Geology and palaeontology of the Telychian (Silurian), reservoir formation of the North Esk inlier, near Edinburgh, Scotland

Thesis

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GEOLOGY AND PALAEONTOLOGY OF THE TELYCHIAN (SILURIAN), RESERVOIR FORMATION OF THE NORTH ESK INLIER, NEAR EDINBURGH, SCOTLAND.

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BSc (Hons) Edinburgh.

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Abstract

The North Esk inlier is one of several outcrops of Silurian sediments in the Midland Valley of Scotland. The lowermost sediments exposed are the Reservoir Formation, and these have been studied in detail. These sediments are interbedded shales and siltstones, deposited as the deepest part of a regressive sequence. The sediments are suggested to have been deposited predominantly by storm processes in an outer shelf or marginal basin environment, and not by turbidity currents into a deep ocean basin as previously suggested. Decreasing water depths can be traced by changes in sedimentary structures and in the animals and their bioturbation traces fossilised therein. A correspondence between the graptolites preserved in the North Esk group and models for distribution of graptolites in depth related zones is observed and is compared with other taxa thought to be indicative of water depth. Cycles of sedimentation are identified and also record fluctuations in the water depth.

The NEI sediments were deposited in the remnant Iapetus ocean basin at the time of a three plate collision. The sediments are currently sub-vertically oriented. Emplacement at this attitude was probably associated with thrusting at depth, in turn related to strike-slip movement of separate terranes along the southern margin of Laurentia. Minor small scale bedding-parallel thrusts are evidence of this at the surface. The North Esk inlier sediments were probably part of a terrane now of unknown extent. Minor folding, local thrusting and faulting, indicating one major phase of tectonic deformation are described. Compressional kink folding took place, with pressure applied obliquely to foliation (bedding). Areas of chevron folding and kink bands correspond to deformation along Caledonian trends. The northern boundary of the NEI, previously thought to be fault controlled, is reinterpreted as the regional unconformity at the base of the Upper Old Red Sandstone. Metabentonite horizons are identified. The volcanic source of these ash falls is suggested to have been of calc-alkaline character, and an increase in alkalinity of the volcanic source in Scotland during the Telychian is suggested.

A study of the fossils preserved has led to a review of late Llandovery graptolite biostratigraphy. A biozonal scheme based on that currently in use in other parts of the world, particularly in Bohemia, is introduced. Three Llandovery graptolite biozones are recognised between the *crenulata* biozone and the base of the Wenlock. The Reservoir Formation sediments are correlated with the middle of the *O. spiralis* graptolite biozone, upper Telychian. Comparisons are made with the biozonal schemes for other fossil groups, and the *P. celloni.* to *P. amorphognathoides* conodont biozone boundary is accurately identified within the Gutterford Burn sediments, facilitating accurate correlation between graptolite and conodont biozonal schemes.

Revised taxonomic descriptions and notes on a number of species of graptoloid and dendroid are presented. Further work on the dendroid *Dictyonema pentlandica* has identified normal and abnormal dendroid growth patterns. The response of dendroids to trauma, and disease are described and possible uses of dendroids as palaeoenvironment and palaeocurrent -direction indicators are discussed. A model for the secretion of dendroid holdfasts by mobile zooids distributed across the sediment surface is suggested, and possible dendroid reproductive processes are outlined.

A new technique of producing graptolite "Profile Plots" is introduced. These plots are used to identify, characterise and compare different graptoloid species, where a number of species with similar thecal structure are known. The rate of expansion of the stipe at different levels within the colony and the thecal size can be compared, and characteristic profiles plotted for each species. This technique has possible future uses in the computerised identification of graptolites.

"....I hope to add one drop to the bucket of geological truth, yet far from full, many thousand of such drops being required ere the geological record is complete." (Haswell 1865).

Chapter 1.

Introduction

1.1 General Introduction

The North Esk inlier is a small outcrop of Upper Llandovery to Wenlock (Silurian) sediments, about 5.8 square km in total area, surrounded on all sides by Devonian sediments (see figs. 1.1 and 1.2). It is one of a group of three in the Pentland Hills, which lie at the eastern end of a chain of inliers running westwards across Scotland and Ireland, and possibly into Newfoundland (see figure 1.3). The North Esk inlier sediments are unconformably overlain by Lower Old Red Sandstone (LORS) coarse conglomerates to the south and Upper Old Red Sandstone coarse sandstones to the north. This small outcrop of sediments has been intensively studied over the years (see chapter 2), mostly because of the abundance of well preserved fossil invertebrates of almost every type occupying the Silurian oceans in the Late Llandovery.

The sediments are presently observed to be lying nearly vertical, with some tectonic folding apparent, and some hill creep (see chapter 5). The general strike direction of these sediments is north-east to south-west. The younging direction is consistently to the North West, without appreciable unconformity or repetition by folding. The sequence is, however, cut by very many small faults, mostly with a throw of just a few metres, which hampers lithological correlation.

As described by Haswell (1865:19) the sediments are very varied,

> "The lithological character of this series of the silurian formation is very variable. They are composed of almost every variety to be found in sedimentary rock. We have hard sandstones, soft shales, mudstones as soft as chalk, which cut easily with the saw or knife. Some are brown, some yellow, gray, reddish, and bluish. Some few beds are hard and suitable for building stone, while others are soft and friable. In fact, you have in this section of the silurian formation such a variety of sedimentary rocks as would point to considerable changes in circumstances and conditions under which they have been deposited."

Within the outcrop of the Silurian sediments, exposure is very poor (fig 1.4), restricted to stream sections, and what can be exposed by excavation in the field. The area is listed as an S.S.S.I, and therefore collection is restricted. Some of the localities have been extensively quarried in the past, such as the Gutterford Burn eurypterid horizon (Laurie 1892-1899), and due to backfilling of these localities and complete quarrying out of lenses of fossils, it is not possible to observe the sediments in situ. Other localities have extensive scree slopes, from which specimens can be obtained.

The sediments of the North Esk inlier have a very high weathering rate, particularly the more calcareous and fossiliferous sediments. Therefore many of the fossils are only known from moulds. Some are excellently preserved however, and in particular some of the graptolites are preserved in three dimensions. Some of the dendroids are well enough preserved in 3-D, to identify the thecal structure.

Throughout this thesis, a few abbreviations are used. In particular, the North Esk Inlier is abbreviated to "NEI", and the Pentland Hills are referred to as "PH". One locality is the focus of much of this work, and it is referred to as the "Gutterford Burn Limestone Bed" locality, "GBLB" hereafter. This locality is shown on all maps included herein, and was the focus of extensive excavation to expose fresh sediments (fig 4.11.a), allowing the logged section to be measured (see chapter 4). The name "Gutterford Burn Limestone Bed" is actually a misnomer, because at this locality there is a series of calcareous horizons. Many have a calcareous matrix and some with abundant, still calcified fossils preserved. They are,ver not limestones but calcareous siltstones and will be discussed in more detail in Chapter 4. The name "Gutterford Burn Limestone Bed" has been retained for historical reasons.

During the (prolonged) course of the study of this project, a number of sections of the work contained herein have been published in advance of the completion of the thesis (Bull 1987, Bull 1991, Bull 1995 in press, and Bull and Loydell 1995 in press). Where sections have been published, this is marked in the text. Collaborations with other authors have also been undertaken (Loydell, Bull and Storch 1992) based on work contained herein, but not directly included in the thesis. It is planned that further sections of the thesis should be developed in the future, such as a joint project integrating the biostratigraphy of the graptolites (Bull), conodonts (Dr. H. Armstrong), corals (Dr. C. Scrutton) and certain brachiopods (Dr. M. Parkes).

1.2 Objectives

The aim of this study was to identify the age of the sediments from biostratigraphy and interpret the depositional environment of the Reservoir Formation of the North Esk Inlier, Pentland Hills, near Edinburgh. This commenced with the study of the dendroids and graptolites, looking at their function and palaeoecology, and biostratigraphy, and moved on to correlation with other taxa and other areas. Work on the stratigraphically higher Formations by Gary Robertson at Edinburgh University, was already nearing completion (Robertson 1989), when this project commenced.

1.3.1 Location

The North Esk inlier forms a tract of gently undulating countryside, situated approximately 20 km south west of the centre of Edinburgh, and just over 1 km north west of the village of Carlops. It is bounded by Grid References NT 1256, NT 1260, NT 1856 and NT 1860 of sheet 15, Midlothian District. NEI sediments are exposed in stream sections of the North Esk River, (north and south of the Reservoir), the Monks, Gutterford, Deerhope, Fairliehope, Henshaw and Lynslie Burns, the Lyne Water, tributary streams known as the

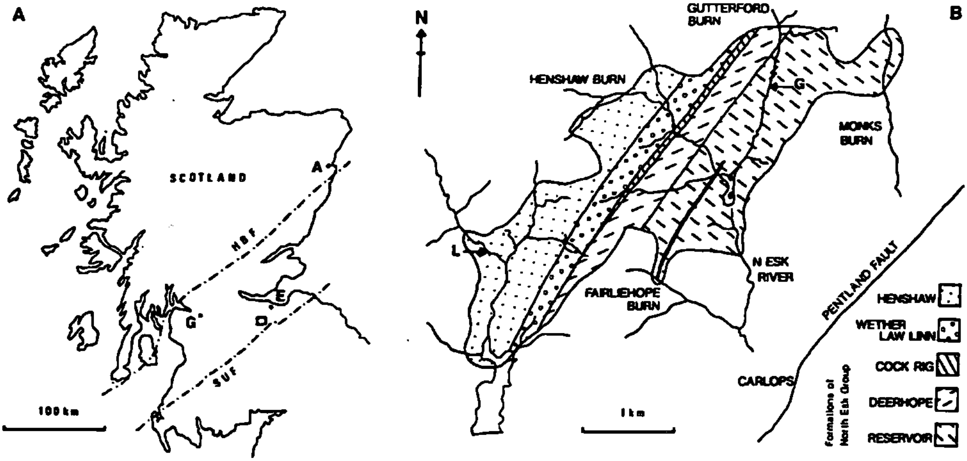

FIG 1.2 A: Location map, with box marked to show position of North Esk Inlier (enlarged as map B) relative to the Midland Valley of Scotland. E : Edinburgh, G : Glasgow, A : Aberdeen, HBF : Highland Boundary Fault, SUF : Southern Upland Fault.
B: Map of outcrop of the North Esk Inlier, Pentland Hills. Rocks lie sub-vertically and young consistently to the north-west. Important localities are marked as, L : Lyne Water Fish Bed, G : "Gutterford Burn Limestone Beds" locality.

Wether Law Linn and that referred to herein as the "Folded Gorge" (NT 155577), and along the shores of the North Esk River and the north shore of the Baddinsgill Reservoir. The two other Silurian inliers in the Pentland Hills, the Bavelaw Castle and Loganlee inliers have not been studied in detail during this project, and are described more thoroughly by Robertson (1986).

1.3.2 Access

The route to the NEI has been described in the past, and never so poetically, nor with as much social comment as by Haswell in 1865 when he was encouraging fellow members of the Edinburgh Geological Society to visit the area:-

> "Suppose we start from the North British Railway station some fine summer morning, by the first train, having taken tickets for Coalyburn, one of the stations on the Dolphington branch, suitably provided with a chipping hammer, a picking hammer or small pick, a compass and clinometer, a good large haversack, two or three old Daily Reviews, - remember Scotsmans do not answer so well as that paper is too hard, and might be apt to crush some of the delicate forms we are likely to meet with in the course of the day." (Haswell 1865:14).
>
> "The village of Carlops through which we pass, was one of the stages in the coaching days on the mail route to Dumfries. It contains a church and two inns, at one of which, the Habbies How Inn, I stayed a few days; and I can recommend any one wishing to spend a few days in this neighbourhood to take up their quarters here. If they do they will find a clean, comfortable house, and an attentive landlady." (Haswell 1865:15).
>
> "Taking Carlops as the starting point of the geological part of the excursion, and having got quit of all exuberance of spirits during our walk over from Coalyburn, we will find near the north end of the village a little picturesque stream, which tumbles over rocks in a romantic looking little glen, past the side of the mill. Here we begin carefully to observe and take note of the geological position of the beds over which we pass." (Haswell 1865:15).

