrence in this association is that of *Cymatiogalea deunffi*. *Solisphaeridium* spp. and *Stellichinitum* spp. also occur here. The chitinozoan component of the assemblages is characterised by low numbers of *Conochitina brevis* and rare *Lagenochitina*? *destombesi* and *L. ventriosa*.

Discussion: Comparison with the zonal scheme of Elaouad-Debbaj 1988b indicates that this association can be assigned to the youngest zone, Zone 6, of that scheme. This is based largely on the presence of the chitinozoan species mentioned above.

Species of note from this association that were recorded from Algeria by Jardine *et al.* (1974) are *Cymatiogalea deunffi* and *Acanthodiacrodium raia* (=*Priscotheca raia* in Jardine *et al.* 1974). The co-occurrence of these taxa in Association 3 suggests that it may be assignable to Zone C2 which is positioned at the base of the Arenig\Llanvirn interval in their scheme (fig. 3). However, abundant *A. raia*, as recorded in Association 3, are reported from Zone C1 by Jardine *et al.* (1979) which suggests an age of latest Tremadoc for the association.

More convincing comparisons of Association 3 can be made with assemblages recently documented from the UK by Molyneux & Rushton (1988) and by Molyneux & Dorning 1989. The co-occurrence of *Cymatiogalea deunffi*, *Cymatiogalea messaoudii* (= *Cymatiogalea* sp. 1 pars.), *Vogtlandia coalita* (= *Vogtlandia* sp. 1) and *Stelliferidium trifidum* is present in the UK assemblages and in Association 3 herein. The age assignation of latest Tremadoc to earliest Arenig for the UK assemblages by Molyneux & Rushton (1988) and by Molyneux & Dorning (1989) appears to be consistent with the age indicated by comparison of Association 3 with the North African zonal schemes. In addition, Mette (1989) reported similar assemblages of acritarchs from SW Spain which he also dated as latest Tremadoc to earliest Arenig.

It is also interesting to note the occurrence of *Tongzia meitana* in sample 304. This taxon has only previously been reported in the literature from the early Arenig of China (Li Jun 1989) and from the late Arenig of Czechoslovakia (Vavrdova 1990). This implies the association in question is Arenig in age, however, making age interpretations from comparison with so few records of this relatively recently published taxon may be misleading.

Arenig.

Thirteen samples believed to be of Arenig age have been analysed which are all assigned to the Fezouata Formation. Of these samples, five have been dated using macrofossils, of which only one yielded palynomorphs. The palynomorphs recovered from the non macrofossil dated samples all indicate an Arenig age. From these samples, several associations can be recognised which are described below. Unfortunately, the relative stratigraphic positions of these associations to each other is not determinable from the lithostratigraphic data available to the author. The relative chronostratigraphic positions of the samples is largely indeterminate due to a lack of data in the literature regarding the evolution of acritarch assemblages during the Arenig. The chitinozoan zonation of Paris (1990) for northern Gondwana is utilised were the samples in question yielded chitinozoans of zonal value, which, in some instances, enables the positioning of samples stratigraphically relative to each other.

Relevant literature: The acritarchs of the Arenig interval in Morocco have been studied previously by Cramer *et al.* 1974a & 1974b, and Cramer & Diez 1977 from subsurface material from the Tadla basin and by Fournier-Vinas (1985) from Zekkara. As there is no macrofossil age control for the sections these authors studied, emphasis has been placed on the macrofossil constrained chitinozoan zonal scheme of Paris 1990 (fig. 16). This zonal scheme incorporates palynological data generated from Arenig-Llanvirn aged sections in the Anti Atlas by Elaouad-Debbaj (1984).

The zonal scheme of Jardine *et al.* (1974) from Algeria is of little chronostratigraphic use through the Arenig interval as Zones C2, D & E are all dated as Arenig/Llanvirn in age.

The palynology of the Arenig series in the UK has been studied by Molyneux 1987. These assemblages are markedly different in their composition to the previously recorded Gondwanan assemblages, notably the chitinozoan component, and they are generally poorly preserved. Both these factors makes them difficult to compare with the assemblages from Morocco.

General composition of the Arenig assemblages.

The Ordovician assemblages are characterised by a general increase in abundance of chitinozoans relative to the older assemblages studied. The generic composition is also markedly different with *Eremochitina* prominent in almost all the assemblages studied, commonly associated with *Belonechitina*, *Sagenachitina* and *Velatachitina*. Within the acritarch component, *Coryphidium* species are characteristic with *Acanthodiacrodium* species far less apparent than in the older assemblages. The genera *Marrocanium*, *Peteinosphaeridium* and *Pirea*, all considered to appear in the Arenig (Downie pers. comm. 1989), are all recorded here.

Detail of the Arenig assemblages.

Association 4 (see Tilia graph 2).

Of the five macrofossil dated samples, only one sample, DW 262, yielded palynomorphs. The sample is dated as Arenig, probably Lower Arenig, on the basis of the shelly macrofauna present (see appendix I). The palynomorph assemblage is a rather impoverished, poorly preserved one with notable occurrences of the acritarchs *Coryphidium ramiferum*, *Frankea sartbernardensis* and *Multiplicisphaeridium inconstans*. Chitinozoans recovered include *Belonechitina micracantha micracantha*, *B. micracantha robusta* and *Eremochitina* sp.

Association 5 (see Tilia graph 3).

This striking association of taxa recorded from the Arenig aged samples was recovered from samples JW 4 and JW 5. The association includes the zonal chitinozoan species *Eremochitina brevis* with the closely related form *E.* cf. *baculata* and with a very interesting acritarch component. The acritarchs are dominated by the abundant occurrence of Acritarch Forms D and N in conjunction with *Coryphidium* cf. *tadlum*, *Dicrodiacrodium ancoriferum minutum*, *Goniosphaeridium polygonale pellucidum*, *Marrocanium simplex*, *Multiplicisphaeridium consolator*, *M. crispum*, common *Polygonium gracile*, *Stellichinitum helosum* and *Striatotheca principalis*.

This association can be assigned to the *E. brevis* Zone of Paris (1990) based on the presence of *E. brevis*. This indicates an age of Whitlandian or 'middle' Arenig for this association.

Association 6 (see Tilia graph 4).

Samples DW 307 and DW 291 are also assignable to the *E. brevis* Zone on the basis of the presence of *E. brevis* but these samples have yielded a noticeably different acritarch assemblages to those recorded in samples JW 4 and JW 5. *Multiplicisphaeridium firmum* and *Tongzia meitana* are present here, however, *Coryphidium* cf. *tadlum*, *Dicrodiacrodium ancoriferum minutum* and abundant *Polygonium gracile* are features of the assemblages in common with those recorded from JW 4 and JW 5.

Association 7 (see Tilia graph 5).

Included here is sample JD 29 which yielded a relatively diverse chitinozoan assemblage including *Cyathochitina campanulaeformis*, *Eremochitina* cf. *baculata*, *Lagenochitina capax*, *Velatachitina nebulosa*, *Sagenachitina* cf. *retifera* and significantly *S. oblonga*. The presence of the latter species indicates that this association is no older than mid *D. ornensis* Zone according to Paris (1990) and hence it is probably younger than Association 5 described from samples JW 4 and JW 5.

Sample DW 303 (see Tilia graph 6) yielded characteristic Ordovician palynomorphs e.g. *Eremochitina* cf. *baculata*, *Velatachitina* sp., *Peteinosphaeridium* spp., *Pirea colliformis*, in association with common Tremadoc-earliest Arenig species such as *Acanthodiacrodium amplium*, *A. constrictum*, *A. raia*, *Cymatiogalea messaoudii*, *C. multarea*, *C. velifera* and *Cymatiogalea* sp. 1. One can only assume that the Tremadoc-earliest Arenig component of this assemblage is recycled.

Llanvirn.

Two samples, DW 309 and DW 310, were studied from the Tachilla Formation, both of which are dated as probable Llanvirn age on the basis of the macrofaunal content, see appendix I.

Relevant literature: Publications regarding the palynology of the Llanvirn aged sediments from Morocco include Fournier-Vinas 1985, Cramer *et al.* 1974, Deunff 1977 and Elaouad-Debbaj 1984. Paris and Deunff 1970 studied comparable Llanvirn age assemblages from France. The chitinozoan zonal scheme of Paris 1990 can be utilised to refine the age of the samples studied from that indicated by the macrofaunal content.

General composition of the Llanvirn assemblages.

The palynological assemblages are characterised by relatively diverse acritarchs and chitinozoans. The generic composition of the acritarch component is rather similar to that recorded from the Arenig assemblages, namely *Coryphidium, Marrocanium, Multiplicisphaeridium* and *Striatotheca*. Notable absentees from the Llanvirn assemblages are the genera *Acanthodiacrodium* and *Polygonium*.

The chitinozoans are characterised by an increase in diversity of species present and the prominence of the genus *Belonechitina*. Other genera of note that are present include *Jenkinochitina, Pogonochitina, Sagenachitina* and *Velatachitina*.

Detail of the Llanvirn assemblages.

Association 8 (see Tilia graph 7).

The acritarch assemblages from samples DW 309 and DW 310 are characterised by a high diversity of acritarch species including *Baltisphaeridium klabavense, Comasphaeridium denseprocessum, Coryphidium elegans, Frankea sartbernardensis*, common *Goniosphaeridium polygonale polygonale, Marrocanium simplex, Striatotheca principalis* and abundant *Veryhachium lairdii*.

The chitinozoan assemblage is dominated by common\abundant *Belonechitina micracantha* with occasional/common *Conochitina chydaea*, common *Desmochitina minor cocoa, Jenkinochitina vulgaris, Pogonochitina? secunda, Sagenachitina oblonga* and *Velatachitina veligera*.

Discussion: Using the zonal scheme of Paris 1990, the chitinozoans present indicate that these macrofossil dated Llanvirn palynomorph assemblages from the Tachilla Formation are assignable to the *Cyathochitina protocalix* Zone based on the co-occurrence of *Belonechitina micracantha, Sagenachitina oblonga, Velatachitina veligera* and *Jenkinochitina vulgaris*. This suggests an early Lower Llanvirn age for the assemblages.

Llandeilo.

Three samples, JHO 220, GAO 388 and GAO 471, dated as Llandeilo on the basis of the macrofossil content were processed for palynological analysis. These three samples of sandy lithology were found to be barren of palynomorphs.

Caradoc.

Thirteen samples believed to be of Caradoc age have been analysed for their palynological content, eight of which, DW 323, DW 336, DW 337, DW 349, DW 353, DW 354, DW 361 and DW 362 have been dated using macrofossils, see Appendix I. All the samples of Caradoc age are assignable to the Ktaoua Formation.

As with the Arenig samples, it is not possible to place some of the samples of Caradoc age that have been studied in lithostratigraphic order. Furthermore, the broad datation of the samples using their shelly macrofossil content does not allow arrangement in a chronostratigraphic order. As a consequence, two palynological associations of the assemblages have been defined, and from these, suggestions are made as to the relative stratigraphic position of each association to the other.

Relevant literature: Caradoc palynological assemblages from Morocco have been studied previously by Elaouad-Debbaj (1986, 1988). Data generated in her 1986 publication on the chitinozoans from the Lower Ktaoua formation has been incorporated into the zonation of Ordovician chitinozoans of Northern Gondwana by Paris (1990). This zonation can be applied to some of the assemblages of Caradoc age documented here. Other relevant publications regarding Late Ordovician palynology of Northern Gondwana include Molyneux & Paris 1985, Molyneux 1988 and Paris 1988 which are all based on subsurface material from Libya. The zonation of Jardine *et al.* (1974) erected on material from Algeria is of little use in the Late Ordovician as only one zone is defined for the Caradoc-Ashgill interval. The palynology of the type Caradoc from the UK has been documented by Turner (1984), who looked at the acritarchs and by Jenkins (1967) who studied the chitinozoans.

General composition of the Caradoc aged assemblages.

The Caradoc aged samples generally contain impoverished, poorly preserved acritarch assemblages dominated by species of *Veryhachium* and *Villosacapsula*. Spheromorphic acritarchs referable to the genera *Leiosphaeridia* and *Lophosphaeridium* are also relatively common.

The chitinozoan components of the assemblages are composed primarily of the genera *Belonechitina*, *Lagenochitina*, notably *L. deunffi*, with *Cyathochitina*, *Conochitina* and *Jenkinochitina* also present. The chitinozoan assemblages are also poorly preserved.

Caradoc aged assemblages in detail.

Two associations of palynomorphs are apparent from the Caradoc aged assemblages. The five samples of Caradoc age that are not assignable to one of these two associations contained very impoverished palynomorph assemblages, generally dominated by indeterminate species of *Veryhachium*.

Association 9 (see Tilia graph 8).

Association 9 is recorded from samples DW 335, DW 336, DW 337 and DW 415. This association is characterised by common *Lagenochitina deunffi* and abundant *Villosacapsula setosapellicum*. *Veryhachium* spp. are abundant with occasional\common *V. reductum* and inconsistent *Veryhachium* sp. 1. *Belonechitina* spp. are consistently present, notably *B. capitata*.

Discussion: The presence of common *Lagenochitina deunffi* indicates that this association is assignable to *L. deunffi* Zone of Paris (1990). This suggests a Costonian, lowest Caradoc age for these samples which is consistent with the Lower Caradoc age indicated by the macrofossils recorded from samples DW 336 and DW 337, see appendix I.

Association 10 (see Tilia graph 9).

Association 10 is recorded from samples DW 352, DW 353, DW 354 and DW 362. This association is characterised by occasional-abundant *Villosacapsula setosapellicum* and abundant *Veryhachium* spp. notably *Veryhachium reductum*, *Veryhachium* sp. 1, *Veryhachium* sp. 3 and *Veryhachium* sp. 4. The chitinozoan component is rather impoverished. Notable occurrences include *Belonechitina capitata* and *Jenkinochitina* spp. in low numbers with *Lagenochitina deunffi* rare or absent.

Discussion: Comparison of this association with assemblages recorded in the literature of Caradoc age from northern Gondwana and the UK appears to indicate the absence of age diagnostic palynomorphs. However, the low numbers of *Lagenochitina deunffi* are indeed significant in this Lower Caradoc macrofossil dated association.

The macrofossils present in samples DW 353, DW 354 and DW 362 enable a Lower Caradoc age assignation for this association, see appendix I. Paris (1990, p.198) in describing the *Lagenochitina dalbyensis* Zone (lower Caradoc) mentions the presence of a few *L. deunffi* specimens persisting into the *L. dalbyensis* Zone from the underlying *L. deunffi* Zone in which they are common. The coincidence of the presence of a Lower Caradoc aged macrofossil assemblage and the rare specimens of *L. deunffi* in this association suggests that this assemblage may be assignable to the *L. dalbyensis* Zone. This indicates that Association 9 containing common *L. deunffi* is older than this association.

Ashgill.

Four samples believed to be of Ashgill age have been studied. Of these, two, TD 17 and GAO 19 are dated using macrofossils but both were found to be barren of palynomorphs. Samples DW 359 and DJ 10 yielded reasonably well preserved assemblages which are comparable to Ashgill aged assemblages described in the literature.

Relevant literature: Palynological assemblages of Ashgill age from Morocco have been studied by Elaouad-Debbaj (1984, 1988). Information from her 1984 publication on the Ashgill chitinozoans has been incorporated into the zonation of Ordovician chitinozoans of Northern Gondwana by Paris (1990). Other relevant publications regarding Late Ordovician palynology of Northern Gondwana include Molyneux & Paris 1985, Hill & Molyneux 1988, Molyneux 1988 and Paris 1988 which are all based on subsurface material from Libya. The zonation of Jardine *et al.* (1974) erected on material from Algeria is of little use in the Late Ordovician as only one zone is defined for the Caradoc-Ashgill interval. The palynology of the Ashgill from the UK, including the type area has been documented by Whelan (1988) and Barron (pers. comm. 1992). Numerous papers regarding the Ashgillian palynology of Anticosti and western Canada have been published by Achab and co-workers, e.g. Achab 1981, 1984, 1987 and 1989.

General composition of the Ashgill aged assemblages studied.

The acritarch assemblages are dominated by the genus *Veryhachium* in association with less frequent spheromorphic forms assignable to the genera *Leiosphaeridia* and *Lophosphaeridium*. The occurrences of *Diexallophasis* and leiofusid forms, notably *Dactylofusa* are regarded as significant.

Ashgill aged assemblages in detail.

The two samples studied yielded quite dissimilar assemblages in terms of species composition.

Association 11 (see Tilia graph 10).