The access today is a little easier. Alas the trains no longer run on the Dolphinton branch, but adequate public transport is available to the village of Carlops, on the A 702 (T) from

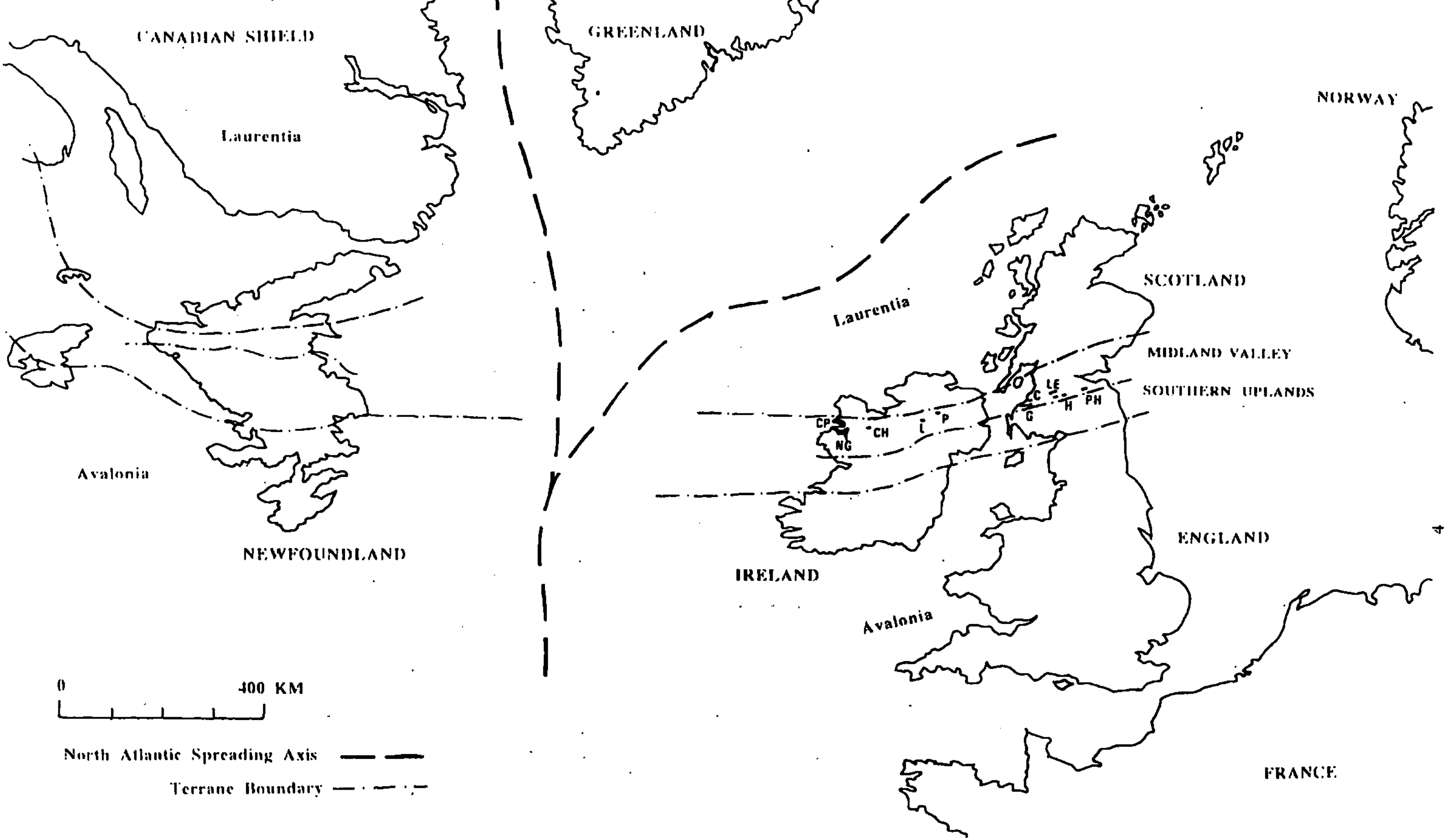

Figure 1.3. Map of the Midland Valley inliers of Scotland and Ireland and the proposed extension of the terrane into Newfoundland.
PH : Pentland Hills, H : Hagshaw Hills, C : Craighead, LE : Lesmahagow, G : Girvan, CH : Charlestown, L : Lisbellaw, NG : North Galway, CP : Croagh Patrick, P: Pomeroy ;
S.U.F. : Southern Upland Fault; H.B.F. : Highland Boundary Fault. (After Colman-Sadd *et al.* 1992 and Doyle *et al.* 1991)

Edinburgh. Ample car parking space is available within the village (admirable refreshment can also still be obtained at the Allan Ramsay Inn in Carlops). Access to the main part of the outcrop around the North Esk Reservoir can be made by two routes. Firstly following the course of the North Esk River as extolled by Haswell (1865:15), and inspecting the LORS conglomerates on the way to the NEI, or by following the (1.5 km long) track past Fairliehope farm to the North Esk Reservoir keepers cottage. This track has been partially surfaced for only half of its length. It is not suitable for low axled or long vehicles due to tight bends, steep slopes and a very uneven surface.

Exposures in the Monks Burn can be accessed by walking from the Gutterford Burn, over Green Law hill to the east from the North Esk Reservoir, or more easily by stopping at Nine Mile Burn and walking up the Monks Burn from there. Exposures at the Baddinsgill reservoir can also be accessed from the main exposure at the North Esk Reservoir by walking to the south west over The Mount from the top of the Deerhope Burn, or along the farm track from West Linton (see fig 1.2). Local farmers are very welcoming and helpful, allowing access to all localities freely. They are also wary of unscrupulous fossil collectors so it is worthwhile introducing yourself to the farmers when passing through their properties. The main NEI fossil collecting localities are to be found at the "Gutterford Burn Limestone Bed" Locality, at grid reference NT 1589 5918, in the Wether Law Linn at grid reference, NT 146 585, the Deerhope Coral bed, at grid reference NT 1471 5806, and the North Esk River at grid reference NT 148 590.

The close proximity of the NEI to Edinburgh, equipped as it is with such an excellent Geology Department in the University, and such an active Geological Society, has meant that the area has been extensively studied over the years. Some of this work has been by experts in their fields (Davidson 1868; Clarkson and Howells, 1981) and has added greatly to science. Some valuable studies have been undertaken by groups or interested individuals with an amateur involvement. Some very interesting specimens have been discovered by many groups on undergraduate field trips and mapping projects. Unfortunately the area is also prone to visits by the less scientific, professional fossil collector.

It should be noted that the area immediately surrounding the North Esk Reservoir has been designated a bird sanctuary, as it has a large breeding population of gulls. Access is denied to the shores of the Reservoir and to the lower reaches of the streams to the north of the reservoir from mid March to mid August (anyone ignoring this is highly likely to be attacked by the gulls) see fig 1.5.a.

1.4 Techniques of Study.

An enlargement of the existing maps of the Gutterford Burn was made to assist accurate mapping, which was proving difficult due to the thinly bedded nature of the sediments of the Reservoir formation. Initially this involved making accurate magnified drawings as enlargements of the aerial photographs using a camera lucida microscope. The edge effect distortion of this method proved fairly inaccurate, and when applied in the field it was seen that the stream had changed course slightly in a number of places. Therefore a further map was constructed, using a tape measure and compass to take bearings of stream direction and position of exposures relative to the stream. Each exposure of sediment was then marked on this map.

Each locality was recorded by sedimentary logging, and comparisons were made between each locality, to find how laterally continuous each sedimentary unit is, to identify mappable units and therefore to ascertain the thickness of the sequence. As the average bed thickness is only a few centimetres, and alternations between shale and siltstone can in some places be observed on a millimetre scale, these logs became quite lithologically detailed, although very few sedimentary structures are observed in situ. A detailed map was therefore produced (Fig 1.1) and sedimentary cycles identified (see chapter 4).

One locality was studied in more detail, the "Gutterford Burn Limestone Bed" (GBLB) locality. Excavation (by pickaxe and shovel, in some places requiring the removal of a metre thickness of fine scree on a steep slope) to expose more sediment was undertaken. The sequence was collected extensively both at a vertical section (12 metres long) which was logged, and along strike for up to 25 metres from this logged section. The sediments exposed at this locality are slightly affected by folding, and instead of the general vertical position for these strata elsewhere, they are slightly overturned. The younging direction remains constant, but these strata are physically overturned. Therefore the base of the logged section is at the top of the slope at this exposure. The sediments of the logged section were collected in detail, many thin sections were made (by the author) to analyse the sedimentary structures, rock fabric and fossil content.

Fossils were collected as often as possible. Due to the very rapid weathering rates in this area, newly exposed calcified sediment leaches out considerably within a few months. Within 6 months the specimen becomes mould material, in a further 6 months the rock matrix will crumble away and within two years the specimen will resemble muddy clay (see figure 5.2B). Therefore specimens were collected as fresh as possible. The exposed sequence, dug during the summer of 1989, is nearly completely covered over again. In part this was due to the excavations of Dr. N. Clark (Hunterian Museum), who dug out the starfish horizon 2 m up into the logged section, and allowed the debris from his excavation to fall into the existing trench.

The original intention was to collect and study in detail all of the fossiliferous material from the Reservoir Formation. This proved overambitious, and whilst collections were made of other material, some thin sections, latex moulds and photographs were produced and the expert opinion of other workers sought, this project has covered only the graptolites and dendroids in depth. In particular, good collections of new specimens of starfish and echinoids exist, and these are shown in figures 10.1 to 10.5. All specimens other than

b

a. General view of North Esk Reservoir and dam, looking due north with the mouth of the Gutterford Burn on the right.

b. Glacial erratic boulder from the Gutterford Burn, visable on air photos. Thin inter-bedded silt and shale.

graptolite material were dusted with ammonium chloride using a pipette and then photographed. The graptolite-bearing slabs were immersed in ethanol in a shallow bowl, with the specimens surrounded by marbles to displace the ethanol.

The extensive collections of the Royal Scottish Museum and the Grant Institute of Geology, Edinburgh University were consulted to supplement new collections. Many exquisitely preserved unregistered specimens of dendroid were discovered in the Royal Scottish Museum, and form the basis of much of this study. Graptolite material was studied using a camera lucida microscope, to produce line drawings. Some specimens both of dendroids, and of "Dictyocaris" (see figs. 10.27-28), were also viewed using a Scanning Electron Microscope.

1.5 Outline of thesis

Within this thesis are 10 chapters.
1) serves as an introduction to the area, the methods of study, techniques used throughout the thesis, and describes the general geology of the area.

2) Presents a brief historical review of past research in the area.

3) Covers a biostratigraphical review of the area and new results obtained by correlation of a number of fossil groups.

4) Covers general geology. The environment and conditions prevalent at the time of deposition of the sediments is discussed, and is based on field and laboratory (thin section analysis) sedimentological observations. Various facies are described. Igneous activity as evidenced by the metabentonite horizons identified, is also discussed.

5) A review of tectonic structures observed in the field, linked in to overall tectonic models for the Midland Valley of Scotland and Ireland in the Silurian.

Chapters 6-9 represent a body of work based on the study of graptolites.
6) Graptolite physiology, covering a review of the current controversies, the state of knowledge of graptolite reproduction and dendroid holdfasts, and new observations made during this research.

7) A study of the growth and regrowth patterns of one dendroid species.

8) A review of benthic graptolites and graptolite faunal provinces. Conclusions regarding the depth of water at the time of deposition of these sediments is also drawn from this work.
This project has involved extensive study of the structure of dendroids and the comments contained herein are based on the author's own observations. Section 8.1 was published as an introduction to the benthic graptolites (Bull, 1991) and whilst some of the comments made may seem elementary, they have not been detailed elsewhere.

9) Contains the systematic section of the thesis, a review of old and new methods of study, taxonomic descriptions and a terminology section.

10) Illustrations of other taxa found during this study.
Some additional taxonomic descriptions and comments, including ichnofossils and *Dictyocaris*.
Appendices contain the raw data for the measurements of various graptolites.

Figure 1.5 a) View looking north across the North Esk Reservoir. Note gull infested island in background.
b) Thin interbedded siltstone and shale typical of Reservoir Formation sediments. Grid ref. NT1585 5897. Lens cap 57 mm diameter.
c) Pale streak of clay indicating the presence of a metabentonite, Grid ref. NT1603 5940, field photo.

Figure 1.5


A
NORTH ESK
WILDLIFE REFUGE
Please – No Access
Mid March to Mid August
B
C

1.6 Summary of Geology

The North Esk inlier exposes generally highly fossiliferous sediments of upper Llandovery to lower Wenlock age, the lower portions of which can be accurately dated by both graptolite and conodont Biostratigraphic schemes. The succession has been recognised as the North Esk Group, and divided into five Formations, which were formally defined by Robertson (1989) (see fig 3.6). A copy of Robertsons (1989:139) palaeoenvironmental interpretation model is given in fig 4.3a.

The sediments record a conformable regressive succession. The base of the sequence is not exposed. The Reservoir Formation sediments are interbedded thin silts and shales (fig 1.5.b). Previously (Robertson 1985; 1989), they were considered to have been deposited as deep ocean-plain (or in non channelised areas of a fan fringe), distal turbidites. Reservoir Formation sediments are reinterpreted here as having been deposited very rapidly by distal to intermediate storm sedimentation on either a low energy, mud dominated shelf, or the infilling of a shallow marginal basin sea. Periodic fluctuations in sea levels are also suggested to have occured at this time. These are overlain by marine-fan facies sediments of the Deerhope formation, representing overbank deposits, and the Cock Rig formation representing fan feeder channels. This was overlain by the Wether Law Linn Formation formed by a shallow marine barrier complex, deposited and modified by (proximal) storm and fair weather processes and repeatedly colonised. The upper member of the Wether Law Linn Formation is interpreted as a restricted lagoonal environment overlain by the Henshaw Formation terrestrial alluvial fan facies (Robertson 1985; 1989).

Correlation between the numerous Midland Valley inliers can be made by the presence of distinctive conglomerate horizons within the Henshaw Formation (Wellman and Richardson 1993). Metabentonites have recently been recognised within the NEI sequence (Batchelor and Clarkson 1993), and further such horizons have been identified within the Reservoir Formation and subjected to geochemical analysis (see chapter 4).

Throughout the sequence, the sediments yield some excellent fossil specimens. In the Reservoir Formation, there are numerous horizons with shelly material, some fresh, some badly abraded. Also there are a number of 'exceptional preservation' horizons, which yield exquisitely preserved specimens of eurypterids, dendroids, graptolites, crinoids, starfish or echinoids. Associations of biostratigraphically significant fossils within the Reservoir Formation, allows excellent, accurate correlation with other areas and biostratigraphic schemes. The Wether Law Linn Formation is also highly fossiliferous, and community associations have been identified and discussed by Robertson (1989).

Further studies of certain fossil groups have resulted in; accurate refinement of the biostratigraphy for the area and for the British upper Telychian (chapter 3); an insight into graptolite palaeoecology based on the interpretation of regrowth structures of dendroid graptolites; a review of graptolite physiology; and some taxonomic revision (chapters 6-9).

The sediments were deposited at the end of a period of major tectonic activity (Caledonian Orogeny), following the closure of the Iapetus ocean. They were emplaced by subduction related, sinistral strike-slip motion along the boundary between two plates. Considerable motion is considered to have taken place, and a number of separate terranes have been identified along this boundary. The basin of deposition for the NEI may have been a pull apart basin controlled by the strike-slip motion. Surface examples of en-echelon folding and thrusting may echo patterns at depth. This may have contributed to the upending of the sediments to their current sub vertical position, and to the LORS alluvial fan conglomerates being domed unconformably over the Silurian sediments. Later tectonic activity, has left the Pentland Hills lying as a block emergent from the surrounding, largely Carboniferous age basin deposits (fig 5.4.b).

The current land surface is the result of glaciation, smoothing and rounding the hills, carving a window through the overlying LORS sediments and exposing the Silurian sediments beneath. Glacial action also scoured out the hollow now occupied by the North Esk Reservoir and creating the topographic highs now forming the islands within the reservoir. Substantial quantities of glacial till and soil, now cover the majority of the area, and some large glacial erratic boulders form useful landmarks, particularly in the Gutterford Burn (fig 1.4).

Chapter 2.

2.1 History of Research

Although these sediments have been studied since as early as 1813 (Davidson, 1868) interest at first was not great until fossils were found. The earliest fossil finds were made by Maclaren (1838) but descriptions were not published until Salter's contribution to the earliest Survey Memoir to the Edinburgh district (in Howell and Geikie 1861), wherein only a few of the fossils are represented, mostly those from higher up in the succession. It is suggested that Salter possibly collected from just a few localities, making only one traverse through the section. The same memoir contained a rough stratigraphy, and it seems that this was enough to fire the members of the Edinburgh Geological Society into action.

In 1865, Haswell published a charming report of the Geology of the Silurian Rocks of the Pentland Hills, acting as a field or excursion guide to the area, extolling its virtues and encouraging others to visit and commence work on "..this most interesting subdivision of the siluria formation" (Haswell 1865:47). Evidently others had already started work there, as Haswell is lavish in his thanks to Mr. Henderson among others, for allowing him to inspect their collections of fossils.

Haswell's comments can be seen in the light of current stratigraphical and tectonic models to have been very far reaching and incisive. He observed-

> ".....the great number of species found in these beds which are not found in the silurian beds of England. No less than twenty five of the fifty two species found in the Pentland Hills are not found in the typical district of Siluria".(Haswell 1865:46).

He also noted that these sediments-

> "....have probably formed part of a different and separate basin of deposit, and have been divided from the English basin by an isthmus, something in the same way as the Gulf of Mexico is separated from the Pacific Ocean by the Isthmus of Darien, thus rendering it very difficult for species living in one basin to travel into the other." (Haswell 1865:46).

He also concluded that this sequence-

> "....has most probably been deposited during the same period as the Wenlock shale." (Haswell 1865:46).

Between 1865 and and 1900 the pages of the *Transactions of the Edinburgh Geological Society*, were aglow with reports of the geology of the area, with lists and descriptions of fossils, refined stratigraphy, satisfactory maps of the whole inlier, and reports of major quarrying undertaken to reveal exquisite eurypterid specimens (Brown, 1866; 1867; Brown and Henderson, 1867; Davidson 1868; Haswell , 1865; Henderson 1866, 1867, 1869, 1874 a,b, 1880; Henderson and Brown 1867; Lapworth 1874; Laurie 1892a-c, 1894, 1898, 1899). A major collection of fossils was made by Mr. Hardie of Bavelaw Castle at this time, and is now lodged in the collections of the Royal Scottish Museum.

Sadly Mr. John Henderson (see fig 2.1) died at the turn of the century, and his obituary (Goodchild 1900) is a cutting reminder of the divisions of society at the time. His work was clearly regarded by the establishment of the Edinburgh Geological Society with scorn as he had done his social standing no good whatsoever by daring to disagree with his "betters". It is particularly pleasing to note that Mr. Henderson's ideas were much closer to the agreed modern stratigraphy than those of Dr. Geikie with whom he disagreed. The Geological Survey completely remapped the area (Peach and Horne 1899; Peach et al. 1910), gave comprehensive cross sections (although invoking isoclinal folding to account for the vertical position of the strata), and gave a full description of the geology.

Fig.2.1 Mr John Henderson. (From Lamont 1943)

It seems that with the passing of Mr. Henderson, interest in the area waned for many years. Work obviously continued to some degree in the area as major constituents of the starfish fauna described by Spencer (1914-1940) came from the NEI; Størmer (1935) described Dictyocaris from the area as crustacean carapace; Lunn (1924) gave the first descriptions of intrusions occurring in the PH (work which was continued by Cockburn in 1952), and Jones (1928) made comment on a brachiopod from the area.

Interest was rekindled by Dr. Archie Lamont, who published his first work on the area in 1942. Interestingly, Lamont (1947) notes that Henderson had made extensive, informed faunal notes on the NEI, but that sadly they were pulped during the war, so obviously he had been able to consult these notes, at least partially, prior to their loss. Extensive jottings made by the late Dr. Lamont on the plates of Dr. Haswell's publication (1865) have been preserved and make very interesting reading. Lamont (1943) produced descriptive and quite imaginative notes for those attending the International Geological Congress, which was presumably the congress (18th Session, Great Britain 1948), for which he wrote the article proposing the new division of the Silurian System in Scotland (Lamont 1952), discussed in chapter 3. Lamont (1942) suggested deposition in close proximity to an island arc, in fairly shallow conditions and also close to a supply of fresh water because of the presence of eurypterids. Lamont produced many papers describing the faunas of the PH (Lamont, 1943, 1947; 1949; 1952; 1954; 1955; 1961; 1978), and the stratigraphy (1947).

Lamont continued to publish privately until his death in 1985. His latest works were restricted to papers on agate veins found near to his home in Carlops (Lamont 1982), as his health had failed, keeping him from the hills, close though they were. His extensive collections are now in the stores of the Royal Scottish Museum awaiting funding to allow this vast resource to be properly catalogued and utilised. Many Edinburgh University geology graduates, who visited the NEI on class field trips in the 70's and early 80's will forever have etched in their minds the picture of the lone figure of Dr. Archie Lamont with his flowing beard, selling copies of his journal to them as they ventured out from the bus.

The area was remapped by the Geological Survey and published (Mitchell and Mykura 1962) as the third edition of the Memoir, the Geology of the Neighbourhood of Edinburgh, explanation of one inch sheet 32. More recently a discussion of the Geology has been included in an account of the Midland Valley of Scotland in the British Regional Geology series (Cameron and Stevenson, 1985:15-17).

The next major integrated study was made by Tipper (1974; 1975; 1976). Careful sampling enabled three animal "Communities" to be described in the Wether Law Linn Formation. This work was based on statistical analysis and new sampling techniques were introduced. These sampling techniques were continued and modified by Robertson (1985; 1989) who refined the lithostratigraphy greatly, formally defining five formations and three members within the Wether Law Linn Formation. Robertson's main contribution however, was the again meticulous sampling and statistical analysis, resulting in detailed taxa distribution diagrams and the description of three animal associations. Robertson also carefully excavated the base of the Henshaw Formation, and was able to identify the shoreline, and recognised periodic marine incursions into the predominantly terrestrially derived sediments of the Henshaw Formation. Robertson (1985) also produced a comprehensive taxonomic review of the bivalves and gastropods, and some other taxa. This has sadly remained unpublished.

Tipper (1976:19) also was the first to identify the volcanic origin, and recognise the importance of, the "ash band" horizons in the area. These metabentonites form important time lines that can be correlated for long distances across the inlier. The geochemistry of the metabentonite horizons from the Wether Law Linn Formation has been studied by Batchelor and Clarkson (1993), but during this present study, further horizons have been discovered and analysed, and are described herein (see chapter 4).

Both Tipper and Robertson were conducting their research at times of copious activity in the sedimentological world, particularly in the interpretation of thin bedded shale and siltstone sequences. During the early 70's a number of papers appeared describing contourites (for review see Stow and Lovell, 1979), and Tipper (1974:28) invoked the corresponding mechanism for the deposition of the Reservoir Formation sediments. When Robertson was scouring the sedimentological journals in the early 80's, the turbidite model had gained favour, and the Reservoir Formation sediments fitted neatly into the deep marine distal fan facies descriptions available to him. Since that time, storm generated deposits have become the mode of deposition generating an avalanche of papers in the journals of the day (see chapter 4 for references) and in this volume, storm generated horizons are at least considered to have contributed to the deposition of the Reservoir Formation. It is tempting to suggest that the depositional model for the Reservoir Formation is as much subject to the vagaries of fashion as the movement of ocean currents, however it is in fact due to increasing availability of information that the models can thus be constantly refined. Each model takes into account more and more diverse information, such as water depth information implied from work on graptolites. It is with increasing confidence that each model is defined as a modification of the previous suggestion, rather than as a completely new model.

Other studies conducted in the area have focussed on individual fossil groups. Nitecki (1971) described the calcareous alga *Amphispongia oblongata.* The trilobites have also been described in detail (Norford, 1973; Clarkson et al. 1977; Clarkson and Howells, 1981), and were the first fossil group to give firm evidence for the suggestion made by Haswell (1865) that the fauna was separated by a land mass from oceans existing further south. Clarkson and Howells (1981) suggested an elongated ocean basin connected laterally to the sites of the other Midland Valley inliers and to Scandinavian regions in the East. The wide range of species present and the very good preservation of fossils from the NEI has attracted much attention. Some have felt the need to invoke exceptional conditions in the Pentlands, to explain the richness of the fauna present. Palmer (1991) suggested that as the dendroids are found with an exceptional fauna, this implies that they were not restricted to shallow, quiet water meadows, a theory not accepted here (see chapter 6).

Brower (1975:633), in his description of the crinoids, notes the presence of evolutionary relicts, three of the crinoids (*Macrostylocrinus silurocirrifer, Ptychocrinus longibranchialis,* and *Dendrocrinus extensidiscus)* having died out elsewhere prior to the late Llandovery and one species found in the NEI *(Pisocrinus campana)* appears dwarfed. The crinoids present led Brower (1975:633) to suggest normal marine, subtidal, conditions at the time of deposition, with some influxes of brackish water possible, and overall a rapid burial rate, and fairly quiet conditions. The echinoid *Aptilechinus caledonensis* was described by Kier (1973). New specimens of this echinoid are figured herein. In particular, some of these specimens are present in orientations not known previously, which may suggest further work is possible on this species, along with new starfish finds, also from the same locality. An integrated study and comparison with the new starfish, dendroid and crinoid finds made by Ward (1989:152) in the "Rough Neuk Starfish Bed", may be possible.

Beautifully illustrated accounts of the eurypterids were published by Waterston (1964;

1979). He described and illustrated the adaptations of the stylonuroid eurypterids to bottom dwelling, requiring them to have walked along the sediment surface or partially buried themselves in the mud. Waterston (1979:315) also suggested a shallow water, near shore environment would be necessary to support the *in situ* fauna of scorpions that he described. Further reference has been made to the Gutterford Burn eurypterids (Philip Manning, presentation at Pal. Ass. conference, 1993), and it has been suggested that they were the first animals to venture out of the water, living so close to the shoreline that they were able to walk on to dry land.

The ostracods from the NEI have regularly provoked interest (Haswell 1865; Lamont 1978; Siveter 1973, 1980; Siveter and Vannier 1990), not least because of the size of *Entomozoe tuberosa* which reaches 11 mm or more in length (hardly a microfossil), but mostly some of the earliest records of certain genera. One sub-species of ostracod (*Craspedobolbina mitrobeyrichia impendens*) , common in the NEI has not been recognised elsewhere (Siveter 1980). Further ostracod finds from the "GBLB" locality, are illustrated in fig 10.8.

The brachiopods from the area are extremely important, and possibly biostratigraphically constrained. The early work of Davidson (1868, and synoptic supplement Cocks 1978) is currently the only reliable reference to the brachiopods from the NEI. New specimens from the Gutterford Burn of *Erinostrophia undata* (M'Coy) (fig 10.8), will form part of a future integrated biostratigraphical study of graptolites, corals and conodonts. Work is currently being undertaken by Clarkson and Taylor on the Deerhope coral bed (Clarkson and Taylor 1989), and on the monoplacophoran mollusc *Pterotheca* (Clarkson *et. al.* 1995).

A number of field guides to the area have been produced in recent years (Clarkson 1981; Clarkson and Taylor 1989; Robertson 1983; 1986); all have concentrated on the slightly more readily accessible and highly fossiliferous section of the Wether Law Linn. Attention has not been drawn to the Gutterford Burn sections, partially to avoid attracting the attention of professional fossil hunters with the lure of rare but commercially far more valuable starfish, eurypterid, dendroid and echinoid fossils. The area in which the North Esk inlier outcrops, is excellent for one day field trips, and an integrated visit looking at the whole of a regressive sequence does not have time to fit in a visit to the Gutterford Burn.

The level of the reservoir has been lowered in recent years as the dam was not considered strong enough to withstand the effects of heavy rainfall. New exposures of less weathered sediment are continuously appearing on the eastern shore of the reservoir, yielding some good sedimentary structures. Periodically during the summer the reservoir is completely drained. Two studies were conducted into recent sediment yield and sedimentation rate in the current reservoir basin (Lovell *et al.* 1973; Ledger *et al.* 1974).

The history of biostratigraphical research, particularly with respect to the Reservoir Formation, is discussed in more detail in chapter 3. Some controversy has been associated with dating of the Henshaw Formation. In the late 19th century various ages were given, ranging from Ludlovian (Henderson and Brown 1870) to Devonian (Howell and Geikie 1861). This was complicated by the fact that the Henshaw Formation represents the onset of deposition of Old Red Sandstone facies (Blieck and Janvier 1991) . It took almost 80 years before a more accurate date was available, established from fish remains (Westoll 1951), found in rare marine incursions. Blieck & Janvier (1991:352) confirmed that these fish beds were marine incursions, and could be correlated with the middle Wenlock *"L" taiti* assemblage of Lesmahagow. The full extent of the *L. taiti* vertebrate biozone is unclear (Cocks and Koren' 1994), and the lower Sheinwoodian zone between the top of the Llandovery L. scotica and base of *L. taiti* zone is marked with a ? on their correlation chart. Wellman and Richardson (1993:155) also considered the Henshaw formation, in their study of the plant microfossils (spores). They concluded that samples from a number of Midland Valley inliers all suggest an early Wenlock age, probably belonging to the *chulus-nanus* Spore Assemblage Biozone.

More recent work has concentrated on integrated projects, linking studies of one fossil group across the whole range of the Midland Valley Inliers. Dr. S. Bruce conducted a study of trace fossils across the inliers (another project sadly not yet published). A further integrated project is currently being undertaken by C. Lovelock at Edinburgh University, studying the sedimentary environments of the central inliers of the Midland Valley; all part of the research team headed by Dr. E.N.K. Clarkson at Edinburgh University.