The assemblage recovered from DW 359 is rather poorly preserved. *Veryhachium* species occur abundantly, notably *V. minutum*, *V. reductum* and *V. subglobosum*, in association with *Dactylofusa ctenista* and primitive forms of *Diexallophasis* including *D. denticulata Gotlandica*. A sparse chitinozoan assemblage composed primarily of *Belonechitina* species and rare ancyrochitinids, notably *Ancyrochitina ancyrea* is also recorded.

Discussion: Sample DW 359, collected from the Upper Ktaoua Formation (*sensu* Destombes *et al.* 1985), see appendix I, yielded a closely comparable assemblage to that recorded from the same stratigraphic level by Elaouad-Debbaj (1988). She recorded a similar suite of *Veryhachium* species, the netromorph *Dactylofusa ctenista* (refered to incorrectly as *Eupoikilofusa striata* by Elaouad-Debbaj 1988) with rare, very poorly preserved specimens of *Aremoricanium syringosagis*. The latter taxon was not recorded from DW 359, maybe as a result of the preservation. Comparison with the data of Elaouad-Debbaj (1984, 1988) suggests an early-'middle' Ashgill age for DW 359. The absence of the species *Armoricochitina nigerica* in this association suggests an age of earliest Ashgill according to zonation scheme of Paris 1990.

Hill and Molyneux (1988) considered *Veryhachium subglobosum* and *Diexallophasis denticulata* to indicate an Ashgill age in Libya, these species occur in Zones As1-As2 of their zonal scheme for the Libyan subsurface. *Veryhachium subglobosum* is also considered to indicate an Ashgill age in the Kingdom of Jordan (Keegan, Rasul and Shaheen 1990). Recent work on the type Ashgill of the UK (Barron pers. comm. 1992) suggests that the first appearance of the genus *Diexallophasis* is in Ashgill aged sediments.

Association 12 (see Tilia graph 10).

The assemblage recovered from sample DJ 10 is reasonably well preserved. The acritarch component is composed of abundant *Veryhachium reductum* and common *V. subglobosum* with *Lophosphaeridium* spp. and *Diexallophasis* sp. also present. Chitinozoans occur in high numbers in this sample (32% of the palynomorph sum). This component is dominated by *Ancyrochitina* sp. 1 with *Armoricochitina nigerica*, *Belonechitina capitata* and *Calpichitina lenticularis* all prominent.

Discussion: The zonation of Paris (1990) is directly applicable here. The abundant occurrence of *Ancyrochitina* spp. within the chitinozoan part of the assemblage in association with *Armoricochitina nigerica* indicates that this sample is assignable to the *A. merga* Zone. This indicates an age of 'middle' Ashgill. Whelan (1988) also reported an increase in ancyrochitinid abundance in the late Ashgill in the UK. The acritarchs present, e.g. *Diexallophasis* sp. and *Veryhachium subglobosum* indicate that the assemblage is assignable to Zones As1-As2 of Hill and Molyneux (1988) which are of Ashgill age.

Assemblages recorded from the Silurian to Lower Devonian aged field samples.

Telychian, latest Llandovery.

The oldest samples analysed from the Silurian in the present study are Telychian in age. Eight graptolite dated samples from the were processed for palynology of which six yielded workable assemblages. There was a major problem in the processing of these samples due to the presence of abundant amorphous sapropelic kerogen. The adoption of fuming Schulze's solution to dissagregate this material was found to be successful.

Relevant literature: The broad nature of the zonations produced by Jardine *et al.* (1974), Taugourdeau & Jekhowsky 1960 and Keegan, Rasul & Shaheen (1990) makes them of little benefit for comparison with the assemblages of refined biostratigraphic dates that have been utilised here. The assemblages are mainly compared with material studied from Libya (Hill, Paris & Richardson 1985, Hill & Molyneux 1988, Paris 1988, Paris 1988), from the Swedish Island of Gotland (Le Herrise 1989, Laufeld 1974) and with the Silurian acritarch distribution charts of Cramer (1970) compiled from American and European data. The zonation proposed by Jardine & Yapaudjian (1968) for the Polignac Basin of Algeria utilises many taxa in open nomenclature at this stratigraphic level which makes comparison with the present assemblages difficult. Hill (1974) divided the type Llandovery from the UK into four acritarch zones, which, due to the difference in the assemblage compositions when compared to the Moroccan assemblages (e.g. the absence of *Deunffia* and *Domasia* species in the Moroccan assemblages), are not applicable.

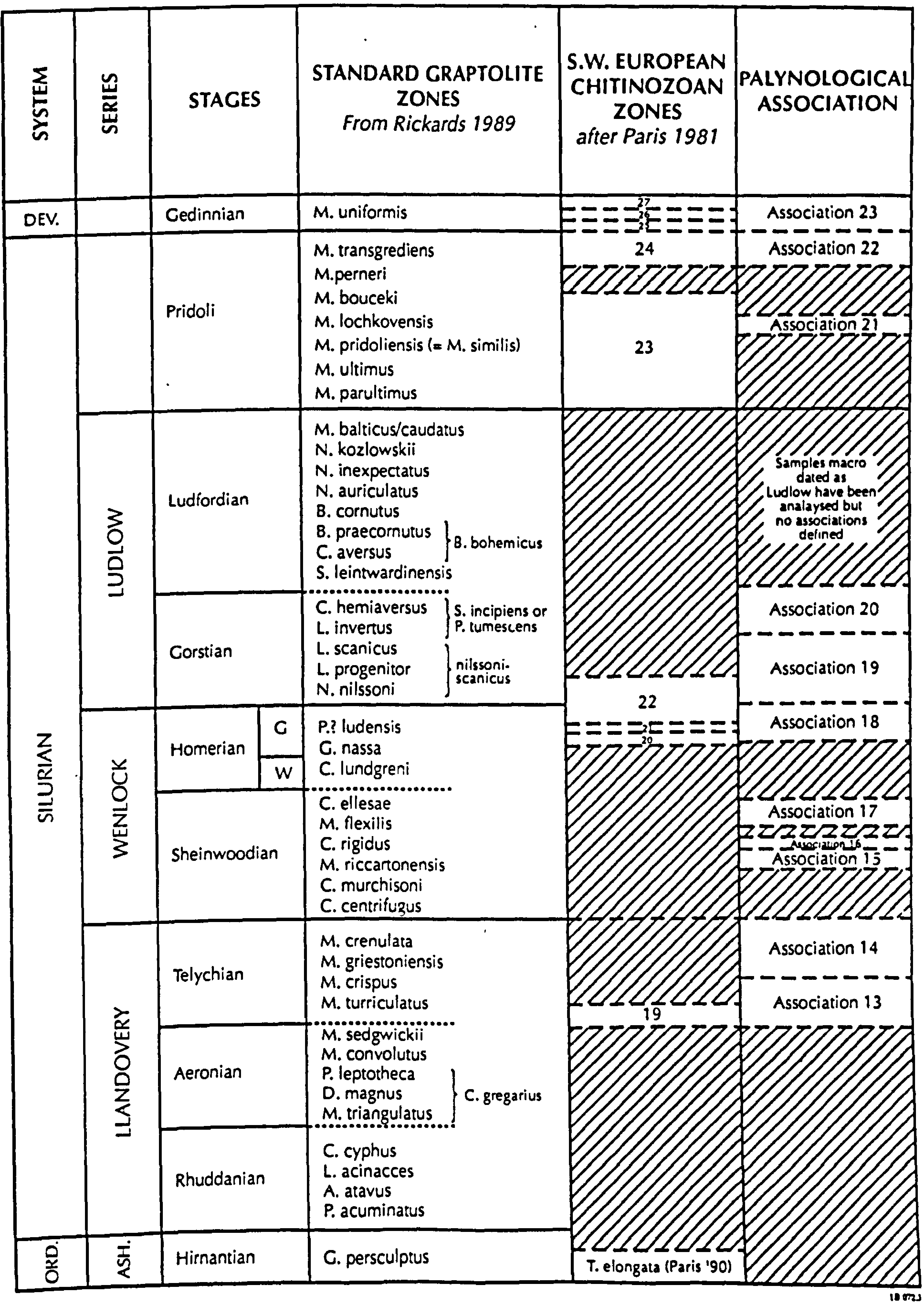
General composition of the assemblages.

Amorphous sapropelic kerogen is abundant in the palynological preparations with palynomorph assemblages generally dominated by spheromorphic acritarchs. The genus *Leiosphaeridia* occurs abundantly with *Dictyotidium* and the prasinophyte *Tasmanites* also common. Of the acanthomorphs, *Ammonidium* species and visbyspherids are frequent. The chitinozoan assemblages are generally poorly preserved and of low species diversity throughout this stratigraphic interval.

Detail of the Telychian aged assemblages.

Two associations of palynomorphs within the Telychian aged samples are apparent (fig. 17).

Figure 17. A correlation of the standard graptolite zones and the Northern Gondwanan chitinozoan zones with the palynological associations defined herein from the Silurian.



SYSTEM	SERIES	STAGES		STANDARD GRAPTOLITE ZONES *From Rickards 1989*	S.W. EUROPEAN CHITINOZOAN ZONES *after Paris 1981*	PALYNOLOGICAL ASSOCIATION
DEV.		Gedinnian		M. uniformis	27 26 25	Association 23
SILURIAN		Pridoli		M. transgrediens M.perneri M. bouceki M. lochkovensis M. pridoliensis (= M. similis) M. ultimus M. parultimus	24 ▨ 23	Association 22 ▨ Association 21 ▨
	LUDLOW	Ludfordian		M. balticus/caudatus N. kozlowskii N. inexpectatus N. auriculatus B. cornutus B. praecornutus } B. bohemicus C. aversus S. leintwardinensis	▨	▨ Samples macro dated as Ludlow have been analaysed but no associations defined ▨
		Gorstian		C. hemiaversus } S. incipiens or P. tumescens L. invertus L. scanicus } nilssoni-scanicus L. progenitor N. nilssoni	▨ 22	Association 20 Association 19
	WENLOCK	Homerian	G	P.? ludensis G. nassa	2 20	Association 18
			W	C. lundgreni	▨	▨
		Sheinwoodian		C. ellesae M. flexilis C. rigidus M. riccartonensis C. murchisoni C. centrifugus	▨	Association 17 ▨ Association 16 Association 15 ▨
	LLANDOVERY	Telychian		M. crenulata M. griestoniensis M. crispus M. turriculatus	▨ 19	Association 14 Association 13
		Aeronian		M. sedgwickii M. convolutus P. leptotheca } C. gregarius D. magnus M. triangulatus	▨	▨
		Rhuddanian		C. cyphus L. acinacces A. atavus P. acuminatus	▨	▨
ORD.	ASH.	Hirnantian		G. persculptus	T. elongata (Paris '90)	▨

Association 13 (see Tilia graph 11).

Monograptus turriculatus-M. crispus Zone in age.

Samples DW 246, JW 249 and JW 46 were analysed from the *Monograptus turriculatus-M. crispus* Zones of which only DW 246 yielded palynomorphs. This association contains an unusually high proportion of acanthomorphic acritarchs (74%) compared with the other Lower Silurian aged samples studied. Important constituents of the association include *Comasphaeridium hirtum*, *Dictyotidium* spp., *Diexallophasis denticulata*, *Oppilatala? frondis*, *Veryhachium* spp. and *Visbysphaera microspinosa* var. A. The poorly preserved chitinozoan assemblage comprises forms including *Angochitina?* cf. *seurata*, *Ancyrochitina* sp. 2, *Cyathochitina campanulaeformis* and *Cyathochitina* sp. 1.

Discussion: Only one palynological zone, Zone L14, is defined for the Telychian age of Libya by Hill & Molyneux (1988). The assemblages recovered by them are of similar species diversity to those studied here, the species compositions, however, are somewhat different. Taxa recorded from sample DW 246 in common with the Libyan Telychian assemblages include *Diexallophasis denticulata* and *Visbysphaera microspinosa*. Significant absentees from the present assemblage include the *Domasia* and *Deunffia* group which are believed to be associated with the low latitude realm. This element, Despite having been recorded in closely proximal Libya (Hill & Molyneux 1988), is not recorded here.

The assemblages recorded by Le Herisse (1989) from the early-middle Telychian Nar Formation of Gotland are of considerably higher species diversity than the present assemblage. Many species recorded from those highly diversified assemblages are present here including *Comasphaeridium hirtum* and *Oppilatala? frondis*. Again, a noticeable difference in the species composition is the absence of *Domasia* and *Deunffia* species in the present assemblage.

Paris (1981) investigated a chitinozoan assemblage of *Monograptus turriculatus* Zone age from SW Europe, his Zone 19, in which he found low species diversity. Assemblages here have no species in common with those observed by Paris (1981). Assemblages recorded from the similar stratigraphic level in Gotland by Laufeld (1974) also lack species in common with the present assemblages.

We should bare in mind that the intense oxidation required to enable the observation of palynomorphs within this thermally mature, sapropelic rich palynofacies may have had an impact on the assemblage compositions recovered.

Association 14 (see Tilia graph 11).

Monograptus griestoniensis-M. crenulata Zone in age.

Four samples, DW 248 (*M. griestoniensis* Zone in age), DW 249, DW 250 and DW 251 (all *M. crenulata* Zone in age) of low species diversity have been analysed from this interval. The cluster analysis (see Tilia graph 11) indicates the close similarity of the assemblage compositions of these assemblages (TSOS less than 1). The assemblages are dominated by *Leiosphaeridia* species, notably *L. microcystis*. *Lophosphaeridium* species are also common as is *Tasmanites medius*. *Buedingisphaeridium lunatum*, *Dictyotidium* sp. 1, *Veryhachium*? sp. 9, *Visbysphaera* sp. 1 and *Visbysphaera* sp. 2 are all particularly diagnostic of this association and *Cymatiosphaera kiryanovii* is inconsistently present. The chitinozoan assemblage is highly impoverished, however, the morphologically distinctive *Pseudoclathrochitina* cf. *carmenchuae* is of note, as is the first appearance in the present study of *Ancyrochitina primativa*.

Discussion: As with Association 13 described above, comparison with Hill & Molyneux 1988 is of little benefit due to the relatively broad nature of their zonal scheme and the considerable differences between the assemblage composition they observed compared to those recorded here.

The chitinozoan assemblages of Zone 7 of Paris (1988) from Libya, which approximates to the *Monograptus griestoniensis-M. crenulata* Zones is also quite dissimilar in composition to the assemblages of that age recorded here. None of the zonal forms quoted by Paris, e.g. *Pterochitina diechaii* and *Margachitina margaritana* are present. The only chitinozoan considered to be of potential stratigraphic significance recorded here is *Pseudoclathrochitina* cf. *carmenchuae*.

The acritarch assemblages of *Monograptus crenulata* Zone age described from the Lower Visby Formation by Le Herisse (1989) have a moderate number of taxa in common with this association, e.g. *Buedingisphaeridium lunatum*, *Dictyotidium dictyotum*, but they are of considerably higher species diversity than the present association containing the *Deunffia* and *Domasia* species typical of low latitude assemblages of Telychian age.

It appears that the previously unpublished taxa e.g. *Dictyotidium* sp. 1, *Veryhachium*? sp. 9, *Visbysphaera* sp. 1, *Visbysphaera* sp. 2 and *Pseudoclathrochitina* cf. *carmenchuae* occurring in conjunction with the high abundance taxa (e.g. *Leiosphaeridia microcystis*) are possibly the best indicators of this interval in Morocco. The reason for the notable differences between these and the Libyan assemblages of a similar age could possibly be associated with the mixing of the low latitude *Deunffia-Domasia* realm with the high latitude *Neoveryhachium carminae* realm in Libya (Hill & Molyneux 1988) in contrast with the high latitude, more provincial flora of the Moroccan assemblages.

Again, it should also be noted that the severe oxidation technique applied to these samples could possibly have an impact on the assemblage compositions recovered.

Wenlock.

Ten graptolite dated samples of Wenlock age have been analysed, eight from the Sheinwoodian (Lower Wenlock) and two from the Homerian (Upper Wenlock). Of the eight samples from the Sheinwoodian, two, both from the *Cyrtograptus ellasae* Zone, were found to be barren of palynomorphs. Four palynological associations have been recorded from the Wenlock aged samples analysed.

Significant literature: As with the Llandovery interval, application of the zonal schemes of Jardine *et al.* (1974), Taugourdeau & Jekhowsky (1960) and Keegan, Rasul & Shaheen (1990) are not of benefit here due to the chronostratigraphically broad ages of their zones. The recent palynostratigraphic publications on north-east Libya, Thusu & Owens (1985) and El-Arnauti, Owens & Thusu (1988), do not cover the mid-late Silurian interval. Comparison of the chitinozoan assemblages is made with Paris (1981) who analysed some Homerian material from south-west Europe, with Laufeld (1974) from Gotland and with Dorning 1981b from the Welsh Basin. The acritarch assemblages are compared with those from Gotland (Le Herrise 1989) and from the type sections in the UK (Downie 1959, 1963 and Dorning 1981a).

General composition of the Wenlock aged assemblages.

The Wenlock aged assemblages are generally poorly preserved. The acritarch component is very much dominated by spheromorphic forms, the vast majority of which are assignable to the genus *Leiosphaeridia* with frequent *Lophosphaeridium* spp. and *Dictyotidium*. spp. present. The prasinophytes *Tasmanites* and *Cymatiosphaera* are also common. Of the acanthomorphic forms, the genera *Ammonidium*, *Oppilatala*, *Tylotopalla* and *Visbysphaera* are commonly present. As with the Llandovery assemblages, the chitinozoan component is generally impoverished with the genera *Angochitina* and *Ancyrochitina* are frequently present throughout this interval.

Detail of the Wenlock aged assemblages.

Four associations of palynomorph assemblages have been recognised in these samples (fig. 17).

Association 15 (see Tilia graph 11).

Monograptus riccartonensis Zone in age.

Three samples, DW 162, DW 357 and DW 358 are assigned to this association. Cluster analysis of the assemblages gives a TSOS of less than 2 which indicates the close similarity of their composition.

Leiosphaeridia microcystis is super-abundant comprising between 46-62% of the palynomorph sum. *Leiosphaeridia* sp. 1, *Dictyotidium* cf. *coarctum* and *Tasmanites medius* are also common. Inconsistently present forms include *Dateriocradus monterossae*, the *Oppilatala eoplanktonica-ramusculosa* complex, *O? frondis*, *Tylotopalla astifera*, *T.* cf. *deerlijkianum*, *Visbysphaera microspinosa* var. A and Acritarch Form L. The chitinozoan recovery is low in this association (less than 4% of the palynomorph sum). The only taxa of note are *Ancyrochitina primativa* and *Cyathochitina* cf. *elinitae* which are both inconsistently present.

Discussion: Dorning (1981) proposed three zones through the Wenlock of the Welsh basin. His zonal taxa do not occur here, however, it is interesting to note the occurrence of *Dateriocradus monterossae* which is restricted to the upper part of his Zone W1 and the lower part of Zone W2. This taxon is coincidentally only recorded from the *Monograptus riccartonensis* Zone in the present study, which is of approximately the same chronostratigraphic position as that record of Dorning. Le Herrise (1989) found this species to range from the latest Telychian to the earliest Homerian in Gotland.

The sparse chitinozoan assemblage has only one taxon in common with the assemblages documented by Dorning (1981) from the UK and Laufeld (1974) from Gotland which is the long ranging species *Ancyrochitina primativa.*

Association 16 (see Tilia graph 11).

Monograptus riccartonensis\Cyrtograptus rigidus Zonal boundary in age.

A single sample, DW 367, comprises this association. It is composed primarily of *Angochitina* sp. 1 which makes up approximately 60% of the palynomorph sum. Other chitinozoans are rare and include *Cingulachitina* sp., *Conochitina* spp. and the *Rhabdochitina magna* complex. The acritarchs are of very low diversity (less than 10 species) with *Leiosphaeridia* spp. dominant and occasional *Visbysphaera microspinosa.*

Discussion: No previously recorded age diagnostic chitinozoans or acritarchs are present in this association. However, it is interesting to note the flood of *Angochitina* sp. 1 at this stratigraphic level.

Association 17 (see Tilia graph 11).

Monograptus flexilis Zone in age.

Assemblages from samples DW 355 and DW 356 comprise this association. The acritarch component is dominated by *Leiosphaeridia* spp. with *L. microcystis* far less conspicuous than in Association 16. *Dictyotidium coarctum* and *Oppilatala*? *frondis* are also prominent. The chitinozoans occur in very few numbers with *Ancyrochitina primativa*, *Angochitina* sp. and *Cyathochitina* sp. inconsistently present.

Discussion: Dorning (1981) recorded *Oppilatala*? *frondis* from the UK as having its youngest occurrence in the middle of his Zone W2 which would appear to approximate to the youngest stratigraphic occurrence of this taxon in the present study. However, Le Herrise recorded this form as high as the Ludfordian (Upper Ludlow) and does not consider it to be reworked.

Two samples from the *Cyrtograptus ellesae* Zone, DJ 84 and JW 9, were processed for palynological analysis but were found to be barren of palynomorphs.

Association 18 (see Tilia graph 11).

Pristiograptus? *ludensis* Zone in age.

Two samples, DW 230 and DW 231, were processed for palynology from the *Pristiograptus*? *ludensis* Zone of which one, DW 231 yielded palynomorphs. The assemblage is relatively diverse compared to the assemblages from older Wenlockian samples and there is a marked change in the palynofacies. The amorphous sapropelic material which was abundant in the Telychian and Sheinwoodian aged preparations is rare here. The acanthomorphic acritarch abundance is markedly increased at the expense of the spheromorphs and the chitinozoan abundance and diversity is slightly increased.

The main constituents of the acritarch component are abundant *Ammonidium* sp. 1 (50%), *Cymatiosphaera octoplana*?, *Diexallophasis* cf. *sanpetrensis*, common *Leiosphaeridia* spp., *Lophosphaeridium* sp. 6, *Lophosphaeridium* sp. 7 and *Onondagella deunffi*. An interesting occurrence in the chitinozoan assemblage is the first appearance of *Cingulachitina* sp. 1.

Discussion: The base of the range of *Onondagella deunffi* in both the UK (Dorning 1981, Upper Ludlow, Zones L3 and L4) and in Gotland (Le Herisse 1989, Ludlow) is younger than that recorded here. It is interesting to note the coincidence of the first appearance of *Cingulachitina* sp. 1 in this study compared with that of *Cingulachitina* sp. A Paris 1981 (=*Cingulachitina* sp. 1 herein) from south west Europe which appears in both cases in the latest Wenlock, in or close to the *Pristiograptus? ludensis* Zone.

Ludlow.

Seven graptolite dated samples of Ludlow age have been analysed. Of these, three, JW 224, DW 34 and JW 10 are biostratigraphically constrained to graptolite zones based on the macrofauna present. The remaining samples, DW 215, DW 232, DW 234 and DW 235 are less well constrained by the macrofossils, DW 215 having been dated as 'middle' Ludlow in age, the remainder are dated as Ludlow in age. The stratigraphic position of these four samples relative to the highly constrained samples, and to each other, is indeterminate from the palynology. For this reason, the general composition of the Ludlow assemblages is described in some detail. This is done in order to give a more comprehensive overview of the palynology of the Ludlow interval studied. A detailed description of the highly constrained assemblages follows the general description.

Relevant literature: Jardine *et al.* (1974) published four zones within what they term the '(Wenlock?) Ludlovien' interval of Algeria. No Pridoli interval is represented in their scheme. The somewhat vague chronostratigraphic interpretation of the ages of the zones is a problem with their scheme at this stratigraphic level. Keegan, Rasul & Shaheen (1990) published just one palynological zone corresponding to the entire Ludlow series from the Kingdom of Jordan, as did Taugourdeau & Jekhowsky (1960) for the Algerian Sahara. The type area from the UK has been studied by Lister (1970) and by Dorning (1981a, 1981b). The palynostratigraphy of the Silurian succession on Gotland is documented by Le Herrise (1989) who looked at the acritarchs and Laufeld (1974) who studied the chitinozoans. The zonal scheme of Paris 1981 covers only the lowermost part of the Ludlow series, namely the *Neodiversograptus nilssoni* Zone.

General composition of the Ludlow aged assemblages.

With the exception of the earliest Ludlow assemblages i.e. Association 19 described below, the Ludlow assemblages are well preserved and of moderately high species diversity. The chitinozoans show a major proliferation of species in the assemblages considered to be younger than the *Lobograptus scanicus* Zone . The acanthomorphic to spheromorphic acritarch ratio is somewhat inconsistent but the acanthomorphs are noticeably higher in abundance than in the earliest Ludlow and Wenlock assemblages. The terrestrial component of the Ludlow aged assemblages studied makes up less than 1% of the palynomorph sum in each of these assemblages.

The acritarch assemblages are composed of inconsistent *Ammonidium microcladum*, *Cymbosphaeridium* spp., notably *C. cariniosum* and *C. bikidium* in the Gorstian aged samples, common *Dictyotidium* spp., common *Diexallophasis* spp., inconsistently common *Leiofusa estrecha*, inconsistently abundant *Multiplicisphaeridium* cf. *saharicum*, and inconsistent *Onondagella deunffi*, *Oppilatala eoplanktonica* and Acritarch Form G. Surprisingly, only one specimen of *Neoveryhachium carminae* was recorded in the entire study which was recovered from a Ludlow aged sample.

The Chitinozoan assemblages are characterised by abundant *Cingulachitina* spp. and common *Ancyrochitina* spp. including *A. fragilis*, *A. primativa* and *A. pachyderma*. *Calpichitina* spp., *Angochitina echinata*, *Plectochitina carminae*? and *Sphaerochitina* spp. are also present.

Detail of the biostratigraphically highly constrained samples.

Only three of the seven samples of Ludlow age are tightly constrained biostratigraphically by the graptolitic faunas present. Two associations appear to be present, both of Gorstian age, (fig. 17) which are as follows.

Association 19 (See Tilia graph 12).

Neodiversograptus nilssoni-Lobograptus scanicus Zone in age.

This rather indistinct association from the earliest Ludlow, recorded from samples JW 224 and DW 34, has many features similar to those of the underlying Wenlock assemblages. The association is characterised by a high proportion of spheromorphic acritarchs and a highly impoverished chitinozoan fauna. The common acritarchs are *Leiosphaeridia* spp, and Acritarch Form L with inconsistent *Cymbosphaeridium* spp. notably *C. bikidium*, *Dictyotidium* spp., *Diexallophasis* spp., *Lophosphaeridium* sp. 7 and *Visbysphaera microspinosa* var. C. The rare chitinozoans recorded include *Ancyrochitina fragilis* var. A.

Discussion: This rather impoverished association contains few taxa of potential biostratigraphic value. *Cymbosphaeridium bikidium* was originally recorded from the Bringewood Beds of Shropshire (upper Gorstian) by Lister 1970 and from a similar stratigraphic level by Dorning 1981 (Zone 2-early Zone 3). This taxon is recorded in the early Gorstian here which is lower than previous records from the UK. The impoverished chitinozoan assemblage of Association 19 contains no taxa in common with Zone 22 of Paris (1981) which occurs at the same chronostratigraphic level. The first appearance of *Ancyrochitina fragilis* var. A in Association 19 is of note.

Association 20 (See Tilia graph 12).

Saetograptus incipiens Zone in age.

This association is only recorded in sample JW 10. It is composed of highly diverse acritarch and chitinozoan assemblages which contrast with the low diversity assemblages of Association 19.

The characteristic acritarchs are common *Cymbosphaeridium bikidium*, *C. cariniosum*, *Dactylofusa striatifera striatifera*, *Leiofusa estrecha*, *Multiplicisphaeridium fisheri*, Acritarch Form G and Acritarch Form I. The chitinozoan assemblage is also diverse in species composition including *Ancyrochitina ancyrea*, *A. fragilis brevis*, *A. pilosa*, *Angochitina echinata*, *A. elongata*, abundant *Cingulochitina* spp. notably *C.* cf. *convexa* and *Cingulachitina* sp. 1, and occasional *Plectochitina carminae*?

Discussion: Several taxa recorded here were reported by Dorning (1981) from the UK. He reported *Ammonidium microcladum*, *Oppilatala eoplanktonica* and *Multiplicisphaeridium fisheri* from sediments no younger than Wenlock in age. These taxa are recorded in the present association which is of late Gorstian age. *Cymbosphaeridium bikidium* has a youngest occurrence in the UK of earliest Ludfordian (the lower part of Zone L3, Dorning 1981) which is consistent with the occurrence of that taxon in the present study. Both *Onondagella deunffi* and *Leiofusa estrecha* are reported to have a range base at the base of Zone L3 (Dorning 1981) in the UK, however, these taxa are recorded in this older association in Morocco. In Gotland, the stratigraphic range top of *Ammonidium microcladum* (Le Herrise 1989) is similar to that recorded here. *Onondagella deunffi* and *Neoveryhachium carminae* are examples of other coincidental taxa from Gotland at this stratigraphic level. The first appearance of diverse and abundant *Ancyrochitina*, *Angochitina* and *Cingulochitina* species and the presence of *Plectochitina carminae*? are all of note at this stratigraphic level.

Pridoli-Lower Devonian.

Nine graptolite dated samples have been analysed from this stratigraphic interval. From the cluster analysis carried out on Tilia graph 13, there appears to be three associations present, the first including assemblages from samples DW 51, DW 52, DW 55 and DW 56, the second including assemblages from DW 94, DW 57 and DW 58, and the third including assemblages from DW 96 an DW 97. However, the second cluster (DW 94, DW 57 and DW 58) is rather misleading. Analysis of the species composition of sample DW 94 shows it to be quite different from samples DW 57 & DW 58. The clustering of the three samples is a result of the coincident numbers of relatively insignificant taxa categories on the Tilia graph plot, e.g. the Acanthomorphic acritarchs indet., Spheromorphic acritarchs indet and Leiosphaeridia spp. For this reason, four rather than three associations are described from the Pridoli to Lower Devonian aged field samples (figs. 17 & 18).

Relevant literature: The chitinozoans of the Silurian-Devonian boundary stratotypes in Bohemia are documented by Paris, Laufeld & Chlupac (1981). The chitinozoan zonation of Paris (1981) also covers this interval in part. The chitinozoans, acritarchs and miospores from the upper Silurian to Devonian of the Algerian Sahara are documented by Jardine & Japaudjian (1968), Jardine *et al.* (1974) and Boumenjel et al. 1988.. In 1983, Wicander published a biostratigraphic catalogue of the North American acritarchs. In addition, there are numerous acritarch assemblages of late Silurian to Lower Devonian age reported from around the globe, notably Cramer 1964, Deunff 1976, 1980, Deunff & Paris 1971, Loeblich & Wicander 1976 and Playford 1977. The miospore component of palynological assemblages generally become more significant biostratigraphically late in the Silurian and through the Devonian. Significant publications regarding Upper Silurian and Lower Devonian spore biostratigraphy include Richardson & Lister 1969, Richardson and McGregor 1986, Streel *et al.* 1987, Massa & Moreau-Benoit 1976 and Steemans 1989.

General composition of the Pridoli to Lower Devonian aged assemblages recovered from the field samples.

The preservation of the assemblages is moderate with generally high abundances of palynomorphs recovered and moderate species diversity. The dominant acritarch genera over this stratigraphic interval are *Cymbosphaeridium, Dictyotidium, Diexallophasis, Leiosphaeridia* and *Visbysphaera*. Biostratigraphically important genera present are *Actinophasis, Hapsidiopalla, Onondagella, Orygmahapsis* and *Thysanoprobolus*. The genera *Cingulachitina, Fungochitina, Muscochitina* and *Plectochitina* are all significant occurrences within the chitinozoan assemblages.

Detail of the Pridoli to Lower Devonian aged assemblages recovered from the field samples.

Association 21 (see Tilia graph 13).

Monograptus lochkoviensis Zone in age.

Assemblages recorded from samples DW 51, DW 52, DW 55 and DW 56 are included in this association. The acritarch component of the assemblages includes *Ammonidium* sp. 2, *Cymbosphaeridium pilar, Diexallophasis denticulata* var. A, *Multiplicisphaeridium variabile, Multiplicisphaeridium* sp. 1, *Orygmahapsis fistulosa*, inconsistent *Hapsidiopalla* cf. *sannemanni, Quadraditum fantasticum* and *Thysanoprobolus polykion*, common\occasional *Visbysphaera microspinosa* var. C and common acritarch form L. The chitinozoan assemblage is relatively impoverished with *Cingulachitina ervensis* and *C.* cf. *serrata* inconsistently present. The only miospores recorded in this association are *Retusotriletes* spp. which consistently make up less than 1% of the palynomorph sum.

Discussion: Taxa recorded here in common with those selected by Jardine *et al.* (1974) and Jardine & Yapaudjian (1968) to be of biostratigraphically value include only *Cymbosphaeridium pilar* and *Quadraditum fantasticum*. These taxa indicate a position of Zones G5-H in the scheme of Jardine *et al.* and Zones IV-Vb of Jardine & Yapaudjian. It is interesting to note that *Thysanoprobolus polykion* is here recorded in the Pridoli having previously only been recorded from the lowermost Devonian (e.g. Wicander 1981). Application of the chitinozoan zonal scheme of Paris (1981) to this association is not possible due to the impoverished chitinozoan assemblages recorded.

Association 22 (see Tilia graph 13).

Monograptus transgrediens Zone in age.