With the recent interest in the tectonic history of the whole region (see chapter 5), information from the Midland Valley inliers is crucial in the development of tectonic models and palaeogeographic reconstructions. Leggett (1980) was the first to recognise this, and envisaged the inliers to have been deposited in an upper slope basin separated from the Iapetus ocean by the emergent southern uplands accretionary prism to the South. Bluck (1983) suggested a modification of this scheme, envisaging the sediments of the inliers to have been deposited in an interarc basin. A basin model for the formation of the Midland Valley of Scotland and Ireland was described by Williams and Harper (1988). Much information in support of this model has since been gathered from other inliers such as Charlestown in Ireland (Parkes 1993). A more recent review, considering the influence of strike slip motion on the tectonic setting is given by McKerrow *et al.* (1991). A series of excellent palaeogeographic maps (Cope *et al.* 1992) helps in understanding the relative positions of the inliers at the time of deposition. In particular, the late Llandovery palaeogeographical reconstruction of the eastern end of the Midland Valley (Cope *et al.* 1992:51), conforms to the model presented here of deposition in relatively shallow water and not the published model of Robertson (1989). This is not made clear in the text (Cave 1992:50), and is probably based on discussions of the present author with Dr. Bluck in Glasgow in 1990. An erroneous version of the NEI stratigraphy was given by Cocks *et al.* (1992) in their revised correlation of the Silurian rocks of the British Isles.

"The only justification [for stratigraphical correlation by fossils] is the purely pragmatic one that such correlation has been found to work in practice"
(Temple, 1988:875).

Chapter 3.

Biostratigraphy

3.1 What is Biostratigraphy ?

Stratigraphical classification is primarily concerned with identifying patterns of stratified rocks and producing an accurate chronology, identifying the order of events, preferably with dates, and with time divided into recognisable periods so that rocks from similar time periods all over the world can be correlated.

The usual aim of the study of biostratigraphy is to identify the **age** of the rocks from which the fossils were discovered. Biostratigraphy in practice, is the process of identifying the fossils preserved as closely as possible, then assessing the known time range for each species. For each new species it is necessary to identify its time range as closely as possible. Each new find of a known species from a new locality, can possibly extend the known time range of each species. A comparison of the ranges of two species might identify an overlap period of time when the two species coexisted. The further addition of the known time range for other species, should gradually narrow down the possible time period in which the rocks were deposited. These time periods are represented by short sections of the geological succession known as **zones.** A concise description of the practical problems facing biostratigraphers is given by Clarkson (1985: 20-21).

In the literature, the word **Zone** is often used when the term **Biozone** is meant (Loydell and Palmer, 1991:88), as the author is referring to a time zone defined by the presence of fossil biotas. Some authors insist that the term Zone was established prior to Biozone and its meaning is clear, and the term Zone will continue to be used.

Increasingly, zonal schemes erected for one fossil group are being refined by more rigorous taxonomy, and enhanced by correlation with other areas in the world (particularly as new localities become available following the opening up of some national boundaries, although some are at present unavailable e.g. Yugoslavia). Much more information is also becoming available as the complementary zonal schemes of two or more fossil groups (eg graptolites and conodonts) are compared and combined.

Care must be taken to consider the fossil assemblage rather than just the **zone fossil.** It is very unfortunate that each biozone has traditionally been named after its most characteristic fossil. In making the point that it is the association that we should be considering, Elles and Wood (1905:515) stated

> "It must be carefully borne in mind that a graptolite zone is characterised by a *special association* of graptolites, and that the form of this association which apparently combines restricted vertical range with wide horizontal distribution is most conveniently selected as the index of the zone."

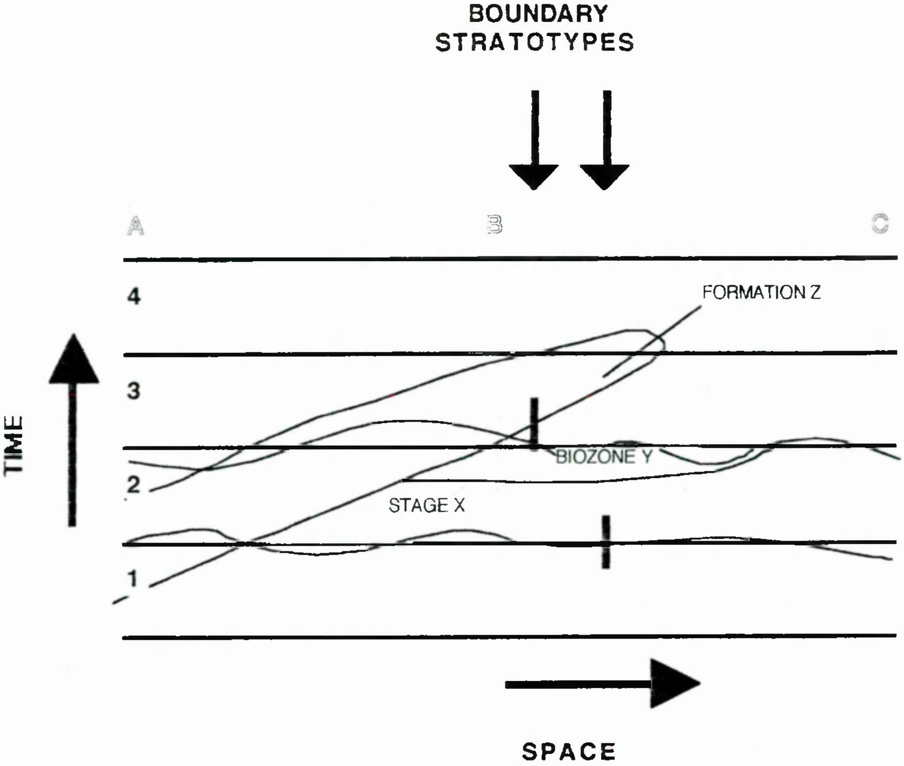

Fig 3.1 Diagramatic representation of relationships between stratigraphical divisions of different categories. The numbered horizontal strips indicate the passage of time. The Stage X, a *chronostratigraphical* division (or part of the Global Standard Stratigraphy), is extended through space A-B-C by correlation involving the total available palaeontological and physical evidence. Its boundaries approach time boundaries but can be *known* to coincide with these only at the boundary stratotypes for the base of the stage and for the base of the stage above (which defines the top of Stage X). Biozone Y is a *biostratigraphical* division used in extending the upper boundary of the stage, but only in the area where its diagnostic fauna is known to occur; it mostly provides a close indication of a time boundary. A flagrantly diachronous *lithostratigraphic* division, formation Z, is added for completeness (after Holland 1989, fig 1)

This has led often to the presence of rocks of that age being confirmed, simply by the presence of specimens of one species, a problem discussed below (see section 3.2). A full discussion of biozone types; Assemblage, Acme, Total-range (or Local-range), Concurrent-range, Partial-range, and Consecutive-range biozones is given by Temple (1988:876) and discussed both therein and in Holland and Bassett (1988).

Temple (1988) points out all of the possible difficulties and inconsistencies in using biozones for correlation. He notes that "Biostratigraphy is the utilisation of fossils for correlation in stratigraphy. Biozones, the units of biostratigraphy, are recognised and specified only by their fossil content' (Holland *et al.* 1978:5). Biozones are therefore conceived inherently in terms of correlation" (Temple 1988). He goes on to discuss the problems inherent in using biozones, and the consequences of using ideal models. Such models imply that all of the taxa characteristic of the biozone, are expected to occur on one bedding plane, or that observation of the sudden disappearance of one taxon is expected alongside the co-occurrence of two other taxa. Temple's discussion is, as pointed out by Holland and Bassett (1988), negative; he outlines many of the problems though his solutions are not necessarily workable either.

This does not mean that the principle of biostratigraphy is fundamentally flawed, merely that there are many problems still to be overcome. The ultimate aim must be to compile enough data that worldwide correlation becomes possible. To this end Standard Sections (stratotypes) have been identified against which all other sections can be correlated (see section 3.5.2). The principle of producing a Standard or Global Standard is to encourage "stability".

If the sections chosen as "Stratotypes" and internationally agreed upon, are less than perfect or have little to commend them to a particular group of biostratigraphers, that is unfortunate but at least there exists a base to compare with, published in an agreed format, that is readily accessible to those perhaps unable to travel to Arctic Canada or Nevada. From within a stable frame of reference, other workers' attention can be drawn to perhaps better preserved sections in other locations. The standard correlation chart given by Cocks, (1989:49) for the Llandovery Series, clearly must be a composite based on information from other (unspecified) areas, as there is no definite record of either the *griestoniensis* or *crenulata* biozones in the Llandovery area. During the current study, a correlation chart was prepared comparing all published stratigraphical columns spanning the late Llandovery (the Telychian Stage see fig. 3.1), known by the author. The composite nature of the chart of Cocks (1989:49), made correlation with this chart inaccurate.The column actually used in fig 3.2 to represent the "Global Standard" is taken from Rickards (1989) wherein more overall information is presented.

Most palaeontologists, and in particular most graptolite workers, are engaged in looking at fossils with direct reference to biostratigraphy and correlation and few are involved in pure taxonomy. Given the amount of work put into studies of correlation, it is alarming to note that drastic differences occur in the interpretation of different authors' biostratigraphical charts. Figure 3.2 shows copies of published correlation charts produced by various authors, drawn as accurately as possible, representing the original authors biozonal pattern, and the inherent differences in interpretation. Particularly apparent was the differing interpretations of Bjerreskov (1992:9) and Loydell (1993:324) of Melchin's chart (1989:1731). It is clear that various authors not only have difficulty in fitting their observations on the graptolites into existing biozonal patterns, they actually have difficulty in interpreting each others' pattern. Obviously, "science is better when individual authors explain what they mean by what they are doing" (Holland and Bassett 1988:881). A great

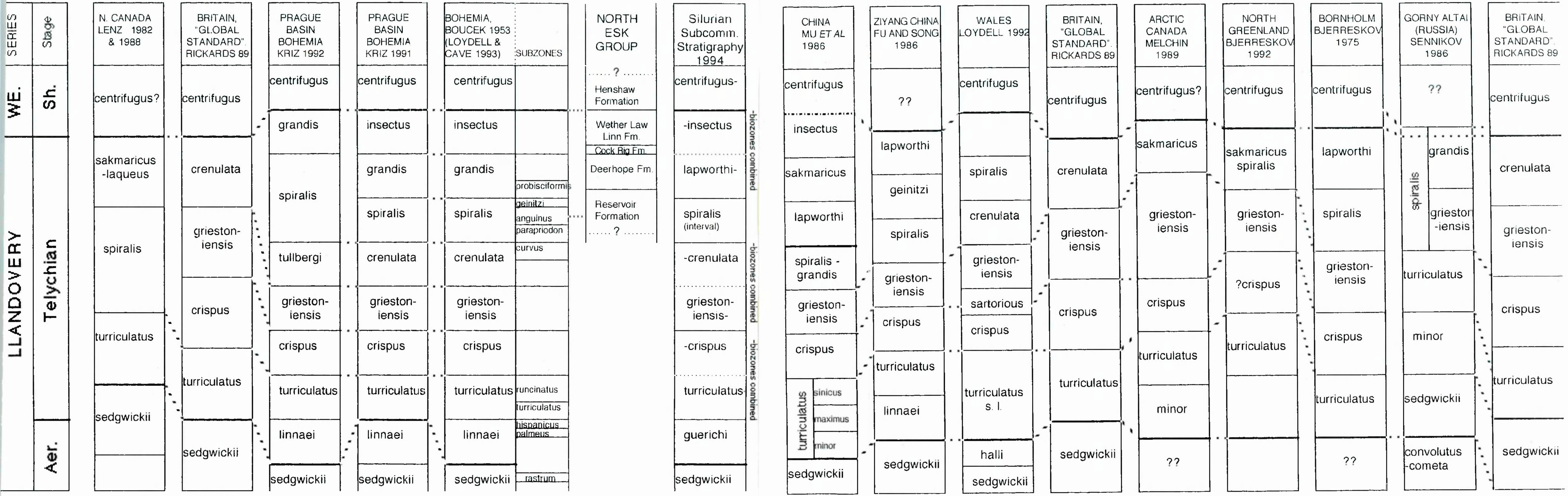
SERIES
Stage
WE.
Sh.
LLANDOVERY
Telychian
Aer.
N. CANADA LENZ 1982 & 1988
centrifugus?
sakmaricus -laqueus
spiralis
turriculatus
sedgwickii
BRITAIN, "GLOBAL STANDARD" RICKARDS 89
centrifugus
crenulata
grieston-iensis
crispus
turriculatus
sedgwickii
PRAGUE BASIN BOHEMIA KRIZ 1992
centrifugus
grandis
spiralis
tullbergi
grieston-iensis
crispus
turriculatus
linnaei
sedgwickii
PRAGUE BASIN BOHEMIA KRIZ 1991
centrifugus
insectus
grandis
spiralis
crenulata
grieston-iensis
crispus
turriculatus
linnaei
sedgwickii
BOHEMIA, BOUCEK 1953 (LOYDELL & CAVE 1993)
centrifugus
insectus
grandis
spiralis
crenulata
grieston-iensis
crispus
turriculatus
linnaei
sedgwickii
SUBZONES
probisciformis
geinitzi
anguinus
parapriodon
curvus
runcinatus
turriculatus
hispanicus
palmeus
rastrum
NORTH ESK GROUP
?
Henshaw Formation
Wether Law Linn Fm.
Cock Rig Fm.
Deerhope Fm.
Reservoir Formation
?
Silurian Subcomm. Stratigraphy 1994
centrifugus-
-insectus
lapworthi-
spiralis (interval)
-crenulata
grieston-iensis-
-crispus
turriculatus
guerichi
sedgwickii
-biozones combined
-biozones combined
-biozones combined
CHINA MU ET AL 1986
centrifugus
insectus
sakmaricus
lapworthi
spiralis - grandis
grieston-iensis
crispus
turriculatus
sinicus
maximus
minor
sedgwickii
ZIYANG CHINA FU AND SONG 1986
??
lapworthi
geinitzi
spiralis
grieston-iensis
crispus
turriculatus
linnaei
sedgwickii
WALES LOYDELL 1992
centrifugus
spiralis
crenulata
grieston-iensis
sartorious
crispus
turriculatus s. l.
halli
sedgwickii
BRITAIN, "GLOBAL STANDARD". RICKARDS 89
centrifugus
crenulata
grieston-iensis
crispus
turriculatus
sedgwickii
ARCTIC CANADA MELCHIN 1989
centrifugus?
sakmaricus
grieston-iensis
crispus
turriculatus
minor
??
NORTH GREENLAND BJERRESKOV 1992
centrifugus
sakmaricus spiralis
grieston-iensis
?crispus
turriculatus
BORNHOLM BJERRESKOV 1975
centrifugus
lapworthi
spiralis
grieston-iensis
crispus
turriculatus
??
GORNY ALTAI (RUSSIA) SENNIKOV 1986
??
spiralis
grandis
grieston -iensis
turriculatus
minor
sedgwickii
convolutus -cometa
BRITAIN "GLOBAL STANDARD" RICKARDS 89
centrifugus
crenulata
grieston-iensis
crispus
turriculatus
sedgwickii

Figure 3.2: Biostratigraphical correlation between published charts of various authors.

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deal of confusion in the literature and requirement for philosophical thought could be alleviated by clear explanations of each author's point, particularly by good illustrations of the taxa concerned (Bull and Loydell 1995). Precise taxonomy should have the distinguishing features clearly described and illustrated, leading to proper identifications.

3.2 Aims of this project

3.2.1. The aims of the biostratigraphy section of this project were :-

-To ascertain the age of the rocks exposed in the North Esk Inlier and to place this in the clearest biostratigraphical setting possible.

-To detail how the biostratigraphical information gained agrees with established patterns and what the implications are for correlation with other areas, and with the "Global Standard" (Holland and Bassett 1989).

-To focus initially on the age of the Reservoir Formation of the North Esk Inlier, as previous projects (Robertson 1989; Tipper 1974) had concentrated on stratigraphically higher strata which contain few biostratigraphical markers.

The strata are preserved in a conformable sequence without repetition by folding. To date the period of sedimentation (age range) it was necessary to date the oldest sediments preserved (the Reservoir Formation) to give us the earliest date. The latest date of the subsequent sediments is already constrained to the early Wenlock by fish remains found in the Henshaw formation (Wellman and Richardson 1993).

Previous projects (Robertson 1989; Tipper 1974) have all assigned an age to the NEI sediments, most citing the presence of certain graptolites as confirmation. It was clear from the literature that the strata now exposed in the NEI were thought to have been deposited during late Llandovery to early Wenlock times. Initial surveys of the literature detailing Late Llandovery sediments and in particular graptolite biostratigraphy, revealed that there were a number of major problems at each stage, not only with details immediately relevant to the NEI, but fundamental problems with worldwide biostratigraphy and basic taxonomy. The subject of research developed into documentation and discussion of these difficulties, and relating solutions as apparent from Pentland Hills fauna.

3.2.2 Problems

As a result of the initial analysis of the existing literature, it appeared that different biostratigraphers studying the uppermost Llandovery or Llandovery/ Wenlock boundary sediments, recorded different names for the biozones, and different faunal assemblages present. Various biozonal schemes were being used in different areas of the world; these schemes were not easily correlated and some were not even considered equivalent (see fig 3.2 for references). Existing correlation charts have a confusing use of time on the vertical scale which seemed to contradict statements made about the apparent duration of each zone. Correlation charts are discussed more fully in section 3.5 and illustrated in fig 3.2.

Figure 3.3 : Silurian graptolite Biozones (the "Global Standard"), taken from Rickards 1989.

DEVONIAN			*Monograptus uniformis*	
PRÍDOLI SERIES			*Monograptus transgrediens*	
			Monograptus perneri	
			Monograptus bouceki	
			Monograptus lochkovensis	
			Monograptus pridoliensis	
			Monograptus ultimus	
			Monograptus parultimus	
LUDLOW SERIES	Ludfordian Stage		*Monograptus balticus / caudatus*	
			Neocucullograptus kozlowskii	
			Neocucullograptus inexpectatus	
			Neolobograptus auriculatus	
			Bohemograptus cornatus	
			Bohemograptus praecornatus	*-Bohemograptus bohemicus*
			Cucullograptus aversus	
			Saetograptus leintwardinensis	
	Gorstian Stage		*Cucullograptus hemiaversus*	*-Saetograptus incipiens*
			Lobograptus invertus	*-Pristiograptus tumescens*
			Lobograptus scanicus	
			Lobograptus progenitor	*-nilssoni-scanicus*
			Neodiversograptus nilssoni	
WENLOCK SERIES	Homerian Stage	G	*Pristiograptus? ludensis*	
			Gothograptus nassa	
		W	*Cyrtograptus lundgreni*	
	Sheinwoodian Stage		*Cyrtograptus ellesae*	
			Monograptus flexilis	
			Cyrtograptus rigidus	
			Monograptus riccartonensis	
			Cyrtograptus murchisoni	
			Cyrtograptus centrifugus	
LLANDOVERY SERIES	Telychian Stage		*Monoclimacis crenulata*	
			Monoclimacis griestoniensis	
			Monograptus crispus	
			Monograptus turriculatus	
	Aeronian Stage		*Monograptus sedgwickii*	
			Monograptus convolutus	
			Pribylograptus leptothecae	
			Diplograptus magnus	*-Coronograptus gregarius*
			Monograptus triangulatus	
	Rhuddanian Stage		*Coronograptus cyphus*	
			Lagarograptus acinaces	
			Atavograptus atavus	
			Parakidograptus acuminatus	
ORDOVICIAN			*Glyptograptus persculptus*	

Disagreements existed about time ranges of individual fossil species. Particularly disturbing being that a given species used as index fossil in one area and defined as restricted to the time range of that zone for that area, was recorded as ranging considerably outwith that biozone in other areas (Bjerreskov 1975; Rickards 1976). How much this was due to taxonomy and each author seemingly having their own interpretation of many of the species was unclear.

The commonly used zone for the uppermost Telychian in Britain is the *Monoclimacis crenulata* Biozone, and was identified by Rickards (1989) as one of the zones "most widely used in international correlation" (see fig. 3.2). The species *Monoclimacis crenulata* had very unclear taxonomy (Loydell, Bull and Storch, 1993), as did all of the *vomerinus* group (Strachan 1971:64). Similarly the most commonly cited biozone index fossil elsewhere (eg. Lenz, 1992) was *Monograptus spiralis* (or *Oktavites spiralis)* with a similarly unclear taxonomy. The specific problems associated with the *crenulata* biozone are discussed at greater length in section 3.6 where the problem of what is the most appropriate scheme of graptolite biozones to use is discussed.

A priority seemed to be, to decide which graptolites were indicative of a Llandovery / Wenlock age, and the fossil assemblage associated with each graptolite Biozone, also what each of these graptolites looked like. Not all authors can agree on the name of each fossil concerned, never mind the description, at both generic and specific (and sub-species) level. Two of the genera involved, *Monoclimacis* (Frech) and *Oktavites* (Levina) need revision and clarification, with some authors refusing to accept the need to introduce new generic names (see section 7.8). Additionally, some of the late Llandovery species attributed to genera not in question (e.g. *Monograptus priodon*), seemed to be the ones associated by some with identification difficulties (Lenz 1974).

Most biostratigraphy in the Upper Llandovery is based on graptolites (see below). However, certain non-graptolite fossils found in the Pentland Hills, have been used to date sediments in other areas as "*crenulata* " biozone age because of their presence in beds of "known" age in the NEI such as the brachiopod *Pentlandella* or the ostracod *Entomozoe*. Thereby the majority of non graptolite biostratigraphical markers are rendered useless for dating these rocks from first principles as the NEI has been used as a reference area. Other faunal elements are however capable of yielding biostratigraphical data in the Telychian, such as corals and conodonts (see section 3.9), and an integrated approach was aimed at here.

Graptolites are not perfect for biostratigraphy. The reasons for these imperfections can yield further information such as depth, faunal provinces, considered further in chapter 8. Were such factors as faunal provinces, depth related faunas, global climatic changes, or biofacies, distorting the biostratigraphy, or is the apparent lack of correlation due to poor taxonomy? Graptolite literature is not easy to access, it is not held in most libraries, and much depends on descriptions in old texts. Many very informative papers are in obscure journals and in foreign languages such as Russian, Czech, and Chinese, often without translation.

Some specimens have been misidentified. This is often a result of different authors having their own view of what each particular species looks like, and sadly this can vary greatly between workers. The taxonomic descriptions given by some authors are rarely detailed enough for the reader to readily discern the dimensions and characteristic growth patterns of a particular species from the text alone. Sometimes it is neccessary to rely on illustrations (often of flattened poorly preserved material) to visually separate the sub-species. The degree of preservation of graptolites is often not good, hence illustration can also be poor. Furthermore, remarks in taxonomic descriptions often concentrate on how to differentiate the species being described from other similar species, which is further complicated when variations in the comparative species have not been fully elucidated (eg *Monograptus tullbergi*) (see Chapter 9).

Why did this stratigraphical unit seem so difficult to correlate? Initially this seemed to be due to lack of information,which has been greatly rectified by the recent glut of papers. Many of these problems have also now lessened due to the formation of BIGG allowing more freedom of discussion between graptolite workers, and exchange of information about recently published papers in obscure journals. The recent work of Dr D Loydell from Aberystwyth has clarified a number of the problems with biostratigraphical correlation worldwide (Loydell 1993). The present work was conducted over the same time and has reached similar conclusions. The discussion below will be made with reference to recently published papers (see section 3.5). Much of the original thought and work was done prior to the publication of these papers.

From existing tectonic models for the late Llandovery (McKerrow *et al,* 1991; Bassett *et al,* 1992) it is clear that the geographical position of the NEI might be crucial in linking with evidence from other areas in the study of such issues as faunal provinces and palaeobiogeography (Berry and Wilde 1990; Rickards, Rigby and Harris 1990; Loydell 1993:325). Clearly, in the Pentland Hills, there is preserved a slightly anomalous fauna (Williams and Harper, 1988:743); this means that the PH can be considered in isolation, but ultimately must fit into any biostratigraphical scheme, if that scheme is to have worldwide application.

Does the unique basin position of the NEI as a remnant of ocean connecting other provinces, record the mixing of faunas? Is the fauna partially endemic, adapted to the basin of deposition as it was such a long established geographical feature? It is in part due to the difficulties of correlating north to south between Scotland and England, that models of land barriers and oceans (Leggett *et al.* 1979) separating the two areas during the Llandovery began to have any initial credence. The Telychian tectonic regime and palaeogeography now envisaged for the south/north British division makes any comparison and correlation envisaged between the different faunas preserved, potentially very important. Very little equality at the species level is observed between these two land masses.

With the current proliferation of papers on the Midland Valley and its place in the Caledonide terrane models, (e.g. Bluck 1983, 1984; Hutton 1987; Leggett 1980; McKerrow *et al*, 1991; Pickering *et al* 1988a; Scrutton and Parkes 1992; Williams and Harper, 1988; Woodcock and Soper 1992) any information that tightens the constraints on our knowledge of the sedimentary and tectonic history of this area is valuable. In particular any new data of this kind might shed light upon the timing of critical events within the Midland Valley of Scotland. Thus the marine regression affecting the Silurian in all of the inliers and especially clearly documented in the North Esk Inlier (Robertson 1989), which has hitherto remained imperfectly constrained, can now be more accurately dated as a result of the work detailed in section 3.6.1.

The information presented here (section 3.6.1) introduces to the Midland Valley a revised time-scale and greatly refines existing information, giving a much more precise definition of Telychian biostratigraphy than has previously proved possible. This new clarification of the biostratigraphy has implications for other areas which have palaeontological similarities to the Pentlands, such as the Charlestown inlier in Ireland (Parkes 1993) and Girvan (Cocks and Toghill 1973) in the Midland Valley, or further afield such as in the Oslo region (Cocks and Worsley 1993). A more detailed review of Telychian graptolite biostratigraphy is given by Loydell (1993).

3.3 Lithostratigraphy/ Chronostratigraphy

3.3.1 *Lithostratigraphy* is the practice of dividing sequences of strata into units dependent on the rock type. This is extremely important in local areas, but decreases in value rapidly with distance, as beds are highly likely to be diachronous. However it can be very important to identify certain lithologies that are indicative of events such as emergence. This has been used regularly to relate the events across the Midland Valley inliers (Williams and Harper 1988; Wellman and Richardson 1993), where the Igneous Pebble Conglomerate is identified as marking the onset of deposition in terrestrial conditions in all of the inliers.

Bentonites are thought by some to serve as accurate time lines (Batchelor and Clarkson 1993). They are understood as representing a fall of ash, therefore recording an instantaneous event, identifiable over a large area. The accuracy of such correlation is doubtful as the falling ash may be winnowed, the resultant beds are often heavily weathered, not always exposed in the field and it is usually very difficult to differentiate between bentonite horizons, making even mapping on a local scale difficult. It is now thought possible that eventually absolute dates for the Silurian from minerals such as zircons present in bentonites may be obtained (Pearce and Cann 1973; Tucker *et al.* 1990). Pentland Hills bentonite horizons are considered in more detail in chapter 4.

Thickness of rock should not be correlated with *time* durations. Thickness of rock is purely a function of sedimentation rate. Only if uniform sedimentation rates are assumed, can any such correlation be made. This assumption is reasonable if rocks such as pelagic black shales are being studied (Carter *et al*, 1980) where a uniform sedimentation rate may be assumed from area to area. In comparison, the rapid sedimentation rate and the relatively large thickness of rock established for the NEI, considered in this study to have been deposited during three graptolite zones, suggest such correlation with rock thicknesses in other areas, to be of no practical use. The position of Formation and Biozone boundaries are often expressed in terms of sediment thickness. Correlation of sediment thickness is clearly unrealistic and misleading.

Great danger arises when attempts are made to correlate similar lithological / lithostratigraphical units and their superimposed biostratigraphical patterns. Clearly not all changes took place at the same time and, for example, a conglomerate marking the onset of a regressive sequence in two areas may not have been deposited at the same time. The gravest error is to place two stratigraphic columns together and to continue the lines of correlation more or less horizontally across them, correlating similar thicknesses of rock. In one area 1m of sediment may be deposited in one million years (the average length of a graptolite zone) whereas in another 1500 m of sediment may be deposited in the same time span.