DW 94 is the only sample from which this association was recorded. The association includes abundant *Cymbosphaeridium* sp. 1, Common *Diexallophasis denticulata* var. A, *Hapsidiopalla* cf. *sannemanni*, *Orygmahapsis fistulosa*, *Triangulina sanpetrensis* and *Visbysphaera microspinosa* var. C. The chitinozoan assemblage is of moderate species diversity including, *Angochitina echinata*, *Cingulachitina* spp., *Muscochitina muscosa* and *Plectochitina* sp. 1.

Discussion: The zonal scheme of Jardine *et al.* (1974) and Jardine & Yapaudjian (1968) are not applicable to this association due to the lack of coincident stratigraphically useful taxa. Paris (1981) defined a zone from this chronostratigraphic level, Zone 24, from SW Europe which has no taxa in common with the association described here.

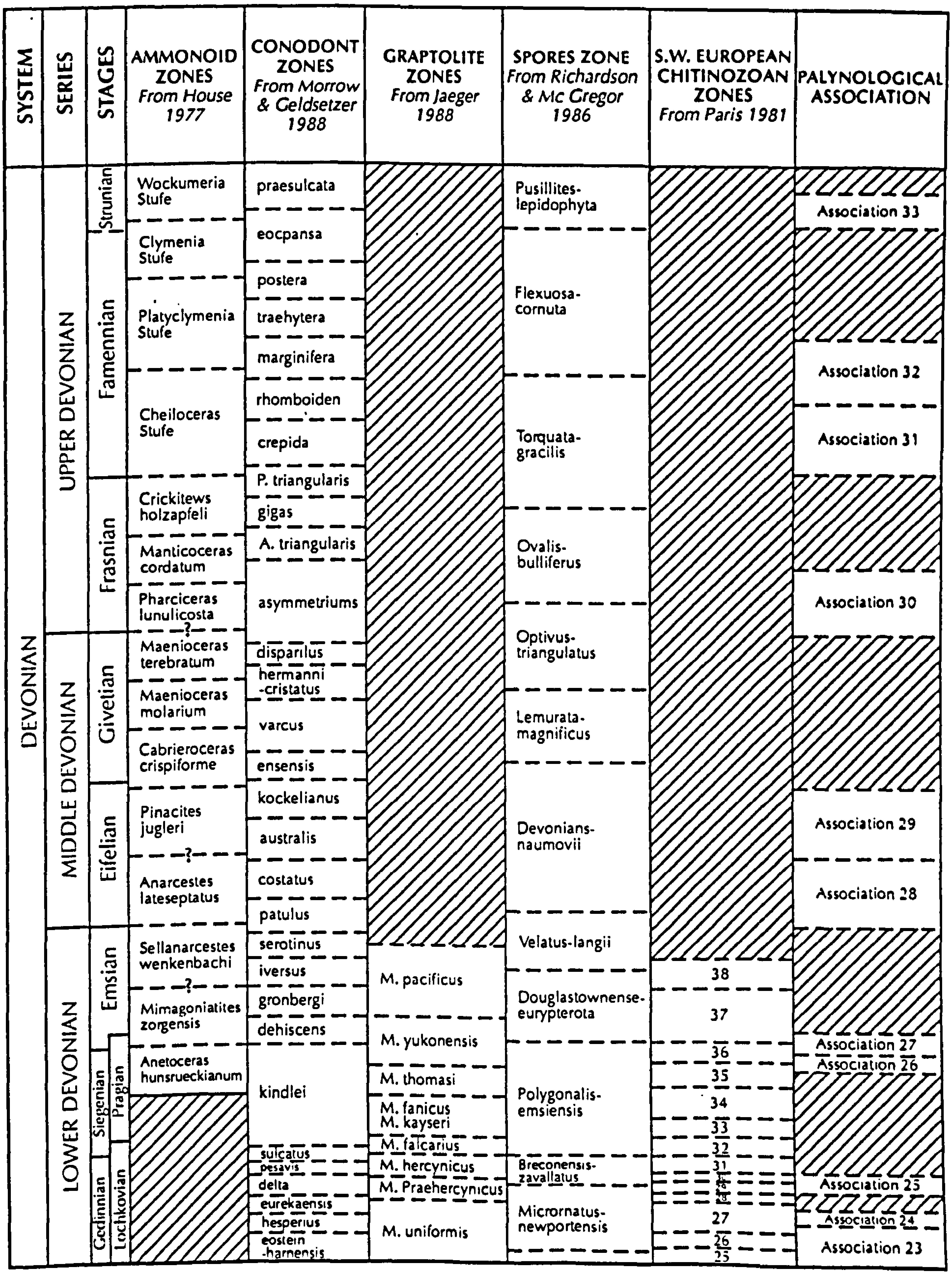
Association 23 (see Tilia graph 13).

Monograptus uniformis Zone in age.

Assemblages recorded from samples DW 57 and DW 58 are included in this association. The significant acritarchs present include common *Diexallophasis denticulata* var. A, occasional *Ammonidium* sp. 2, *Cymbosphaeridium pilar pilar* and *Multiplicisphaeridium variabile*, *Orygmahapsis fistulosa*, *Triangulina sanpetrensis*, *Visbysphaera microspinosa* var. C, Acritarch Form G and inconsistent *Diexallophasis remota* var. A and Acritarch Form J. The sparse chitinozoan assemblages include *Angochitina crassispina*, occasional *Hoegisphaera* cf. *glabra*, and occasional *Cingulochitina* spp.

Discussion: It is interesting to note the first occurrence of *Cymbosphaeridium pilar pilar* s.s. as late as the Gedinnian in the present study. Specimens of *Cymbosphaeridium pilar* recorded from the older samples have a less prominent ornamentation than this variety from the Gedinnian. The youngest

Figure 18. A correlation of the standard ammonoid, conodont and graptolite zones, the Northern Gondwanan chitinozoan zones and the O.R.S. continent spore zones with the palynological associations defined herein from the Devonian.



SYSTEM
- DEVONIAN

SERIES
- UPPER DEVONIAN
- MIDDLE DEVONIAN
- LOWER DEVONIAN

STAGES
- Strunian
- Famennian
- Frasnian
- Givetian
- Eifelian
- Emsian
- Siegenian / Pragian
- Gedinnian / Lochkovian

AMMONOID ZONES *From House 1977*
- Wockumeria Stufe
- Clymenia Stufe
- Platyclymenia Stufe
- Cheiloceras Stufe
- Crickitews holzapfeli
- Manticoceras cordatum
- Pharciceras lunulicosta
- ?
- Maenioceras terebratum
- Maenioceras molarium
- Cabrieroceras crispiforme
- Pinacites jugleri
- ?
- Anarcestes lateseptatus
- Sellanarcestes wenkenbachi
- ?
- Mimagoniatites zorgensis
- Anetoceras hunsrueckianum

CONODONT ZONES *From Morrow & Geldsetzer 1988*
- praesulcata
- eocpansa
- postera
- traehytera
- marginifera
- rhomboiden
- crepida
- P. triangularis
- gigas
- A. triangularis
- asymmetriums
- disparilus
- hermanni -cristatus
- varcus
- ensensis
- kockelianus
- australis
- costatus
- patulus
- serotinus
- iversus
- gronbergi
- dehiscens
- kindlei
- sulcatus
- pesavis
- delta
- eurekaensis
- hesperius
- eostein -harnensis

GRAPTOLITE ZONES *From Jaeger 1988*
- M. pacificus
- M. yukonensis
- M. thomasi
- M. fanicus
M. kayseri
- M. falcarius
- M. hercynicus
- M. Praehercynicus
- M. uniformis

SPORES ZONE *From Richardson & Mc Gregor 1986*
- Pusillites-lepidophyta
- Flexuosa-cornuta
- Torquata-gracilis
- Ovalis-bulliferus
- Optivus-triangulatus
- Lemurata-magnificus
- Devonians-naumovii
- Velatus-langii
- Douglastownense-eurypterota
- Polygonalis-emsiensis
- Breconensis-zavallatus
- Micrornatus-newportensis

S.W. EUROPEAN CHITINOZOAN ZONES *From Paris 1981*
- 38
- 37
- 36
- 35
- 34
- 33
- 32
- 31
- [illegible]
- [illegible]
- [illegible]
- 27
- 26
- 25

PALYNOLOGICAL ASSOCIATION
- Association 33
- Association 32
- Association 31
- Association 30
- Association 29
- Association 28
- Association 27
- Association 26
- Association 25
- Association 24
- Association 23

occurrences of *Ammonidium* sp. 2, *Diexallophasis denticulata* var. A and *Orygmahapsis fistulosa* are recorded at this level. *Angochitina crassispina* is only recorded in this association in the present study.

Associations 24 and 25.

These associations are described from the assemblages recorded from Oum Doul-1 and are documented later in this chapter.

Association 26 (see Tilia graph 13).

Monograptus yukonensis Zone in age.

The assemblages recorded from samples DW 96 and DW 97 comprise this association. The association is dominated by abundant *Cymbosphaeridium pilar pilar*, Acritarch Form U and *Cingulachitina* spp., notably *C.* cf. *convexa*, *C. serrata* and *Cingulochitina* sp. 1. Other significant occurrences include *Actinophasis* cf. *compluritala*, *Triangulina sanpetrensis*, *Visbysphaera microspinosa* vars. B and C, *Fungochitina pistilliformis* and inconsistent *Quadraditum scutiferum*, *Ancyrochitina tormentosa*, *A. tumida* and questionable *Pterochitina perivelata*.

Discussion: As with the assemblages from the *Monograptus uniformis* Zone, the specimens of *Cymbosphaeridium pilar* are ornamented with relatively coarse grana. *Actinophasis complurilata* has only previously been recorded from the Late Gedinnian of North America (Loeblich & Wicander 1976), the closely related morphotype *Actinophasis* cf. *complurilata* is recorded here from slightly younger sediments. Comparison of the chitinozoan part of the assemblage with Paris 1981, table 39, shows marked contradictions of the supposed chronostratigraphic ranges of some of the species recorded by that author. For example, several of the *Cingulachitina* species supposedly restricted to the Pridoli and Gedinnian e.g. *Cingulachitina* sp. A (=*Cingulachitina* sp. 1 herein), *C. serrata* and *C.* cf. *serrata* are recorded here in the latest Siegenian in considerable numbers. Other notable occurrences occurring younger than the records of Paris (1981) include *Ancyrochitina tormentosa*, *A. tumida*, *Pterochitina perivelata*?, *Fungochitina pistilliformis lata*. These latter forms occur in far fewer numbers than the *Cingulachitina* species.

Assemblages recovered from Oum Doul-1.

Twenty-six core samples from between 1496m (Strunian) and 4215.4m of Oum Doul-1 have been analysed. The assemblages are described from the oldest to the youngest for reasons of continuity with the descriptions of the Ordovician-Lower Devonian field samples. No macrofossil data for the well is available to the author, hence the dates assigned are derived solely from the palynological assemblages.

Lower to Middle Devonian.

Twenty samples from this interval have been analysed, the assemblages from which comprise five palynological associations (fig. 18).

Relevant literature: The relevant palynostratigraphic literature for this stratigraphic interval has already been discussed in the section describing the Silurian to Lower Devonian aged field samples. The most significant comparative papers include Paris, Laufeld & Chlupac 1981, Paris 1981, Jardine & Japaudjian 1968, Jardine *et al.* 1974, Boumenjel *et al.* 1988, Wicander 1983, Cramer 1964, Diez & Cramer 1977, Deunff 1976 and 1980, Deunff & Paris 1971, Loeblich & Wicander 1976, Playford 1977, Richardson & Lister 1989, Richardson & McGregor 1986, Streel *et al.* 1987, Massa & Moreau-Benoit 1976 and Steemans 1989.

Association 24 (see Tilia graph 14).

This association is described from the four lowemost core samples from the well which are from the Lmhaifid Formation between 4214.5m and 4217m depth. The assemblages are generally of high species diversity. The acritarchs occurring in high abundance include *Cymbosphaeridium pilar pilar, C. pilar scabratum, Diexallophasis denticulata, D. remota, D. remota rabiosum* and *Multiplicisphaeridium ramispinosum*. Several taxa of biostratigraphical value occur in lower numbers including *Dateriocradus lindus, Multiplicisphaeridium lobeznum, M. raspum, Onondagella deunffi, Ozotobrachion palidodigitatus, Pterospermella onondagaensis*, and *Quadraditum fantasticum*.

The chitinozoan assemblages are also diverse in species composition with *Angochitina chlupachi, Cingulachitina* spp, *Hoegisphaera* cf. *glabra* and *Sphaerochitina sphaerocephala* all prominent. The other notable occurrences within the chitinozoan assemblages include *Pterochitina perivelata, Urnochitina urna* and *Calpichitina sphaerica*. The spores make up approximately 30% of the palynomorph sum. This component is dominated by *Retusotriletes* spp. with rare *Apiculiretusotriletes* spp. The presence of *Brochotrletes* spp. and zonate spores (plate 136, figs.3 and 6 respectively) is significant for biostratigraphic purposes.

Discussion: The previously published stratigraphic ranges of many of the taxa recorded appear to indicate contradictory ages for this association. Within the chitinozoan component of the assemblages, several species are significant biostratigraphic markers. Paris (1981) considered *Pterochitina perivelata* and *Urnochitina urna* to be zonal species, lending their names to his two zones from the Pridoli (Paris

1990, table 40). The ranges of these two species and the also present *Sphaerochitina sphaerocephala* is illustrated by Paris (1981, table 39) as being restricted to the Pridoli. However, the presence of *Angochitina chlupaci* and *Calpichitina sphaerica* is not consistent with a Pridoli age for this association. The stratigraphic range of these species does not extend down into the Pridoli but would appear to indicate a Lower Gedinnian age.

The acritarch assemblages appear to be dominated by forms having previous stratigraphic records from the Lower Devonian. These include *Ozotobrachion palidodigitatus* (Gedinnian-Emsian, Cramer 1966, Playford 1977), *Diexallophasis remota* var. *rabiosum* (Siegenian-Emsian, Cramer 1964, 1970), *Multiplicisphaeridium lobeznum* and *M. raspum* (both Middle Siegenian-Emsian, Cramer 1964). Both *Quadraditum fantasticum* and *Onondagella deunffi* which occur in the late Silurian are reported to range into the Gedinnian (Diez & Cramer 1977). It is interesting to note that *Cymbosphaeridium pilar pilar* s.s. was recorded from the macrofossil dated field samples studied here that are Gedinnian and younger in age.

Within the spore assemblages, the presence of rare zonate spores and *Brochotriletes* spp. is important. Richardson & McGregor (1986) record the first appearance of zonate miospores within their *micrornatus-newportensis* Zone which is of Gedinnian age. Forms with foveolate ornamentation are also interpreted as having their first appearance at this level.

Consideration of the acritarch and spore assemblages would appear to indicate a Gedinnian age for this association. The chitinozoan assemblages also possess species indicative of a Gedinnian age, however they do contain forms that have previously been reported as being restricted to the Pridoli, e.g. *Pterochitina perivelata*, *Urnochitina urna* and *Sphaerochitina sphaerocephala*. These latter species may either be interpreted as ranging into the Gedinnian or, more likely, they are reworked.

The presence of zonate spores and *Brochotriletes* spp. suggests that this association is younger than lowermost Gedinnian (Richardson & McGregor 1986) which implies that this association is younger than Association 23.

Association 25 (see Tilia graph 14).

This association incorporates the assemblages recovered from three core samples between depths 4069.8m and 4071.5m from the Lmhaifid Formation. The diverse acritarch component of the assemblages is dominated by common *Cymbosphaeridium pilar pilar*, abundant *Diexallophasis denticulata* and common *D. remota* var. *rabiosum*. Biostratigraphically significant taxa occurring in fewer numbers include *Baltisphaeridium anfractum*, *Daisypilula compacta*, *Demorhethium* cf. *lappaceum*, *Diexallophasis remota* var. A, *Onondagella deunffi*, *Onondagella* sp. 1, *Ozotobrachion* *furcillatus, O. palidodigitatus, Pterospermella circumstriata, Quadraditum fantasticum, Thysanoprobolus polykion* and *Triangulina alargada.*

The chitinozoan assemblages are of moderately high diversity but only moderate abundances of taxa recorded. The genus *Ancyrochitina* is represented by rare *A. tormentosa* and *A. tumida.* Five species of *Cingulachitina* are recorded including the biostratigraphically significant form *C. plusquelleci. Eisenackitina* species are prominent including common *E. taugourdeaui* and rare *E. raucheri.* Other significant occurrences include *Fungochitina pistilliformis lata, Margachitina* spp. notably *M. catenaria crassipes* and *M. catenaria tenuipes, Muscochitina muscosa* and *Pterochitina perivelata.* The spores make up less than 5% of the palynomorph sum in this association with *Retusotriletes* spp. dominant and tripapilate forms common. Zonate spores also occur in low numbers.