3.3.2 *Chronostratigraphy* is the process of relating strata to a standard hierarchical scale of system, series and stage. In this case we shall only consider the Silurian System, the Llandovery and Wenlock **Series** and the Telychian **Stage.** These are chronostratigraphical units and the chronostratigraphical classification for the Silurian System, as ratified by the International Commission on Stratigraphy, and all the discussions as to how these decisions were made, along with descriptions of the boundary stratotypes and parastratotypes are contained in Holland and Bassett (1989). The Global Standard Stratigraphy is outlined in fig. 3.1.

3.3.3 Discussion. It is envisaged that eventually enough evidence will be available worldwide that it will be possible to identify biozones that can be referred to as chronozones. Holland 1989 (in Holland and Bassett 1989:8) states:-

> " As to biostratigraphy, it is necessary in terms of principles only to reiterate the point that *biozones*, that is biostratigraphical divisions depending for their definition and recognition on the presence of particular fossils, are different in kind from *chronozones*, which are simply the lowest category of the chronostratigraphical hierarchy, coming below the Stage. Chronozones have scarcely as yet become the business of the Commission on Stratigraphy. Within the Silurian System two such divisions have been properly defined, named and explained from the type (and standard) area for the Wenlock series in the Welsh Borderland (Bassett *et al.* 1975). They are the Whitwell and Gleedon chronozones of the Homerian Stage."

The contribution of the information available from the Pentland Hills is detailed here, in the hope that all such information takes us one step closer to the eventual identification of chronozones, and as close as possible to the standardisation of usage of biozonal schemes. Meanwhile, it is important that chronostratigraphical, lithostratigraphical and biostratigraphical units and classifications do not become confused. Diagrammatic representation of this is given in figure 3.1.

Unfortunately there are examples of such misuse of stratigraphical divisions, particularly with reference to the Pentland Hills and the Midland Valley Inliers. Most of these are found in important and often quoted papers. It should be noted that despite reference to previous work (Robertson 1985; 1989; Tipper 1976), the age range of the Pentland Hills deposits as depicted in the correlation charts of Cocks *et al.* 1992 (Fig. 8:16), and Williams and Harper (1988, Fig. 4:743), are clearly in error. The correlation presented in fig. 3.2 suggests that the North Esk Group sediments range from Upper Telychian to Lower Wenlock stage and there is insufficient evidence to suggest that the uppermost and lowermost unfossiliferous deposits of the group, are significantly older or younger than the biostratigraphically constrained beds.

The first clear lithostratigraphical correlation was made by Leggett (1980:415), discussing the Midland Valley as an upper slope basin, noting the presence of the Igneous Pebble Conglomerate, marking the transition from marine to terrestrial conditions, occurring almost simultaneously in the inliers to the east of Girvan. Similarly, the Quartzite Conglomerate, within the Wenlock is also correlated across the inliers. His figure 8 is clearly marked as *not to scale*, however the uppermost units of the Pentland Hills stratigraphic column are suggested to encompass the Wenlock and ?Ludlow. There is no actual field evidence to suggest this may be true. Other than this, the figure is a good representation of the proposed correlation.

The second inaccurate correlation is to be found in Williams and Harper (1988:743, fig.4). All of the biostratigraphic evidence so far available for the marine sediments in the Pentland Hills suggests a level not below uppermost Mcl. griestoniensis Biozone (from graptolites, this author). Fish scales, gastropods and crinoid ossicles found in the Henshaw Formation in the North Esk Inlier, suggest the youngest sediments to have been deposited fairly early on in the Wenlock (Wellman and Richardson 1993). However, according to Williams and Harper (1988, fig. 4), the Pentlands range from approximately convolutus to nilssoni Biozones, the Reservoir Formation ranges from the base of the sedgwickii biozone to mid-crispus biozone and the Henshaw Formation ranges up into the Ludlow, therefore correlating with Aeronian to Gorstian Stages. This is somewhat clarified in the text, but simply ascribing the problem to “atypical community development” and lack of exposure is not sufficient. It is thought that Williams and Harpers’ figure was drawn using sediment thicknesses to define each column, which was then superimposed on the biozonal vertical scale.

The most important mis-correlation is in Cocks *et al.* (1992:16). Here the lithostratigraphical correlation of the Igneous and Quartzite Conglomerates is illustrated along with further correlation by rock thicknesses. This is projected against a chronostratigraphic scale. Their correlation chart depicts North Esk Inlier sediments ranging from mid Aeronian to upper Wenlock, with the top of the Reservoir Formation implied to be equivalent to the base of the Telychian. It is quite reasonable to suggest that the base of the Henshaw Formation correlates with the base of the Wenlock. Biostratigraphic evidence presented in this thesis suggests that good correlation with the chronostratigraphic scale can be made at this point, but lithostratigraphical correlation is very misleading directly as a result of the great thickness of sediment found in the Pentland Hills. It is quite possible for all of this pile of sediment to have been deposited during the equivalent of one graptolite biozone, and there is no need to suggest that the biozone was particularly longer or shorter (Cocks and Toghill 1973) than the average 1 million years (Rickards 1989:268).

There is a difference between:-
1) placing a date on a particular formation (from biostratigraphy) and therefore saying that the (tectonic or sedimentary or palaeoenvironmental) events recorded in that formation, happened at that time, and b) stating that events happened at a certain time, and hence the rocks must be of that age.

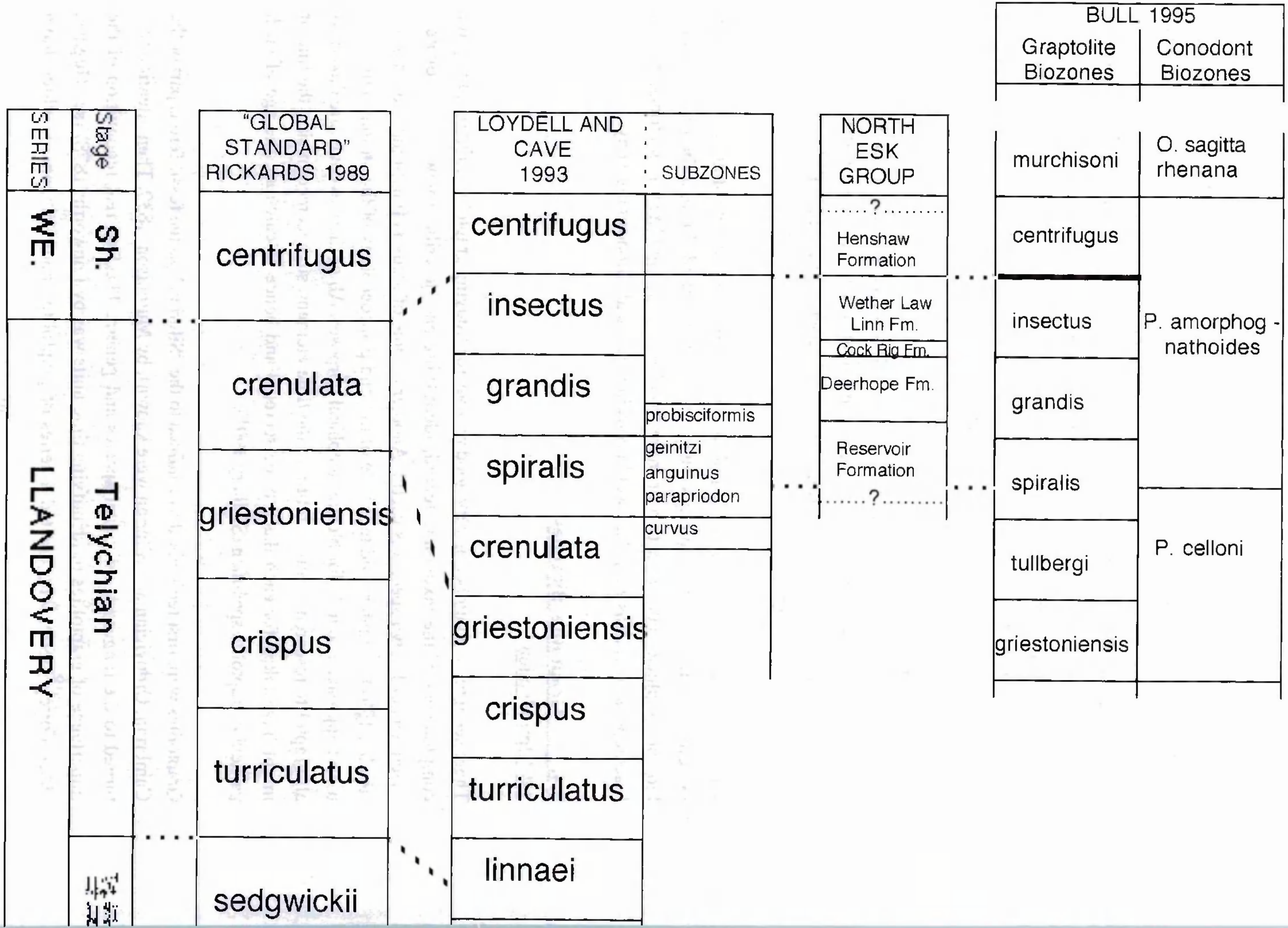
The ideal situation is a combination of the two, preferably with absolute dates given by radiometric dates from minerals such as zircons found in metabentonites, and biostratigraphical data from two or more fossil groups (graptolites, conodonts, corals, brachiopods, acritarchs etc.). This would constitute an ideal chronostratigraphy.

3.4. Graptolite Biozones

3.4.1 Introduction

There seem to be a number of very good reasons for studying graptolites. Firstly purely for completeness of the taxonomic record, identifying and describing new species or new specimens of known species is useful. Another avenue of study is functional morphology (Rigby, 1991), to understand the mode of life and palaeoecology of the animal. The other useful approach is purely for biostratigraphical purposes. All of these avenues are linked, as all graptolite research seems to return to the time element, such as recognising the time it might have taken for each theca to be secreted and hence to calculate the age of each particular graptolite specimen (Sudbury 1991).

Graptolites were first recognised as confined to the "Silurian" (as the fossiliferous part of the Cambrian, Ordovician and Silurian were known), by Murchison, 1839. Then attention was turned to the ranges of individual species and genera. The first real recognition of the importance of graptolites in identifying time units was by Lapworth (1878) (see Hughes, 1995, Fortey 1993), who erected a series of graptolite zones (biozones), which have


SERIES
Stage
WE.
Sh.
LLANDOVERY
Telychian
"GLOBAL STANDARD" RICKARDS 1989
centrifugus
crenulata
griestoniensis
crispus
turriculatus
sedgwickii
LOYDELL AND CAVE 1993
SUBZONES
centrifugus
insectus
grandis
probisciformis
spiralis
geinitzi
anguinus
parapriodon
crenulata
curvus
griestoniensis
crispus
turriculatus
linnaei
NORTH ESK GROUP
?
Henshaw Formation
Wether Law Linn Fm.
Cock Rig Fm.
Deerhope Fm.
Reservoir Formation
?
BULL 1995
Graptolite Biozones
Conodont Biozones
murchisoni
O. sagitta rhenana
centrifugus
insectus
P. amorphog - nathoides
grandis
spiralis
tullbergi
P. celloni
griestoniensis

remained largely unchanged to the present day. Lapworth recognised that individual species are restricted in range to definite zones (biozones) and could be employed as indices.

For a fossil group to be suitable for biostratigraphy they should be (Clarkson 1986:21) :-
a) widely distributed around the world, preferably occurring on a number of continents.
b) present in only a short vertical range, relatively short lived, hence defining a short section of the geological column.
c) easily distinguishable, with enough readily identifiable morphological features.
d) robust enough to be commonly preserved.
e) independent of facies so that they may be found in a variety of sediment types.

In some areas, biozones are being identified almost entirely by the presence or absence of the index fossil alone (particularly common for the *crenulata* Biozone (White *et al.* 1992)), and not by clear assemblages. This has led to the presence of rocks of that age being recognised, simply by the presence of one species. This can cause particular difficulties when either a species is misidentified, or if a species is discovered to have a different range in a different area. Two authors may therefore quote the presence of rocks of say *Oktavites spiralis* Biozone age and mean two completely different things (see fig 3.2). Cocks and Toghill 1973, identified the presence of the *crenulata* Biozone by the record of *Mcl. crenulata* itself, though these specimens are now thought to be *Mcl. geinitzi* and not indicative of *crenulata* Biozone age.

Assignation to a particular zone of a sequence of rocks is often done by implication. When strata of, for example *Mcl. griestoniensis* Biozone are identified beneath a packet of sediment, and strata of Wenlock age are identified above the sediment packet, then the biostratigraphically unconstrained sediment are assigned to the *crenulata* Biozone. In some instances this extrapolation has taken place without even clear evidence of early Wenlock strata .

A study was made of the common graptolite species of the Upper Llandovery, involving detailed examination of type material, consultation with available literature and discussion with other authors, in order to clarify the features of each of the species involved. As a result, identification of the graptolites from the NEI collected during recent field work, and of existing museum specimens was made possible. This involved accurate observation, illustration and collection of statistical data for each of the specimens known (see taxonomic descriptions chapter 9). The Robertson and Tipper collections of graptolites contained a few identifiable specimens. However, in the Royal Scottish Museum, drawers full of exquisite dendroids, previously unregistered but well located, were discovered. These were worked on as part of this project (Bull, 1987 and chapter 9). Whilst the dendroids did not yeild appreciable further information about the age of the sediments, but may do so in the future, as more dendroid finds are made worldwide.

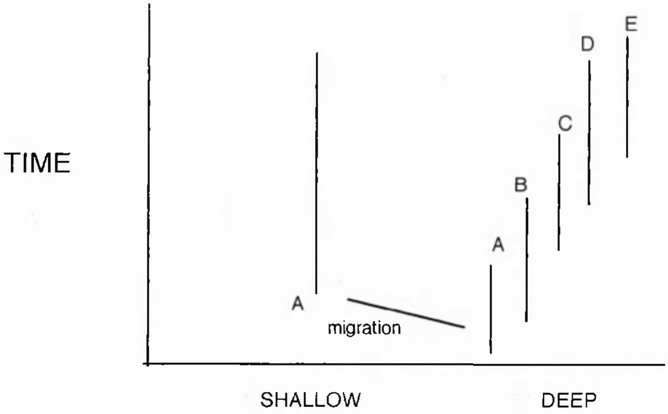


Fig 3.a

3.4.2 Discussion

Graptolites are generally very good as time indices as they satisfy most of the above criteria. Most species were generally relatively short lived with a good rate of evolution, pandemic, eurythermic and well dispersed between the epipelagic and shelf strata (although some degree of depth stratification and some faunal provincialism is recognised and discussed in Chapter 8).

In the practical application of biostratigraphy, the single most important factor is accuracy of identification of specimens. Clearly nothing can be gained by the correlation of the strata of two different areas, based on incorrectly identified fossils.

Composite descriptions are a further complicating factor for biostratigraphy (Loydell 1993:330). The monograph of Elles and Wood (1901-1918) is such a standard text that it is often the first step towards identifying a specimen, most importantly for new graptolite workers, who do not yet have experience of the common species. Many of the descriptions therein were composite. The effect of preparing descriptions of material from a number of localities is that evolutionary lineages and intraspecific variations are obscured. It is far better to have geographically localised collections, then local variations can be described. This may in future lead to the ranges of minor (local) variations in each species being identified, hence avoiding the confusion produced by the introduction of more and more sub-species. A comprehensive graptolite bibliography is given herein and see also Hutt (1975:2), and "Fossils Illustrated : Graptolites" (Palmer and Rickards, 1991), which introduces and explains most of the avenues of study and controversy.

It is as well to consider the possible difficulties with assuming that graptolites are perfect stratigraphic markers. Each biozone can have a species either confined, starting, ending or ranging through the biozone. It is possible that some species may not have evolved at the same rate everywhere (fig 3.a), giving rise to singular difficulties in correlation. For example one species (A) may have evolved in deep water, spread from there to shallow water, found a niche, and continued there for many millions of years. In deep water on the other hand, it may have become extinct almost as soon as it had spread to shallow water, and in the deep been succeeded by descendent species B-E.

Some major factors to be considered are :- depth control, dependence on food density, water mass specificity and current control, tolerance to changes in temperature and geography (ocean currents and land barriers).

Given all of the possible factors detrimental to the actual use of graptolites as biostratigraphical markers, the following (taken from Fu and Song 1986:175) remains true and of primary importance :-

> "German palaeontologist Jaeger (1980) reminded us .... "graptolites enable intercontinental and even global equations to be made with unsurpassed precision" which plays a role as a standard for the correlation of International Silurian. Therefore a continuous and complete graptolite section is the most ideal Silurian stratigraphic type."

In the absence of the perfect section, with all of the stratigraphically restricted faunas such as conodonts, certain brachiopods and acritarchs preserved, then the presence of graptolites in Silurian rocks will remain of primary importance to biostratigraphers.

(Bio)zonal definition is currently an area of debate. Not all authors agree with the way that zonal boundaries are defined. The argument is presented most succinctly by Rickards in a recent issue of "Silurian Times" (Rickards 1994:7) wherein the differences between identification of a biozone by the first appearance of a species, and the far more widely accepted concept of recognition of a *faunal assemblage* are outlined. The "golden spike" where "time-rock and time can be known to coincide in space" (Holland 1978:88), is an ideal horizon (Rubel 1994:6). Unfortunately insufficient of these golden spikes are identifiable. It is very rare to find a point within a sequence where the incoming of more than one species at one point is identifiable (other than as a preservational artifact). The best horizons will always be those in the middle of a biozone when the most representative assemblage is found, and more species with overlapping time ranges can be compared. In stratigraphy the search always seems to be for the base of each succession, and establishing the top may be very difficult. To facilitate international correlation, boundaries must be defined. At a purely local level however, or with the determining of the age range of a succession such as the NEI, it is far more important to identify the total faunal assemblage present at each level and fit this into the overall scheme, without the initial need to look for boundaries.

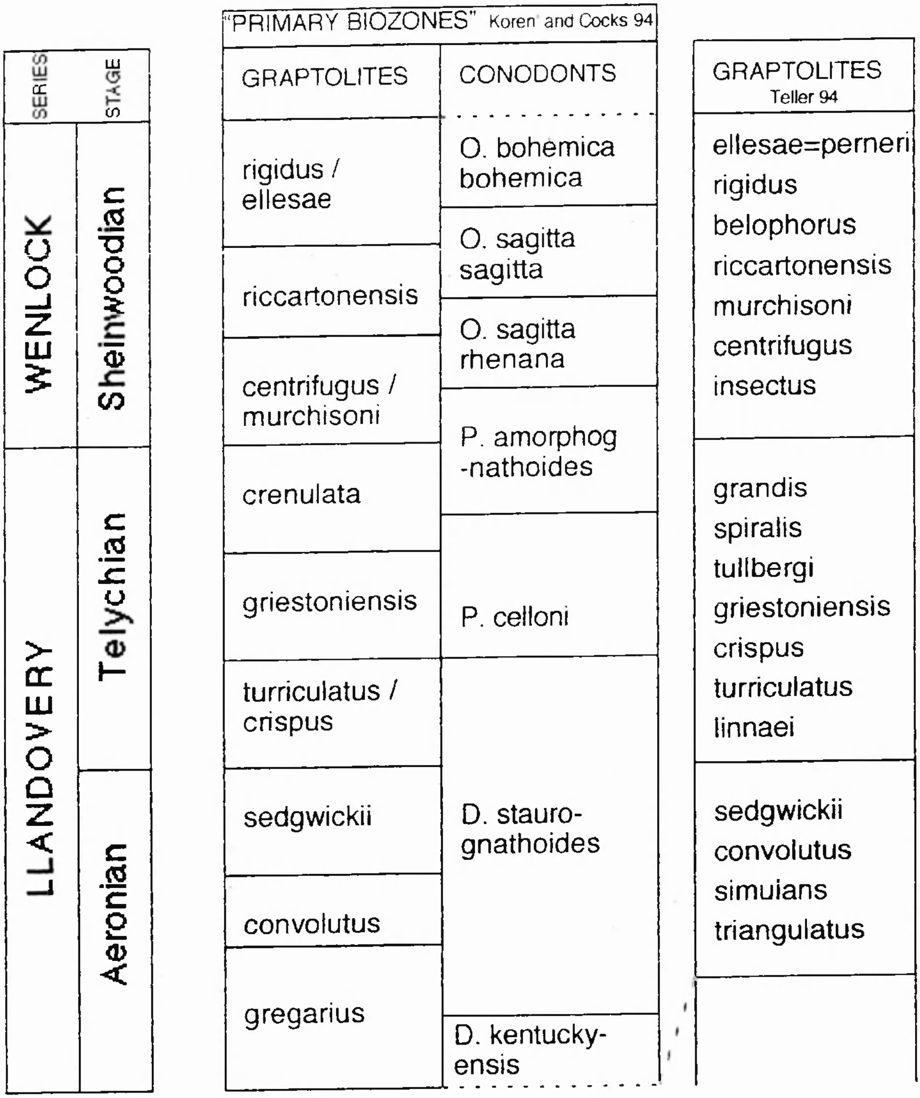
Further clear discussion of graptolite biozones is given by Obut and Sennikov, 1986:155. The criteria for distinguishing stratotypes are presented, and considered so carefully that it is suggested that "In sections with one or two zonal assemblages, 'beds with graptolites', and not formal zones, ought to be distinguished." The nature of teilzones, interzones, acme (epibole) zones, phylozones, range zones, assemblage zones, interval zones and biozones are discussed, and the important point is made that ".... authors ought always to mention exactly what they mean by graptolite zones and what criteria they have used in defining such zones." (Obut and Sennikov, 1986:155).

3.4.3 Correlation: discussion of problems with correlating graptolite biozones.

Biozonal schemes, charts and their correlation are given in figure 3.2 to 3.5
The uppermost Llandovery graptolite *crenulata* biozone was established by Wood (1906) in the Tarannon river section in Wales, and was included in the classic Table B, *Vertical Range of the Zones of British Graptolites I* p. 526 of Elles and Wood 1913. Having been included in this standard text, the British *crenulata* Biozone became widely accepted in the geological literature as the uppermost graptolite biozone of the British Llandovery (Rickards 1976). This was recently reinforced by its inclusion in the list of zones "most widely used in international correlation" (Rickards 1989:269) (see figure 3.3), and by being referred to as the "global standard" by Holland and Cave (1992:37). In Bohemia however, there are three Llandovery biozones recognised, which succeed the *crenulata* Biozone (Boucek 1953). These (and correlative biozones) have now also been recognised in North America (Lenz 1982; Melchin 1989), Scandinavia (Bjerreskov 1975), and elsewhere in Europe, China (Fu and Song 1986) and Russia (Sennikov 1976). Loydell and Cave (1993) have recently recorded for the first time in Britain one of these post-*crenulata* biozones, the *Oktavites spiralis* Biozone.

In this present work the "British" biozonal scheme *sensu* Rickards (1989) or Cocks (1989:49) is not used and instead the system shown in figure 3.8 (see also fig 3.2), is employed, with the "British" arrangement illustrated for comparison. This updated scheme in fig 3.4 is based on biozones and subzones established by Boucek (1953) for Bohemia, and currently in use in the Prague basin (Kríz 1991:181; 1992:7). In this stratigraphical system, the uppermost Telychian, between the *griestoniensis* and the Wenlockian *centrifugus* Biozones, is divided into four successive biozones; the *crenulata, spiralis, grandis,* and *insectus* Biozones. These in turn can be further divided into the recognisable subzones as shown in figure 3.4. (further discussion of correlation of Biozones and "primary Biozones" and the "left hand side" of correlation charts is contained in section 3.5 and fig 3.5). The *spiralis* Biozone is considered to be a succeeding zone to the "*crenulata*" Biozone in this scheme, rather than directly equivalent. It should be noted that most references to the *spiralis* zone in the literature are accompanied by correlation with the *crenulata* Biozone, whereas references to the *crenulata* Biozone, are generally not tied in to the *spiralis* Biozone.

If a revised biozonal scheme proposed for the uppermost Telychian stage, incorporating all of the new information about subzones, is to remain correlatable with the worldwide

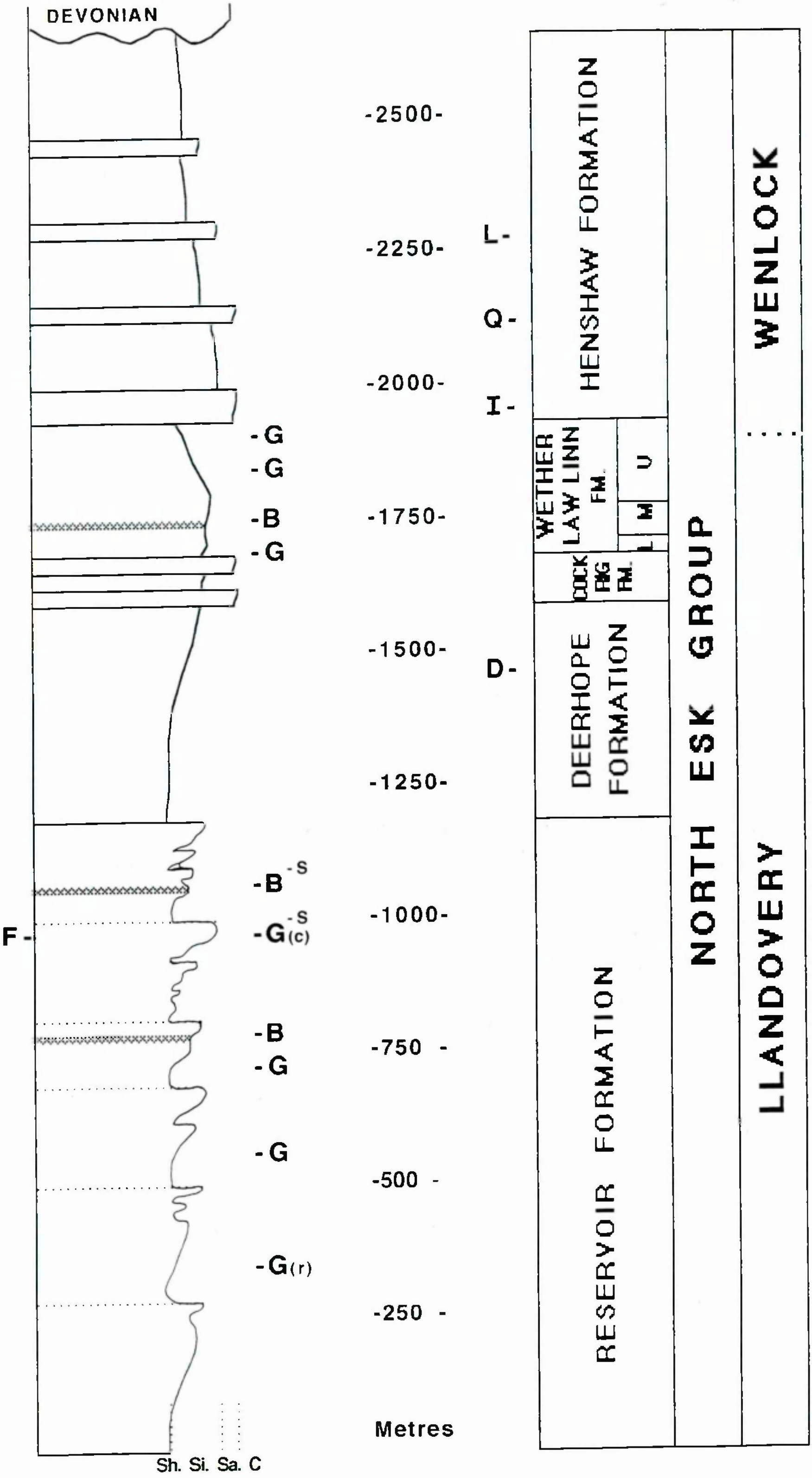


ure 3.5. Primary Biozones (from Cocks and Koren' 1994). Proposed left hand side to be used in all llation diagrams so that all corelation charts have a standard pattern and scale. Right hand column is the eme of primary biozones proposed by Teller (1995) in response to the Cocks and Koren' scheme.

findings, then it creates a problem for British stratigraphers in that "gaps" may be created. Where sections had been described as spanning the Llandovery/Wenlock boundary, if we propose the existence of a new graptolite biozones this could imply strata missing from other sections, suggesting unconformities. There are very few sections that this affects, as there are very few records of "*crenulata* " Biozone faunas being located on mainland Britain. Where a complete record is found, most have poor graptolite faunas and unfossiliferous horizons at this interval.