Discussion: Several of the chitinozoan species recorded here were reported from south-west European sections by Paris 1981. The co-occurrence of *Muscochitina muscosa, Ancyrochitina tormentosa, Cingulachitina plusquelleci, Margachitina catenaria tenuipes, Eisenackitina raucheri, E. taugourdeaui* and *Fungochitina pistilliformis lata* here clearly indicates that this association is assignable to Zones 29 to 30 of Paris (1981, table 39). This would indicate an age of late Gedinnian for the association. The occurrence of *Pterochitina perivelata* and *Margachitina catenaria crassipes* at this stratigraphic level is rather anomalous (see Paris 1981, table 39). This could be interpreted as further evidence for the reworking of Pridoli aged sediment during the Gedinnian.

The age indicated from the acritarch assemblages is clearly consistent with that derived from the chitinozoans. Forms such as *Daisypilula compacta* (late Gedinnian, Loeblich & Wicander 1976), *Demorhethium lappaceum* (late Gedinnian, Loeblich & Wicander 1974, 1976; Gedinnian, Deunff 1980), *Ozotobrachion furcillatus* (Late Gedinnian-Middle Devonian, the late Gedinnian records include Loeblich & Drugg 1968 and Loeblich & Wicander 1974), *O. palidodigitatus* (Gedinnian-Emsian, Cramer 1966, Playford 1977), *Pterospermella circumstriata* (late Gedinnian-Emsian, Loeblich & Wicander 1976), *Quadraditum fantasticum* (Llandovery-latest Gedinnian, Diez & Cramer 1977; Gedinnian, Deunff 1980), *Thysanoprobolus polykion* (late Gedinnian, Loeblich & Tappan 1970, Loeblich & Wicander 1976; Gedinnian, Deunff 1980) and *Triangulina alargada* (Gedinnian-Givetian, Diez & Cramer 1977; Gedinnian, Deunff 1980) are all typical of Gedinnian aged assemblages.

The taxon *Diexallophasis remota* var. A was recorded in the macrofossil dated field samples or earliest Gedinnian age and would appear to range upto the late Gedinnian on the evidence of the associated palynomorphs found here. *Baltisphaeridium anfractum* appears to occur at a younger stratigraphic level in Morocco compared to previous records from North America (Wicander 1983). *Onondagella* sp. 1 is a distinctive palynomorph of potential biostratigraphic use and has previously been reported by Al-Ameri (1986) as *Pulvinosphaeridium* sp. from the Lower Devonian of North Africa.

The rather indistinct miospore assemblages contain zonate forms suggesting an age younger than earliest Gedinnian (Richardson & McGregor 1986).

The acritarch and chitinozoan assemblages strongly indicate an age of late Gedinnian for this association.

Association 27 (see Tilia graph 14).

The assemblages from two samples from the Assa Formation between depths 3675m to 3677.5m are included in this association.

The assemblages are of moderate species diversity dominated by the acritarchs *Diexallophasis remota rabiosum* and *D. remota remota*. Other notable acritarchs present in lower numbers include *Ammonidium*? *alloiteauii*, *Candelasphaeridium* cf. *insolitum*, *Florisphaeridium toyetae*, *Pterospermella onondagaensis*, *Triangulina alargada* and *Winwaleosia distracta*.

The sparse chitinozoan assemblage includes *Cingulachitina serrata*, *Margachitina catenaria catenaria* and *Sphaerochitina sphaerocephala*.

The spores are relatively high in abundance making up over 40% of the palynomorph sum within the assemblages. Biostratigraphically significant occurrences include *Dictyotriletes emsiensis*, *D. richardsoni* and *Dibolisporites variverrucatus*.

Discussion: There appears to evidence of the mixing of palynomorphs from two stratigraphic intervals. The spores *Dictyotriletes emsiensis* and *Dibolisporites variverrucatus* were recorded by Massa & Moreau-Benoit (1976) from Libya within their Zone 2, for which an age of late Siegenian to earliest Emsian was proposed. The stratigraphic range of *D. emsiensis* on the Old Red Sandstone continent, Siegenian to early Emsian (Richardson & McGregor 1986), supports the datation of Zone 2 by Massa & Moreau-Benoit. The acritarch *Florisphaeridium toyetae* is previously recorded from the middle Siegenian-Emsian (Cramer 1964). The co-occurrence of *D. emsiensis*, *D. variverrucatus* and *F. toyetae* indicate an age of late Siegenian to early Emsian for this association.

However, several taxa indicative of a Gedinnian age are also recorded in this association. These include the acritarch *Candelasphaeridium* cf. *insolitum* (Gedinnian, Deunff 1980; Steemans 1989), the chitinozoans *Cingulachitina serrata* (Pridoli-Gedinnian, Paris 1981), *Margachitina catenaria catenaria* (middle Gedinnian, Paris 1981) and *Sphaerochitina sphaerocephala* (Pridoli-earliest Gedinnian, Paris 1981), and the spore *Dictyotriletes richardsoni* (Gedinnian, Steemans 1989). This appears to be further evidence of reworking of latest Silurian and early Devonian sediments during the Lower Devonian interval.

Association 28 (see Tilia graph 14).

The assemblages from seven samples from the N'Kheila Formation between the depths 3239m and 3504.2m are included in this association.

The acritarch assemblages shows a marked contrast in composition to these of the underlying association. There is a distinct increase in the abundance of *Ammonidium*? *alloiteauii* and *Gorgonisphaeridium telum* with several forms making their first up-section appearance including *Craterisphaeridium sprucegrovensis*, *Cymatiosphaera carminae*, *Navifusa bacilla*, *N. minuta Onondagella asymmetrica*, *Polyedryxium evolutum*, *P. embudum*, and *P. pharoane*. There is a notable reduction in the abundance of *Diexallophasis remota* compared to the underlying association.

The chitinozoan assemblages also show a marked change in this association. The *Angochitina philippoti* complex of species is very conspicuous here with the presence of *Bursachitina bursa* and *Eisenackitina castor* also of stratigraphic significance. *Ancyrochitina ancyrea* var. A is inconsistently present in this association.

The spores assemblages are dominated by large grandispores and includes stratigraphically important species such as *Emphanisporites annulatus*, *Grandispora douglastownense*, *G. gabesensis* and *G. protea*. *Diatomozonotriletes* sp. and *Hystrichosporites* spp. are also present. A single specimen of *Ancyrospora nettersheimensis* was recovered from the uppermost sample included in this association.

Discussion: Comparison of the spore assemblages of this association with assemblages from the Ghadamis Basin, Tunisia (Loboziac & Streel 1989) indicates an Eifelian age. This is based on the co-occurrence of *Emphanisporites annulatus*, *Grandispora douglastownense*, *G. gabesensis* and *G. protea*. Comparison with the zonation scheme of Richardson & McGregor (1986) shows that the association is probably assignable to their *G. douglastownense*-*A. eurypterota* Zone based on the presence of *G. douglastownense*, *G. protea* (=*Calyptosporites proteus*) and *Ancyrospora nettersheimensis*. This zone is indicated to occupy the latest Emsian to earliest Eifelian interval by the authors. Consideration of spore data from both Northern Gondwana (Loboziac & Streel 1989) and the Old Red Sandstone continent (Richardson & McGregor 1986) indicates an age of early Eifelian.

The acritarch component of the assemblages is consistent with a Middle Devonian age for the association. *Navifusa minuta* , *N. bacillum*, *Onondagella asymmetricum*, *Polyedryxium embudum*, *p. evolutum* and *P. pharoane* are all typical in the Eifelian (Deunff 1955, 1966, 1971, Legault 1973, Playford 1977, Wicander 1983). The abundance of *Ammonidium*? *alloiteauii* and the first upsection records of *Craterisphaeridium sprucegrovense*, *Stellinium octoaster* and *Cymatiosphaera carminae* are notable stratigraphic occurrences.

The notable feature within the chitinozoan component of the association at this stratigraphic level is the marked increase in abundance of chitinozoans with abundant\common forms assignable to the *Angochitina philippoti* complex. *Bursachitina bursa* and *Eisenackitina castor* and *Ancyrochitina ancyrea* var. A are the other morphologically distinct forms of note here but these forms do not occur in all the assemblages included in this association.

Association 29 (see Tilia graph 14).

The assemblages from four samples from the N'Kheila Formation between the depths 3130.65 and 3186.5 are included in this association.

The composition of the assemblages is not dissimilar to those of the underlying association 28, however there is a marked change in abundance of several of the taxa present. This is confirmed by the dendrogram illustrating the cluster analysis on Tilia graph 14. Within the acritarch component, the most notable change is the increase abundance of *Veryhachium* species, notably *V.* cf. *arcarium* and *V.* cf. *cymosum.* The other acritarchs with a notable increase in abundance are *Polyedryxium pharoane* and cf. *Tunisphaeridium* sp. A notable decrease in abundance from the underlying association is that of *Ammonidium*? *alloiteauii.* *Multiplicisphaeridium*? sp. 2 is the only acritarch to makes its first upsection appearance in this association.

The chitinozoans are far less numerous than in Association 28. Forms assignable to the *Angochitina philippoti* complex are still prominent with *Bursachitina bursa* and *Ancyrochitina ancyrea* var. A present.

The spore assemblages are once again dominated by *Grandispora* spp. which, due to poor preservation, were found difficult to speciate. A notable aspect of this assemblage is the increase in abundance of *Ancyrospora nettersheimensis*.

Discussion: The presence of *Ancyrospora nettersheimensis* suggests that the association is no younger than Eifelian in age (Loboziac & Streel 1989). This is substantiated by the absence of the ubiquitous species *Geminospora lemurata* which has a Givetian and younger range. *Ancyrospora nettersheimensis* has been recorded in over 50 wells from the subsurface of Libya with a similar trend in abundances as that recorded in the present study (P. Swire pers. comm 1992). The increase in abundance as recorded in this association is believed to occur in the late Eifelian.

As with the underlying association, the acritarchs and chitinozoans recorded e.g. *Navifusa minuta* , *N. bacillum*, *Onondagella asymmetricum*, *Polyedryxium evolutum P. pharoane* and *Bursachitina bursa* are consistent with a Middle Devonian age (Deunff 1955, 1971, Legault 1973, Wicander 1983).

Upper Devonian.

Twenty samples from this interval have been analysed, the assemblages from which comprise five palynological associations (fig. 18).

Relevant literature: The publications concerning material from Libya and Algeria (Paris *et al.* 1985, Streel *et al.* 1988, Loboziac & Streel 1989, Boumenjel *et al.* 1988, Massa & Moreau-Benoit 1976) and the Ardennes and Belgium (Martin 1981, 1982, 1984, Streel *et al.* 1987) for this stratigraphic interval are most comparable with the assemblages recorded in the present study. Comparison with previous studies in the UK and Eire (Richardson & McGregor 1986, Higgs Clayton & Keegan 1988), North America (Wicander 1974, 1983, Wicander & Playford 1985, Wicander & Loeblich 1977, Jenkins & Legault 1977) and Brazil (Brito 1967) are also made where relevant.

Association 30 (see Tilia graph 14).

The assemblage from a single sample, OD 2409.65 from the Anou Smaira Formation comprises this association.

The association is markedly different in species composition to the previous. This association includes the first appearances of the acritarchs *Ammonidium grosjeanii, Daillydium pentaster, Diexallophasis remota tyrea, Maranhites* spp. notably *M. britoi* and *M. stockmansii, Palacanthus tripus, Pratulasphaera novacula, Quisquilites buckhornensis, Stellinium comptum* and *Umbellasphaeridium deflandrei*. Also prominent are abundant *Tasmanites* spp. and *Craterisphaeridium sprucegrovense*.

The chitinozoan assemblage is dominated with the species *Sphaerochitina pilosa* which makes up approximately 4% of the palynomorph sum.

The poorly preserved spore assemblage lacks the *Grandispora* species that dominated the assemblages of Association 29.

Discussion: The chitinozoan *Sphaerochitina pilosa* has a stratigraphic range of late Emsian through Frasnian (Jenkins & Legault 1979, Streel *et al.* 1988) indicating an age of no younger than Frasnian for this association.

The diverse acritarch assemblage suggests an age of Famennian, probably lower Famennian based on comparison primarily with material documented from outcrop in Belgium (Martin 1981, 1982, 1984) and also from the subsurface of Libya (Streel *et al.* 1985, Paris *et al.* 1988, P. Swire pers. comm.

1992). When compared to material of Late Devonian age from Belgium, the present assemblages have many species in common. The material studied by Martin (1981, 1982, 1984) is dated by shelly macrofaunas and ranges between early Frasnian and early Famennian in age. In her 1981 publication in which she documents the latest early Fammenian aged assemblages, the coincidence of taxa present with the present study is greater than those from the Frasnian. These coincident taxa include *Maranhites britoi, M. stockmansii, Daillydium pentaster, Polyedryxium pharoane* (=*Eisenackidium martensianum*), *Ammonidium grosjeanii, A. sprucegrovensis* and *Stellinium comptum*. However, it is notable that *Ephelopalla gorkae*, recorded in the overlying Association in the present study, is typical of the latest early Frasnian interval in Belgium and it may be concluded, therefore, that this association is older than the latest early Frasnian.

In Libya, several prominent species observed here and in Belgium e.g. *Maranhites* spp. are not recorded, however taxa such as *Umbellasphaeridium deflandrei* and *Craterisphaeridium sprucegrovensis* are recorded from the Frasnian of Libya. It is interesting to note the occurrence of a flood of tasmanitids in Libya during the early Frasnian (P. Swire pers. comm. 1992). Similarly high abundances of *Tasmanites* spp. are recorded in the present association, however, one can not be over cautious in correlating such events from one sedimentary basin to another.

The only previously published record of *Pratulasphaera novcular* appears to be from the Frasnian of Iowa, USA (Wicander & Playford 1985). This record is consistent with the age assignation of the present association.

From the chitinozoan and acritarch data available from North Africa and Belgium, a Frasnian, probably early Frasnian age can be assigned to this association.

It is interesting to note the absence of *Geminospora lemurata* from the present study. This taxon occurs in greatest abundance in the early\middle Givetian at which time it appears to be almost ubiquitous (Streel *et al.* 1987, Loboziac & Streel 1989, Loboziac pers. comm. 1992). It occurs in lower numbers and is more sporadic geographically in the Frasnian (P. Swire pers. comm. 1992). This species is not recorded from the Frasnian aged Moroccan assemblages studied here.

Association 31 (see Tilia graph 14).

The assemblages from two samples from the Draa Formation at depths 1809m and 1809.3m are included in this association.

The acritarch assemblages are diverse in their species composition with the most notable change from the underlying association being the abundant presence of *Gorgonisphaeridium* spp, notably the *G. spicatum* complex of forms. Also prominent are *Baltisphaeridium*? sp. 5, *Cymatiosphaera leonensis*, *Daillydium pentaster, Diexallophasis remota* var. *tyrea, Ephelopalla gorkae, Maranhites mosessii, M. stockmansii, Muraticavia* sp. 1, *Pterospermella eruptio, Stellinium comptum, S. octoaster Umbellasphaeridium deflandrei* and Acritarch Form P. Biostratigraphically significant forms occurring in low abundances include *Crassiangulina tesselita* and *Palacanthus tripus. Ammonidium grosjeanii* is far less common than in the underlying association 30.

No chitinozoans are recorded in this association.

Within the spore assemblages, the stratigraphically useful species *Auroraspora torquata* and *Ancyrospora furcula* are present.

Discussion: The presence of *Auroraspora torquata* in the association enables the application of the zonal scheme of Richardson and McGregor (1986). Its presence suggests that the present association is assignable to the *torquata-gracilis* Zone or younger, implying an age no older than latest Frasnian.

This age is refined by the acritarch assemblages when they are compared with those from Belgium documented by Martin (1984). The composition of the present association indicates a correlation with her assemblages III to V. This is based on the co-occurrence of *Ammonidium grosjeanii, Daillydium pentaster, Diexallophasis remota* var. *tyrea, Maranhites mosessii, M. stockmansii, Craterisphaeridium sprucegrovense* (=*Ammonidium sprucegrovense*), *Palacanthus tripus, Polyedryxium pharoane, Pterospermella eruptio, Stellinium comptum* and *S. octoaster* here and in Belgium. An early Famennian age for the association can therefore be inferred.

The broad nature of the published studies concerning material from the subsurface of Libya (Streel *et al.* 1985, Paris *et al.* 1988) and Algeria (Jardine *et al.* 1974) makes comparison of the present assemblages impractical.

Association 32 (see Tilia graph 14).

The assemblages from two samples from the Draa Formation at depths 1612m and 1612.1m are included in this association.

The assemblage is dominated by the super-abundance of *Gorgonisphaeridium* spp. There is a change in the composition of the *Gorgonisphaeridium* component of the assemblages from the underlying association which is dominated by the *Gorgonisphaeridium spicatum* complex. The present association is dominated by the *Gorgonisphaeridium ohioense* complex with the first stratigraphic occurrence of *Gorgonisphaeridium*? sp. 2 and *Gorgonisphaeridium* sp. 3 also at this level. Taxa occurring in fewer numbers include *Crassiangulina tesselita, Craterisphaeridium sprucegrovensis, Ephelopalla gorkae,* *Muraticavia* sp. 1, *Polyedryxium pharoane*, *Stellinium comptum*, *S. octoaster* and *Veryhachium downiei downiei*.

No chitinozoans and no age diagnostic miospores are recorded in assemblages constituting this association.

Discussion: Comparison of this association of acritarchs with the literature indicates an age of Famennian or older (Streel *et al.* 1985, Paris *et al.* 1988, Jardine *et al.* 1974). Recent unpublished work on the subsurface of Libya (P. Swire pers. comm. 1992) indicates that *Craterisphaeridium sprucegrovensis* has a stratigraphic top in the early Famennian by the calibration of the occurrences of this form with the associated miospore assemblages. The presence of this form, therefore, and the stratigraphic position of the association in the well (i.e. above Association 31 which is interpreted as early Famennian in age) indicates an age of early Famennian.

There is evidence of reworking at this stratigraphic level indicated by the presence of the Upper Silurian to Lower Devonian species *Onondagella deunffi*. The presence of several other taxa within the association as a result of reworking (e.g. *Ephelopalla gorkae*, *Muraticavia* sp. 1, *Polyedryxium pharoane*) can not be ruled out.

Association 33 (see Tilia graph 14).

The assemblage from one sample, OD 1496 from the Lefdar Formation at depth 1496m in the well constitutes this association.

As with Associations 32 and 33, the acritarch component of this association is dominated by the super-abundance of *Gorgonisphaeridium* spp. with the *Gorgonisphaeridium ohioense* complex predominating. The *Gorgonisphaeridium spicatum* complex, *Gorgonisphaeridium*? sp. 2 and *Gorgonisphaeridium* sp. 3 are also prominent. Other stratigraphically significant forms occurring in low numbers are *Crassiangulina tesselita*, *Maranhites* spp. notably *Maranhites* sp. 1, *Tetraporina horologia*, *T. quadrispina* and *Umbellasphaeridium saharicum*. Several acritarchs present are discussed below as having been reworked e.g. *Craterisphaeridium sprucegrovensis*, *Polyedryxium pharoane* and *P. embudum*.

One specimen of *Sphaerochitina pilosa* was recovered from this assemblage which is believed to be strong evidence for the presence of reworked palynomorphs (see discussion below).

The diverse miospore assemblage recovered includes several age diagnostic forms including *Retispora lepidophyta*, *Velatisporites pusillites*, *Discernisporites micromanifestus*, *Spelaeotriletes granulatus* and *Auroraspora torquata*.

Discussion: The miospores present in this association enable a refined biostratigraphic age to be assigned. The presence of *Retispora lepidophyta, Velatisporites pusillites, Discernisporites micromanifestus* and *Auroraspora torquata* suggests that the association can be assigned to the *pusillites-lepidophyta* Zone of Richardson & McGregor (1986). This indicates an age of early Strunian. An age no more refined than Strunian is indicated by the application of the zonal scheme of Higgs, Clayton and Keegan (1988) in which the co-occurrence of *R. lepidophyta* and *V. pusillites* implies the present association is assignable to their LL-LN Zones. Further unpublished evidence from Libya of an early Strunian age comes from the presence of common *Spelaeotriletes granulatus* in association with *R. lepidophyta* (P. Swire pers. comm. 1992).

The acritarchs *Crassiangulina tesselita, Tetraporina horologia, T. quadrispina* and *Umbellasphaeridium saharicum* are all previously recorded from the Strunian of North Africa (Streel *et al.* 1985, Paris *et al.* 1988, Jardine *et al.* 1974), however, it is interesting to note that the latter three, *Tetraporina horologia, T. quadrispina* and *Umbellasphaeridium saharicum*, are not recorded in the Frasnian to early Famennian assemblages here which differs from the pervious records in Libya (see Paris *et al.* 1988).

There are no unequivocal records of Strunian aged chitinozoans in the literature to my knowledge. The species recovered in the present assemblage, *Sphaerochitina pilosa*, has a published stratigraphic range top in the Frasnian (Jenkins & Legault 1979, Paris *et al.* 1988), hence it safe to say that the occurrence of this form in Strunian aged sediments indicates the presence of reworked palynomorphs. Further evidence comes from the acritarch component of the assemblages in which the previous records of several forms e.g. *Polyedryxium embudum* (Emsian-Givetian, Deunff 1966, 1971, Playford 1977) indicate recycling has occurred. It should be noted, therefore, that taxa whose stratigraphic occurrence is not previously documented from this level (e.g. *Craterisphaeridium sprucegrovensis, Daillydium pentaster, Polyedryxium pharoane* and *Pterospermella eruptio*) could very possibly be recycled.

Chapter 8. Environmental palynology.

Previous studies regarding the spatial distribution of palynomorphs (e.g. Muller 1959, Staplin 1961, Aldridge *et al.* 1981, Dorning 1987) have revealed trends in the gross morphology of the constituents of palynological assemblages from the terrestrial realm through the continental shelf and out into abyssal areas. In the present study, the relative abundance of palynomorph groupings have been calculated in order to investigate the palaeoenvironments of deposition of the samples studied. The environmental model of Dorning (1987), constructed on data from the Palaeozoic, is applied here and the results are considered in conjunction with the sedimentalogical data available.

The groupings utilised are the acritarchs, which are split into 'acanthomorphs', 'spheromorphs' and 'other acritarchs' *sensu* Cramer & Diez 1979, prasinophytes, chitinozoans and spores. The proportions of these groups are illustrated on Tilia graphs 1-14.

In summary, Dorning (1987) recognised trends in the gross composition of palynological assemblages recovered from i. sediments deposited in the littoral or nearshore zone, ii. sediments deposited in the neritic zone (on the mid to outer shelf) and iii. sediments deposited in the bathyal and abyssal zone (figs. 19 & 20.)

Within the littoral zone, low diversity marine palynofloras are dominated by thin walled spheromorphic acritarchs. These simple acritarchs may be accompanied by flask shaped chitinozoans without long spines e.g. *Sphaerochitina* (Laufeld 1974). In the late Ordovician, Silurian and Devonian (i.e. the period of primitive land plant colonisation and diversification), the marine element is commonly associated with high proportions of miospores derived from the adjacent landmass. The proportions of the allochthonous terrestrial element is obviously strongly influenced by the sedimentation rates prevailing at the time of deposition, however, the proportions of miospores in the assemblages can give a general indication of the distance from shoreline of the site of deposition. The abundance of miospores present can be generally interpreted as being inversely proportional to the distance from the palaeoshoreline.

The mid to outer shelf area supports a higher diversity microflora with acanthomorphic acritarchs dominant. The associated chitinozoans include forms with complex and elaborate ornamentation e.g. *Ancyrochitina, Plectochitina.*

Assemblages recovered from sediments deposited in the abyssal realm have a low diversity composition dominated by spheromorphic acritarchs as in the littoral zone. However, spheromorphic forms recovered from sediment deposited in deeper parts of the basin are noticeably thicker walled e.g. *Leiosphaeridia microcystis*. Prasinophycean algae are also commonly associated with such deposits, notably *Tasmanites*

Figure 19. Palynomorph distribution across the continental shelf for the Ordovician (Caradoc) and the Silurian (Wenlock).

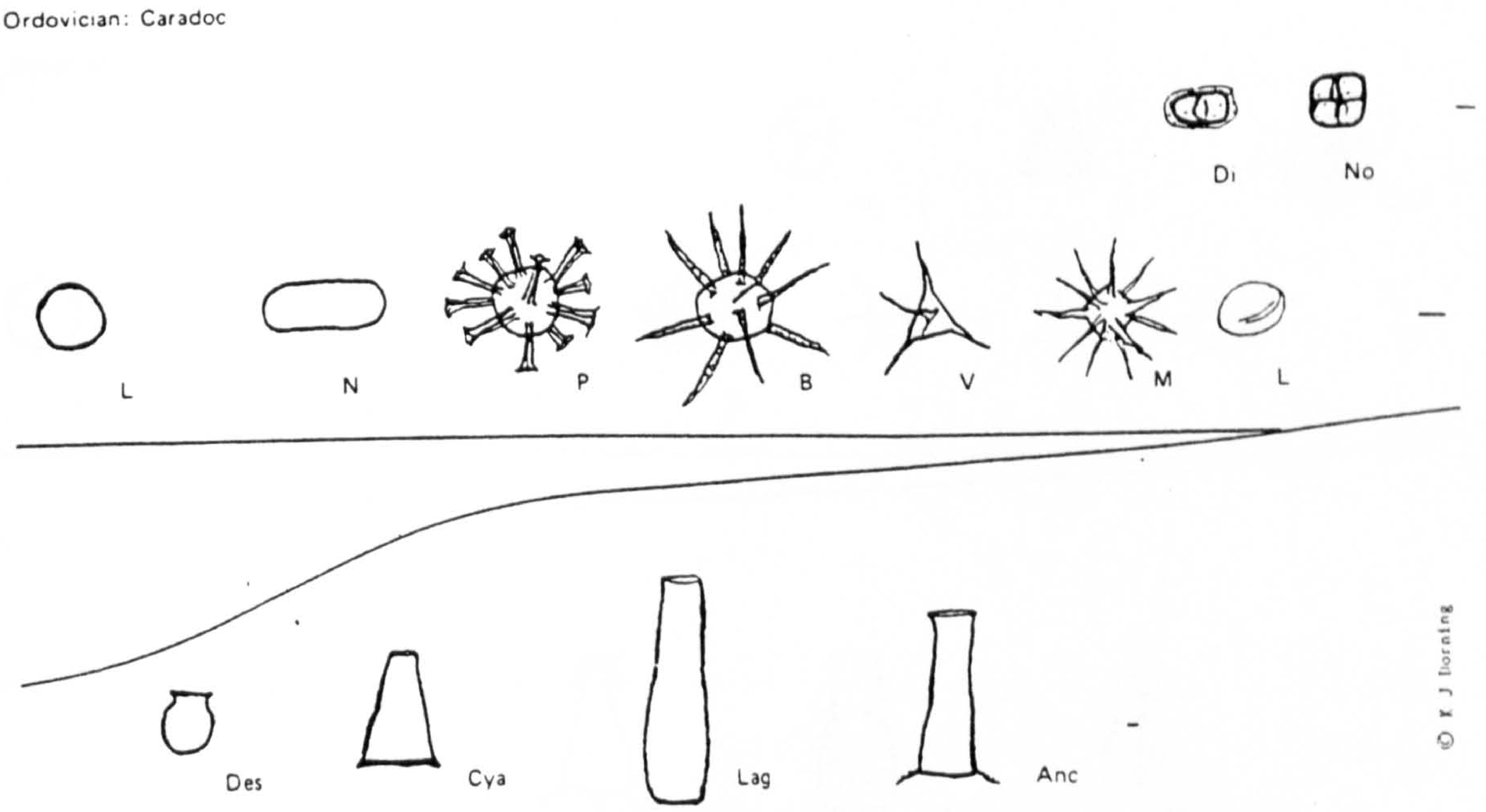


Fig. 14.4 — Ordovician organic palaeontology; diagrammatic sketch of selected palynomorph distribution from the Caradoc carbonate shelf. L. *Leiosphaeridia*, N. *Navifusa*, P. *Peteinosphaeridium*, B. *Baltisphaerosum*, V. *Veryhachium*, M. *Micrhystridium*. Spores: Di. *Diadospora*, No. *Nodospora*. Chitinozoans: Des. *Desmochitina*, Cya. *Cyathochitina*, Lag. *Lagenochitina*, Anc. *Ancyrochitina*.

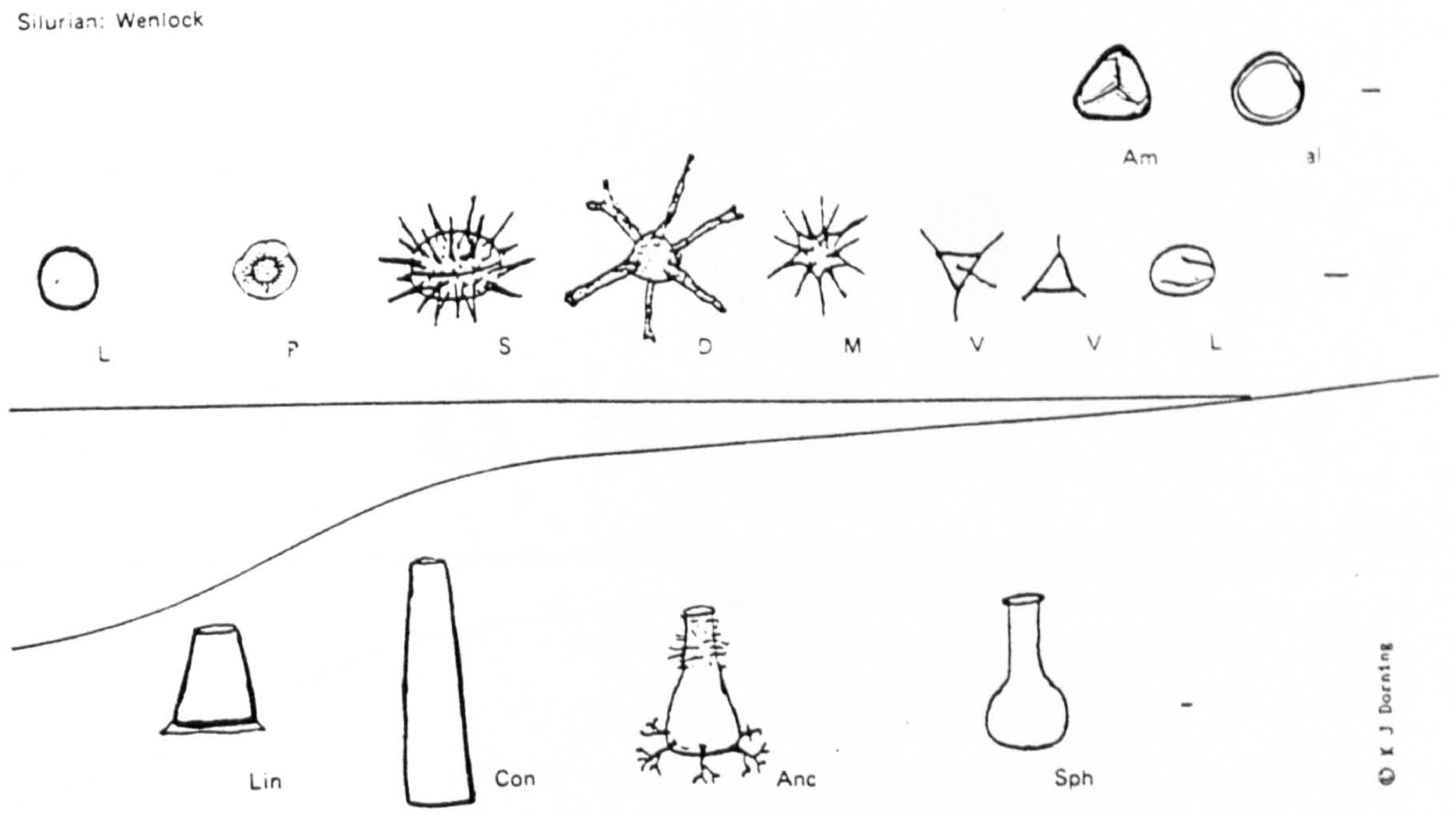


Fig. 14.5 — Silurian organic palaeontology; diagrammatic sketch of selected palynomorph distribution from the Wenlock carbonate shelf. L. *Leiosphaeridia*, P. *Pterospermella*, S. *Salopidium*, D. *Diexallophasis*, M. *Micrhystridium*, V. *Veryhachium*. Spores: Am. *Ambitisporites*, al. alete spores with thickened equatorial margin. Chitinozoans: Lin. *Linochitina*. Con. *Conochitina*, Anc. *Ancyrochitina*, Sph. *Sphaerochitina*.

Figure 20. Palynomorph distribution across the continental shelf for the Devonian (Givetian) and the early Carboniferous (Tournasian).

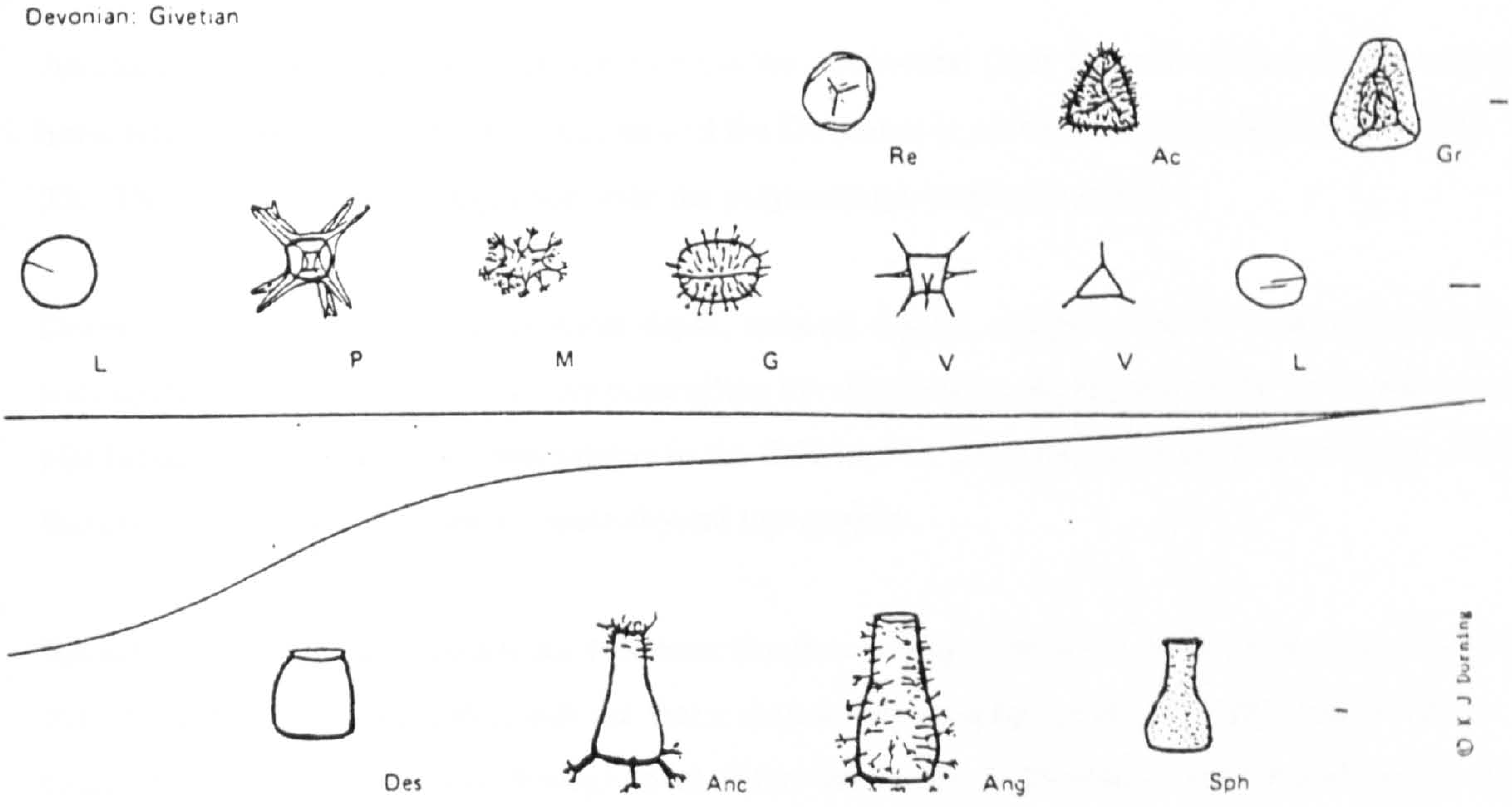


Fig. 14.6 — Devonian organic palaeontology; diagrammatic sketch of selected palynomorph distribution from the Givetian carbonate shelf. L. *Leiosphaeridia*, P. *Polyedrixium*, M. *Multiplicisphaeridium*, G. *Gorgonisphaeridium*, V. *Veryhachium*. Spores: Re. *Retusotriletes*, Ac. *Acinosporites*, Gr. *Grandispora*. Chitinozoans: Des. *Desmochitina*, Anc. *Ancyrochitina*, Ang. *Angochitina*, Sph. *Sphaerochitina*.

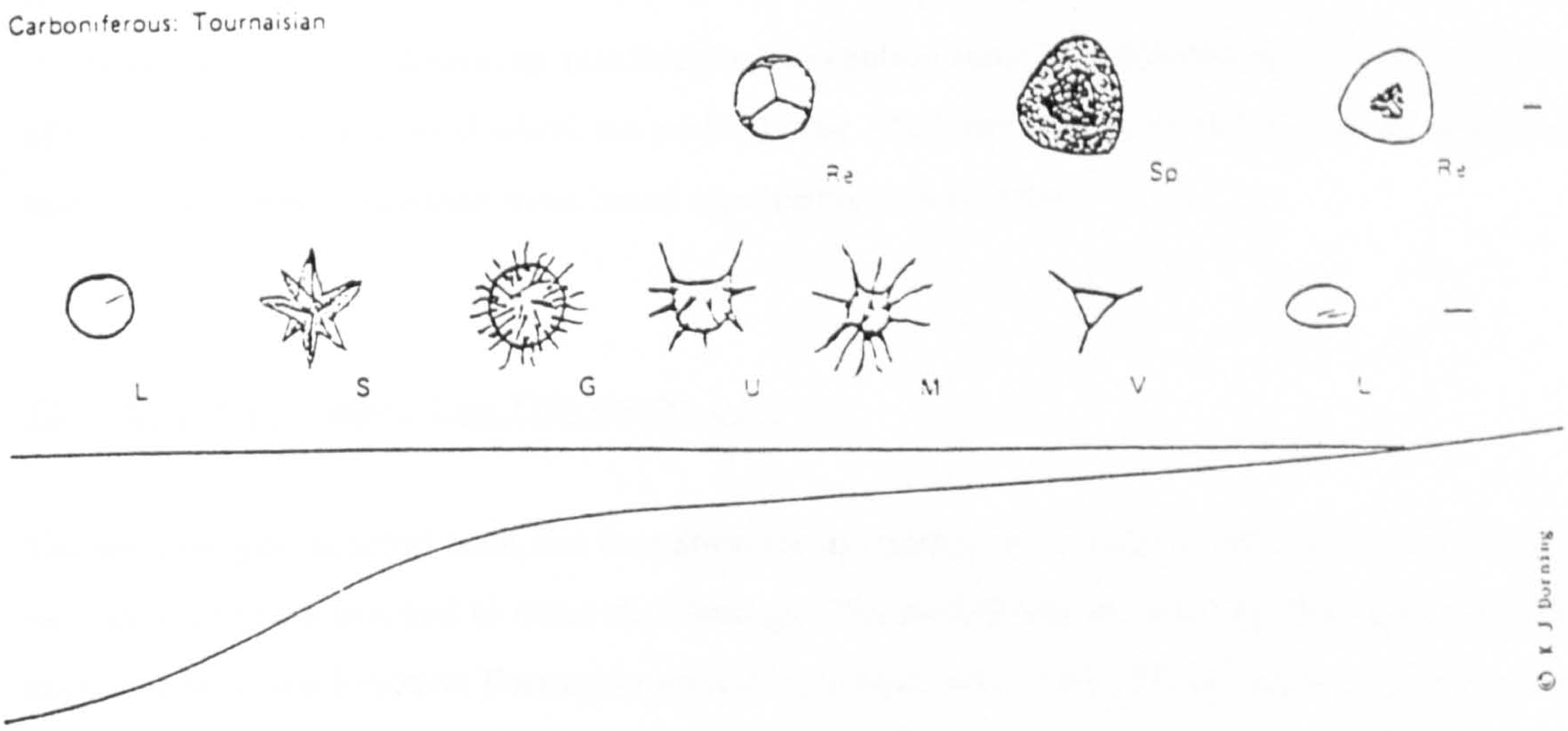


Fig. 14.7 — Carboniferous organic palaeontology; diagrammatic sketch of selected palynomorph distribution from the Tournaisian carbonate shelf. L. *Leiosphaeridia*, S. *Stellinium*, G. *Gorgonisphaeridium*, U. *Unellium*, M. *Micrhystridium*, V. *Veryhachium*, Spores: Re. *Retusotriletes*, *Sp*. *Spelaeotriletes*.

spp. The chitinozoans recovered from deep water sediments tend to be small forms, such as *Desmochitina* spp., and lack the elaborate ornamentation of those commonly recovered from shelf deposits.

An example of palynomorph distribution across the continental shelf for each of the systems studied here, namely the Ordovician, the Silurian and the Devonian is presented by Dorning (1987), figs. 19 & 20. These are useful for comparison with the palynomorph trends observed.

Dorning (1987) considers relative water depth, nutrient supply, oxygen availability and the rate of sedimentation to be the major factors controlling the distribution of palynomorphs in the marine realm. His broad model is based on observations in the field and on the consideration of the interplay of these factors across a typical terrestrial-shelf-abyssal topography.

Recent palaeogeographic models for Northern Gondwana (e.g. Scotese & McKerrow 1990, Paris 1992, T.P. Young pers. comm. 1992) indicate that a shallow topography, relatively stable continental situation prevailed in Morocco through most of the Ordovician to Devonian interval during which an almost complete sequence of sediments were deposited (Destombes, Hollard & Willefert 1985).

The Ordovician.

All the assemblages analysed from the Ordovician in the present study are marine in origin. In general, the preservation of palynomorphs is rather poor so caution must be expressed in making interpretation of the assemblages recovered which are probably not a full representation of the original assemblage that was deposited. However some broad conclusions can be drawn.

The Fezouata Formation, (see Tilia graphs 1-6).

The assemblages recorded from this formation are dominated by acanthomorphic acritarchs which indicate deposition in a mid to outer shelf setting. The assemblage included in Association 2 is the only exception from the Fezouata Formation assemblages analysed. Here, the assemblage is of a much lower species diversity, dominated by one species, *Cymatiogalae messaoudii*, of the 'other acritarch' group. The high abundance of this form is at the expense of the acanthomorphic acritarchs. This may indicate a more stressful environment of deposition (e.g. high salinity, near shore) at that time. There is no lithological reflection of this apparent change in the depositional conditions.

The Tachila Formation (see Tilia graph 7).

The assemblages recorded from the Tachila Formation are also dominated by acanthomorphic acritarchs. The spheromorphs present are relatively thick walled. The chitinozoan element is diverse in species which commonly possess relatively elaborate ornamentation for this stratigraphic interval e.g. *Belonechitina micracantha*. The environment of deposition envisaged for this association of palynomorphs is outer shelf. The fine grained nature of the shale lithology supports the idea that deposition occurred in a relatively low energy environment.

The Ktaoua Formation (see Tilia graphs 8-10).

The samples analysed from the Caradoc aged part of the Ktaoua Formation yielded particularly poorly preserved assemblages. Low diversity acanthomorphic acritarchs predominate and the chitinozoans, when preserved, are generally forms of modest or low ornamentation. Deposition of these sediments probably took place in a mid to outer shelf setting.

The assemblages of Ashgill age from the Ktaoua Formation contain acritarch assemblages of moderate species diversity. The assemblage included in Association 11 possesses abundant acanthomorphic acritarchs with common leiofusids. Poorly preserved *Ancyrochitina* spp. are also recorded. No more than a mid to outer shelf depositional setting can be inferred from this association.

The assemblage included in Association 12, however, possesses forms indicative of outer shelf deposition. Evidence for this comes from the low diversity of acritarch species present which, although dominated by acanthomorphic forms, contain significant abundances of thick walled spheromorphs e.g. *Lophosphaeridium*? sp. 9. Further evidence comes from the abundant presence of the elaborate form *Ancyrochitina* sp. 1. The siltstone lithology of the sample from which this assemblage was extracted indicates low-moderate energy levels at the time of deposition.

The Silurian.

All the sediments analysed from the Silurian in the present study are marine in origin. Palynomorph preservation is moderate to good relative to the assemblages analysed from the Ordovician.

The Carbonaceous Shale Formation, (see Tilia graph 11).

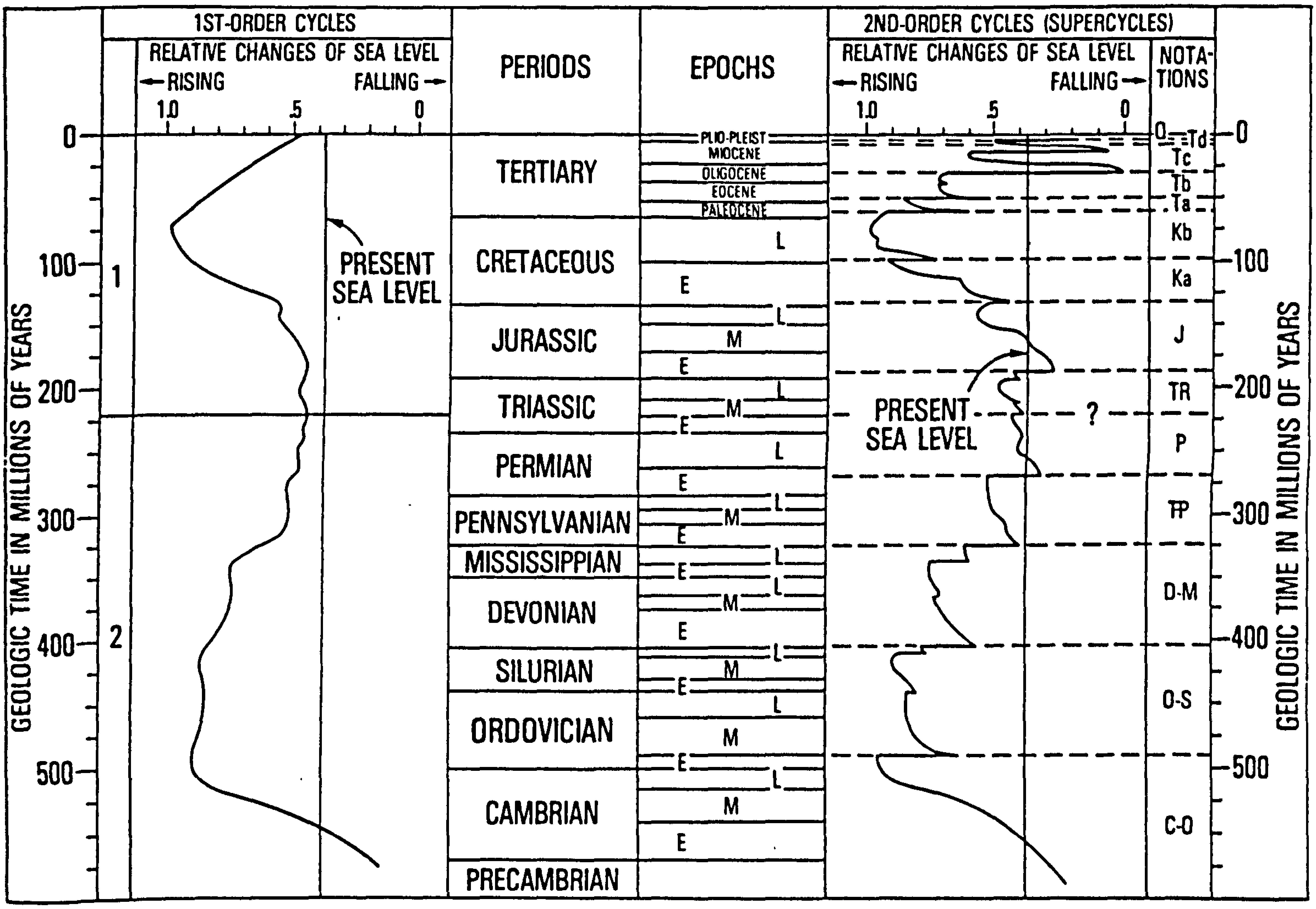
The palynomorph assemblages recorded from the Carbonaceous Shale Formation are accompanied by abundant amorphous sapropelic material. The assemblages themselves are largely dominated by thick walled spheromorphic acritarchs (e.g. *Leiosphaeridia microcystis*) and prasinophycean algae (e.g. *Tasmanites medius*). The acanthomorphic acritarch and the chitinozoan assemblages are generally impoverished in this formation. A probable anoxic, low energy, deep water abyssal environment of deposition can be inferred for these assemblages. This is consistent with the carbonaceous, very fine grained nature of the lithology of the samples.

Within this formation, there are two stratigraphic levels at which the gross composition of the assemblages is somewhat different. At the *Monograptus turriculatus-M. crispus* Zone (early Telychian), the assemblage recovered from sample DW 246, acanthomorphs are dominant over the spheromorphs with a higher diversity of acritarchs recorded. This suggests a difference in the depositional regime at this level, probably related to increased nutrient supply associated with a more oxygenated water column as a result of higher energy conditions. This may also be the case for the time interval at the *Monograptus riccartonensis-Cyrtograptus rigidus* Zonal boundary (mid Sheinwoodian, early Wenlock). The sample analysed from this level, DW 367, has an acritarch assemblage dominated by spheromorphic forms but also contains a flood of *Angochitina* sp. 1. The abundant occurrence of this relatively small but non the less elaborately ornamented form, in association with the spheromorphs, implies a depositional setting on the outer part of the shelf.

It is interesting to note the coincidence in age of these basinal palynofacies with the postulated high stand situation prevailing during the Middle Silurian (Vail, Mitchum & Thompson 1977), fig. 21. Given the relatively stable tectonic situation in Northern Gondwana at this time, it would appear likely that such major fluctuations in the palynoflora are a reflection of eustatic as opposed to tectonic influences.

From a palaeogeographic view-point, it is interesting to note the absence of the *Deunffia* and *Domasia* group of acritarchs in Morocco in early Silurian aged sediments. The records of this group in palaeolatitude parallel Libya at this stratigraphic level (e.g. Hill & Molyneux 1988) suggests the control on their distribution to be more complex than suggested by the model of latitudinal control of microplankton first proposed by Cramer (1970). Further investigation of the palaeogeography of the Northern Gondwanan domain, a subject beyond the scope of this thesis due to time constraints, may well provide answers to these anomalies.

Figure 21. First and second order global cycles of relative change of sea level during Phanerozoic time, from Vail, Mitchum & Thompson 1977.



The Argillaceous Shale Formation, (see Tilia graphs 11 & 12).

The assemblages recovered from samples from the Argillaceous Shale Formation are generally of moderate to high species diversity. The thick walled spheromorphs which dominated the underlying Carbonaceous Shale Formation are relatively insignificant in terms of abundance and the acanthomorphic forms are far more evident. The chitinozoan assemblages are also more diverse in their species composition with very elaborate forms evident e.g. *Ancyrochitina* spp. The miospores are rare constituting less than 1% of the palynomorph sum in each assemblage.

The palynomorph assemblages studied generally indicate a mid to outer shelf setting for the samples analysed from this formation, possibly more towards the outer shelf based on the rarity of spores. The proportions of taxa groupings recorded from sample JW 224 (earliest Ludlow) would appear to indicate that a deeper basinal setting would be more appropriate for this assemblage which is largely composed of indeterminate spheromorphic acritarchs. Such an interpretation could be seriously questioned on the basis of the very poor preservation of this particular assemblage.

The *Orthoceras* Limestone-Shale Formation, (see Tilia graph 12).

Only one sample was analysed from this formation, DW 215. The sparse palynoflora recovered is too poorly preserved to make any confident interpretations of the depositional environment based on the proportions of palynomorphs alone. However, the high proportion of acanthomorphic acritarchs recovered indicating a mid to outer shelf depositional setting is consistent with the environment indicated by the bio sparitic packstone limestone lithology. This lithology suggests a high energy, probably mid shelf depositional setting with negligible clastic input.

The Calcareous Shale Formation, Black Shale Member, (see Tilia graph 13).

The assemblages recovered from this formation are consistent in their gross composition. Acanthomorphic acritarchs are dominant (*ca.* 60% of the acritarch sum) with spheromorphic forms present in significant numbers (*ca.* 40% of the acritarch sum). The miospores are rare, consistently making up less than 1% of the palynomorph sum and the chitinozoans are relatively modest in their gross morphology with ancyrochitinid forms rare in these assemblages. An outer shelf setting can be interpreted for the deposition of these sediments which is supported by the fine grained nature of the lithology indicating deposition under low energy conditions.

The Devonian.

The Devonian aged samples analysed are all marine in origin. The preservation of the assemblages is good relative to those from the Ordovician and Silurian.

The Lmhaifid Formation, (see Tilia graph 14).

The two palynological associations defined from the Lmhaifid Formation each have characteristic gross palynological compositions. Association 24 has a relatively high proportion of spores in the assemblage (*ca.* 30 %) with acanthomorphic forms dominating the acritarch element. Simple flask shaped forms dominate the chitinozoan assemblages. A mid to inner shelf position for the deposition of this association can be inferred from the acanthomorphic acritarchs, the flask shaped chitinozoans and the abundance of terrestrially derived miospores. A low energy environment of deposition can be inferred from the dark, micaceous shale lithology.

Association 25, in contrast, has a relatively low proportion of spores in the assemblages making up approximately 4 % of the palynomorph sum. Acanthomorphic acritarchs are very abundant and Ancyrochitinid chitinozoans are common. This combination of morphotypes implies a probable outer shelf setting of deposition for the assemblages of association 25 which, when compared with the depositional setting proposed for the assemblages of Association 24, indicates fluctuations in the depositional regime within the Lmhaifid Formation with time.

The Assa Formation, (see Tilia graph 14).

The assemblages analysed from the Assa formation are similar in gross composition to those from Association 24 within the Lmhaifid Formation. The miospores are prominent making up approximately 45 % of the palynomorph sum, with acanthomorphic forms dominating the acritarch component. The chitinozoan assemblages are primarily composed of flask shaped forms with ancyrochitinid forms rare. An inner shelf setting can be proposed for the deposition of this assemblage. The dark, micaceous shale lithologies indicate that low energy conditions prevailed.

The Mdaour el Kbir-N'Kheila Formations (see Tilia graph 14).

The samples analysed from this interval yielded palynological assemblages of similar gross composition.

The assemblages are dominated by acanthomorphic acritarchs with the terrestrially derived miospores comprising between 10-33% of the palynomorph sum. Spheromorphic acritarchs and prasinophytes are low in numbers. The chitinozoans, when recorded, are commonly elaborate forms of the genera *Ancyrochitina* and *Angochitina*. The depositional setting inferred from the relatively high proportion of miospores, the dominant acanthomorphic acritarchs and the elaborate chitinozoans is inner to mid shelf. The dark, fine grained, largely micaceous shale lithologies indicate deposition under low energy conditions.

The Anou Smaira Formation (see Tilia graph 14).

The notable feature of the assemblage analysed from this formation is the high numbers (21% of the palynomorph sum) of Prasinophycean algae recorded (e.g. *Tasmanites* spp.). Miospores form approximately 14% of the palynomorph sum and the acritarch component is once again dominated by the acanthomorphs (*ca.*46% of the palynomorph sum). The chitinozoans are represented by an almost monospecific assemblage of the flask shaped species *Sphaerochitina pilosa*.

There appears to be contradictory elements within this assemblage when we try and apply the environmental model of Dorning (1987). The abundant acanthomorphic acritarchs, the common miospores and the monospecific flask shaped chitinozoan assemblage all indicate an inner shelf depositional setting. The abundant tasmanitids would appear to contradict this idea, these forms commonly proliferating in deep water, low energy, anaerobic conditions. The dark, laminated, fine grained shales support the interpretation of probable deeper water sedimentation under low energy conditions.

The Draa Formation (see Tilia graph 14).

The two palynological associations described from the Draa Formation, Associations 29 and 30, possess abundant acanthomorphic acritarchs with negligible spheromorphic forms suggesting deposition of the assemblages comprising these associations occurred on the continental shelf. Association 29, however, has a noticeably higher proportion of terrestrially derived miospores which make up approximately 9% of the palynomorph sum. In contrast, Association 30 has a negligible proportion of the assemblages composed of miospores. It can be inferred that the assemblages of Association 29 were deposited in a more proximal setting, probably inner to mid shelf, while the assemblages comprising association 30 were deposited more distally, probably in the outer shelf region.

The Lefdar Formation (see Tilia graph 14).

The assemblage analysed from this formation is dominated by acanthomorphic acritarchs with a significant abundance of miospores present (ca. 19% of the palynomorph sum). A probable mid to inner shelf setting for the deposition of this assemblage can be inferred from this gross composition. The fine grained, laminated shale lithology of the sample indicates that deposition took place under low energy conditions.

Chapter 9. Conclusions.

Of the approximately 300 samples processed for palynology in the first year of the study, 118 were selected for further palynological investigation based on three criteria. Firstly, that they could be assigned to a lithostratigraphic formation on the evidence available from field notebooks, the Moroccan geological maps and the lithology; secondly, wether the samples had been dated by their macrofossil content and thirdly, wether the samples had yielded palynomorphs. The geographic and stratigraphic information for the 118 samples that was available prior to the onset of the palynological investigations is collated in Appendix I.

Palynological preparation of samples proved to be a problem from the onset of the study due to the high thermal maturity and the commonly indurated nature of the rocks. As stated in the aims and objectives of the study (chapter 2), it was intended to develop a preparation technique that would be applicable for industrial practice. Initial attempts to process large amounts of rock (> 75g) to enhance the abundance of palynomorphs recovered were found to be unsuccessful due to the indurated sediments requiring several weeks to break down in cold HF. Between 20-50g of rock were found to be the optimum quantity depending on the lithology of the sample. Intense oxidation of the majority of samples was necessary for meaningful palynological analysis. Extended oxidation times in normal Schulze's solution of the 'baked' and brittle palynomorphs had adverse effects on their preservation resulting in complete fragmentation of the palynomorphs present. This problem was resolved by the use of a *short sharp shock* technique using fuming Schulze's solution as the oxidising agent. The time period involved in this technique is as little as 1-15 minutes which is also advantageous in terms of time saved compared to other techniques.

Investigation of the suprageneric schemes in current use for the acritarchs and the chitinozoa has revealed inherent problems in adopting purely morphological schemes for biological groups whose affinity is, as yet, unknown to us. The unknown relative biological significance of morphological features has brought about a plethora of schemes from authors stressing the importance of particular morphological features of the individuals concerned. It is concluded that the adoption of such arbitrary classification schemes at the suprageneric level can only lead to frustration for future workers wishing to locate taxa in a scheme when that scheme is no longer in vogue. The acritarchs and chitinozoa are consequently arranged in alphabetical order in the present study pending further biological information as to the relative significance of the respective morphological features of the taxa included in these groups.

The taxonomy adopted at the generic and specific levels is based on observations using the light microscope. No SEM analysis are included in the study due to time constraints. Splitting of some of the rather broad 'bucket' species below the level of species has been attempted, e.g. *Diexallophasis denticulata*. The introduction of varieties within these broad species was attempted to enhance their biostratigraphic value. This approach has been found to be successful in several cases revealing certain morphological variants of broad species (e.g. *Diexallophasis denticulata* var. A , late Pridoli-early Gedinnian) apparently having restricted biostratigraphic ranges.

The biostratigraphic analysis of the palynomorph assemblages recovered from the samples studied was the major objective of the project. Assemblages from a broad stratigraphic interval, Ordovician-Devonian, have been investigated which have been grouped into 33 defined palynological associations. The initial aim, to produce a complete palynological zonation for the Ordovician to Devonian interval, was found not to be possible due to the limited samples available for the project. However, the adoption of an association concept enables the recognition of a series of biostratigraphically useful palynological associations with the stratigraphic gaps in the data acknowledged. The associations are defined on the basis of the presence and abundances of taxa recorded with the aid of cluster analysis of the assemblages generated by the computing package *Tilia.*

Within the Ordovician interval, 12 Associations are defined on the basis of the generally poorly preserved acritarch and chitinozoan assemblages. Dating of the associations is primarily by comparison with previous palynological studies from Northern Gondwana (e.g. Paris 1981, Elaouad-Debbaj 1984, 1986 & 1988), however, dated shelly macrofossil assemblages recorded in some of the Arenig, the Llanvirn and the Caradoc samples provide substantive evidence.

The Silurian samples selected for the study are all biostratigraphically constrained by the graptolitic assemblages recorded from them. Ten palynological associations are defined from this interval and comparisons are made with palynological assemblages previously recorded in the literature, e.g. Paris 1981, Hill & Molyneux 1988, Le Herrise 1989.

The Devonian assemblages are generally well preserved and are composed of diverse acritarchs, prasinophytes, chitinozoans and spores. Eleven associations are defined through this interval, the ages of which are largely defined on the basis of comparison with the well established spore stratigraphy (e.g. Loboziac & Streel 1989, Richardson & McGregor 1986, Steemans 1989). Previous Lower and Upper Devonian microplankton records were also found to be useful for comparison, e.g. Deunff 1980, Playford 1977, Wicander 1983, Martin 1981 & 1984, as were the Lower to Middle Devonian chitinozoan studies of Paris (e.g. 1985, 1988) and co workers. In addition to these microfossils, rich graptolite assemblages in some Lower Devonian samples provide independent evidence for their age.

The palaeoenvironmental model of Dorning (1987) has been applied to the palynological assemblages recorded. Taxa have been grouped into broad morphological categories and the trends in the relative abundances of these morphogroups have been illustrated and analysed using the *Tilia* package. A general interpretation of the environment of deposition from the palynological data, in conjunction with the lithological evidence, can be drawn (i.e. basinal, outer shelf, inner shelf, littoral). However, one must beware of interpreting poorly preserved assemblages, such as those recorded from the Ordovician in the present study, in which selective preservation of the palynomorph groups can be misleading.

The analyses revealed evidence for marine deposition in all of the formations studied from the Ordovician through Devonian and it appears that varying continental shelf settings of deposition prevailed for much of this interval. However, during the Llandovery and the Wenlock (Carbonaceous Shale Formation) there appears to be a notable change in the gross palynological composition with thick walled spheromorphic acritarchs totally dominating the low diversity assemblages. The high abundance of amorphous sapropelic kerogen and the fine shale lithologies corroborate the palynological evidence for deep basinal, low energy deposition through this stratigraphic interval. A similar trend is evident in the Frasnian (Anou Smaira Formation) with abundant tasmanitids suggesting a basinal depositional setting at this level. It is believed that such fluctuations in sea level in Morocco are largely eustatically controlled given the relatively stable tectonic situation prevailing through the Ordovician to Devonian interval.

Chapter 10. Further work.

The broad nature of the study undertaken has revealed much scope for future palynological work in the Anti Atlas region and in the North African-Middle Eastern realm.

With regard to palynological techniques, despite the success of the processing procedure adopted here, I feel there is much potential for processing of problematic Palaeozoic samples using the microwave technology currently undergoing research at Sheffield University. This rapid breakdown and oxidation method would appear to have considerable advantages for indurated and thermally mature samples which are common from the Palaeozoic and should enhance palynological recovery.

There are many taxa recorded in the present study that remain in open nomenclature primarily due to the need for further detailed investigation of the taxa before I consider them to be worth formalising in the literature. The further investigation prior to formalisation of these taxa will involve biometrical analysis and, in some instances, particularly with the chitinozoans, SEM analysis.

Within the Ordovician of the Anti Atlas, detailed sampling of outcrop sections additional to those studied by Elaouad-Debbaj (1984, 1986, 1988) would fill gaps in the existing data. Emphasis should be placed on sampling of the oolitic ironstone deposits reported to be widely extensive over Northern Gondwana through the Ordovician system (Young 1989, pers. comm. 1992; Paris pers. comm. 1992). Investigation of the age and extent of such deposits would enhance our understanding of the genetic relationship of the Ordovician sequences in this realm. It would also give insight into the eustatic fluctuations in sea level for this period given that the region was relatively tectonically stable at that time.

A study of samples collected across the Ordovician-Silurian boundary in North Africa would be informative as to the apparent climatic effects on the microplankton due to the well documented glaciation that occurred during that time. The considerable data base that has now accumulated on the effects on the microplankton across the Quaternary glaciations (e.g. Harland 1983, Dale 1976, Wall *et al.* 1976) would make for interesting comparison.

As with the Ordovician, there are several gaps in the data from the Silurian interval in the Anti Atlas that need to be addressed. The prolific graptolite assemblages present in sediments of this age provide considerable incentive for further biostratigraphical work on the apparently near complete Silurian succession. The graptolite assemblages themselves are largely unpublished from the Anti Atlas (Destombes, Hollard & Willefert 1985) and several new lineages are apparent from the assemblages incorporated into the present study that were analysed by Dr. R.B. Rickards (pers. comm. 1991).

Previous biostratigraphic palynological investigations of the Devonian strata of Northern Gondwana have their age interpretations based on comparisons with other palynological investigations which equally lack independent age data from other biostratigraphically useful groups. Goniatite dated sections are present in the Anti Atlas in carbonate facies (G. Wade pers. comm. 1990) which, to date, have been avoided by palynologists due to the relatively low yields of palynomorphs per gram from such sediments. Palynological information from such independently dated sections would be invaluable to resolve some of the conjecture involved in the dating of Devonian sections in Northern Gondwana.

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