Graptolites representing zones between the *Monoclimacis griestoniensis* and *Cyrtograptus centrifugus* (basal Wenlock) biozones are absent in the Howgill Fells (Rickards 1970:22), Lake district (Hutt, 1975), and only represented by one thin graptolite band in a considerable thickness of penecontemporaneously eroded red beds in the Cross Fell area (Burgess, Rickards and Strachan 1970). In the Southern Uplands of Scotland, Kemp and White (1985) record no graptolites of "*crenulata*" Biozone age, whilst White *et al.* (1992) record the presence of a small number of specimens that are referred to the"crenulata" Biozone, mostly because of the hooked nature of the proximal thecae of their *Monoclimacis* specimens. This may as suggested imply "*crenulata*" Biozone, but are also equally likely to be referred to a new subspecies of *Mcl. vomerina* (Bjerreskov, 1975), found in the lowermost *M. spiralis* Biozone on Bornholm. One further mention of a"*crenulata*" Biozone outcrop in the south of Scotland is made by Cocks and Toghill (1973), where they "confirm" the occurrence of "*crenulata*" Biozone age rocks in the Girvan area by the presence of the index fossil itself. From the figure and material given by Cocks and Toghill of their crenulata specimens, they are thought by this author to be closer to *Mcl. geinitzi* due to their small size, wide thecal spacing, straight stipe and lack of hooked thecae proximally. Cocks and Toghill (1973) also record the presence of *Monoclimacis geinitzi* from the Lauchlan Formation (*greistoniensis* Biozone) of the "Main Outcrop" Girvan. It is unclear without extensive new collections and re-study of Cocks and Toghills' material, exactly which Biozone these rocks can be assigned to. This could include the taxonomic study of the excellent dendroid fauna recorded by Ward (1989), who unfortunately used the data from Cocks and Toghill (1973) for her biostratigraphical evidence and did not attempt further collection of graptolites (Ward, 1989:231, fig. 10.3). Therefore the introduction of a new biozonal scheme would not adversely affect the described stratigraphy in the Southern Uplands or Northern England.

Figure 3.6 Sedimentary log of North Esk group and current accepted lithofacies.
Left hand side: General sedimentary log of North Esk Group, Reservoir Formation sediments predominantly interbedded shale and siltstone, therefore curved line represents average grain size at that level in the column ; *Right hand side* : Accepted current lithostratigraphy for the Silurian sediments of the North Esk Inlier (After Robertson 1989, Figure 4). G: horizons which have yielded graptolites ((c): common, (r): rare). B: Metabentonite. s: Starfish bearing beds. D: Deerhope Coral Bed. I: Igneous Pebble Conglomerate. Q: Quartzite Conglomerate. L: Lyne Water Fish Bed. F: Fossiliferous "Gutterford Burn Limestone Beds", Sh : shale, Si : siltstone, Sa : sandstone, C : conglomerate. The Reservoir Formation is cut by many small faults, making correlation between stream sections and different localities inaccurate.


DEVONIAN
-2500-
-2250-
-2000-
-1750-
-1500-
-1250-
-1000-
-750 -
-500 -
-250 -
Metres
Sh. Si. Sa. C
L-
Q-
I-
D-
F-
-G
-G
-B
-G
-B-S
-G(c)-S
-B
-G
-G
-G(r)
HENSHAW FORMATION
WETHER LAW LINN FM.
U
M
L
COCK RIG FM.
DEERHOPE FORMATION
RESERVOIR FORMATION
NORTH ESK GROUP
WENLOCK
LLANDOVERY

Other descriptions of rocks of "*crenulata*" Biozone age in Britain, are isolated occurrences (Rickards, 1973), which from the fauna recorded could be assigned to either the *crenulata* or *spiralis* Biozones. In Wales further research by Loydell (Loydell and Cave 1992, Loydell 1991) has confirmed that there is a place for the inclusion of more biozones over this interval. The type locality for the *Monoclimacis greistoniensis* and *Mcl. crenulata* Biozones is in the Tarannon section in central Wales (Wood 1906), and is greatly in need of revision. Most other references to "*crenulata*" Biozone are by inference from the presence of other taxa such as corals (Scrutton and Parkes 1992, for the Charlestown Inlier in Ireland), and brachiopods (Bassett, 1989:234). This information can only be enhanced by the redefinition of graptolite biostratigraphy, particularly where actual co-occurrences of these faunas can be recorded such as in this work.

The application to ICZN (Loydell, Bull and Storch 1992) to change the author of the species *Monoclimacis crenulata* from Nicholson (1876) to Elles and Wood (1911), helps to preserve the established name of the Biozone and removes the necessity to use the nomenclatural addition '*sensu* Elles and Wood, 1911'. Some nomenclatural problems still exist however, for example the name *Monograptus vomerinus crenulatus* could still be used by anyone refusing to recognise the genus *Monoclimacis*.

In the Llandovery Stratotype section (Cocks, 1989:49), no definite records of the "*crenulata*" (or *griestoniensis)* Biozones are found. Similarly in the Stratotype for the overlying Wenlock Series, no mention of confirmatory graptolites from underlying sediments is made. In fact the British graptolite biozonal schemes published throughout the volume 'A Global Standard for the Silurian System' (Holland and Bassett 1989) are largely based on inference from other areas (not credited) and quite rightly based on the important work of Rickards (1976). It is largely due to lack of exposure in the British Isles of good uppermost Llandovery graptolite bearing horizons that has led to the continued use of zonal schemes dating back to Elles and Wood (1911). Therefore the name of the "*crenulata* Biozone" for the single biozone representing the uppermost Llandovery has become the "one most widely used in international correlation" (Rickards 1989:269), and referred to in the description for the Stratotype. There is no clear reason why the British graptolite biozonal scheme should not be updated to fall into line with the potentially more accurate biozonal scheme presented here. Many authors use the "*crenulata* Biozone" in their correlation charts (e.g. Parkes and Palmer 1994 fig 2), as they are unaware of the existence of revised schemes (Parkes pers. comm. 1995). The publication of the revised scheme employed here for the NEI (Bull and Loydell in press) and the discussion covered in section 3.5 will hopefully begin to rectify this.

3.5 Recent advances

3.5.1 Discussion

The age of rocks, particularly as far back as the Silurian, has only recently been approximated using "absolute" measurements. Bentonite deposits yield zircons that can be dated on a "Shrimp" microprobe (Claoué-Long *et al.* 1992, and Compston *et al.* 1992). This process has not yet been applied to bentonites relevant either directly or indirectly to this study, but the time scale for the Silurian can only be enhanced when this is attempted in the future. Biozonal schemes have recently been greatly enhanced by the work of Dr. David Loydell of Aberystwyth (1992 and references therein), however this work was not available at the start of my project and still is partially in conflict with results determined from the Pentland Hills.

There have been a number of papers published, spanning relatively large time scales, and without attached taxonomy. Whilst taxonomy, as such, is currently undervalued and underfunded (Loydell 1993a:332), it has however been very difficult to begin taxonomic studies without a conceptual framework. The further problem exists of the tendency to produce identifications based on what is expected rather than considering what is observed. This may ignore the possibility that a specimen might be a completely different species, simply because that species has not previously been recorded from that zone, i.e. the stratigraphy and range of each species are predetermined.

The trend seems to have been subdivision, both of biozones and of genera, for example the subdivision of *Monograptus* into *Oktavites*, *Spirograptus*., *Torquigraptus* ..etc (see chapter 9 and Loydell 1993b:326). Loydell (1993a:326) actually criticises the practise of 'lumping' slight variations into one species. Whilst his example seems valid, illustrating the misuse of this process, it is also dangerous when the taxonomy of a particular species is unclear, such as *Oktavites spiralis*. There is a need for some 'overall taxonomy', the collecting together of all of the figured material for a group of species, or each genus, rather than literature surveys. This work is particularly necessary for the *monoclimacids*. If this work were published widely and scientifically conducted (using recognised parameters such as 2TRD, Howe, 1983) then we would have a solid base for stratigraphical correlation.

3.5.2 Standard Zonal scheme (Global standard)

The establishing of stratotypes and standard sections worldwide, is well advanced (Holland and Bassett 1989). Standardisation and correlation between reference sections, fossil groups and absolute time scales, is an ultimate aim, and a standard text (Holland and Bassett 1989) now exists with which such correlation can be made. Rickards (1989), suggests and discusses Silurian standard graptolite zones, as distinct from biozones, heading towards a formal definition of such zones. Rickards (1989:286) also suggests that units of correlation down to 100,000 years or less should soon be possible. This will give an accuracy of dating in the Silurian using graptoloids, to within 0.1% (Tunnicliffe, Hughes and Zalasiewicz 1991:81).

The process of setting up global standards is underpinned by the identification of basal units. This makes the identification of the top of any unit (biostratigraphical or lithostratigraphical) very difficult if the base of the overlying unit is not clearly defined in the section being studied. Just as in the discussion of graptolite biozones, the zonal assemblage, and the fauna most indicative of the zone (probably indicating the centre of the zone) are of fundamental importance. There is little merit in being able to define the base, if it is unclear what is representative of the majority of the zone, because most fossil bearing horizons are likely to represent the middle of a zone, not the start or end. Any information that can "narrow the window" is clearly useful, be it identifcation of the onset of a new zone, or simply that a certain boundary must be below a certain level, even if that level cannot be accurately defined.

3.5.3 Discussion

Inevitably biozones will be calibrated on an absolute geochronological scale. Attempts have already been made at estimating the length of time represented by each graptolite zone (Carter, Trexler, and Churkin, 1980; Churkin, Carter, and Johnson, 1977.) Some authors seem to have no difficulty in greatly increasing the number of biostratigraphical divisions, for example Loydell (1991:212) introduces one new zone and seven subzones of the known *turriculatus* Biozone. Whilst this refinement of scale is welcomed, it is appropriate that authors should consider their "vertical scale". Loydell (1991) does not make it clear whether his introduction of a new biozone is intended to represent a proposed extension in the duration of time represented by the established biozone, and by implication the stage, or a refinement of the scale used, against a constant time scale. Clearly it is important that biostratigraphical scales should be drawn in a consistent way and meaningful correlations made. Although biozonal schemes are not measures of absolute time, it must be possible to correlate between them or they become valueless (see section 3.5.4).

If the ultimate aim is to refine biostratigraphical zones far enough for them to become chronostratigraphical units, diagrams presented should represent the assumptions being made. If it is to be assumed that all graptolite biozones are of approximately equal length, that is about one million years (Rickards, 1989:268) with subzones representing shorter subdivisions of each biozone, then this is how they should be represented in biostratigraphic charts. If, however, it is considered that some biozones represent relatively longer or shorter periods of time then this should be clearly stated. In some areas it has already been noted (Loydell, 1991:214 and this thesis) that rapid deposition of a large quantity of sediment (possibly in excess of 1000m Ma-1) creates collecting problems, but does not imply a biozone of longer duration, In contrast, a slow sedimentation rate (possibly implying deposition a great distance from the palaeo-coastline), can result in thicknesses of sediment representing a zone of only 3-18 m with graptolites being found almost continuously in such successions resulting in more than 20 collection levels in some zones (Obut and Sennikov, 1986:160). Similarly the statement " The *crenulata* Zone is poorly developed in most districts of Britain and may be plausibly postulated as short..." (Cocks and Toghill, 1973:242) is clearly erroneous and misleading. In the Pentland Hills 1500 m of sediment is attributed to the biozones as illustrated in figure 3.4. Similarly, in North Greenland, Bjerreskov (1989:30) notes that the comparable *spiralis* Biozone reaches a thickness of

2,800m. This highlights the problems of lithostratigraphical correlation as discussed in section 3.3.

3.5.3."New Left Hand Side For Correlation diagrams" ; Silurian Times 1994.

A scheme was set forward, ostensibly on behalf of the Silurian Subcommission, in the first edition of Silurian Times (Nowlan 1994). This was suggested as a standard left hand side to be used in all future published correlation charts. It was laid out with different vertical heights corresponding to the relative thickness of these zones, and lists of "Primary Biozones" for both graptolites and conodonts (with schemes for chitinozoa, spores and vertebrates also included for comparison). Comments were invited. Comments indeed were received, and by the publication of the second edition of Silurian Times, a number of points became clear, common to the authors that replied.

All seem to welcome the concept of an absolutely basic set of reference zones, indicating a level of global correlation that can be achieved, particularly if this scale presents an indication of chronostratigraphy, and a basic scale with subdivisions (even at the stage level, but preferably at the "primary Biozone" level) that will remain constant. It is clear however, that the scheme so far presented is unacceptable (see fig. 3.5).

There is fundamental disagreement between authors as to the nature of the "primary biozones' presented. Almost every one of the zones listed (graptolite and conodont) is questioned in some way. Some of the species mentioned are thought to be synonymous with others, and some established separate zones are not included. It is not clear what is meant by "Primary Biozones", nor if these primary biozones have chronostratigraphic implications. Would any further subdivisions of the finally accepted "primary biozones" be regarded as sub-zones, or locally recognised subdivisions?

Further basic disagreement exists about how biozones are defined. In particular whether a zone should be defined by the first appearance of a particular species, or by recognising a faunal assemblage, using the appearance of a number of species close together to define the base of the biozone.

From the assemblage of fossils described in this volume and biostratigraphical correlation presented, it is clear that the author supports the inclusion of a number of equal length zones above the "*crenulata*" biozone (scheme as defined herin see fig 3.8). Without having worked directly on the graptolites of the *insectus* and *centrifugus* biozones, comment cannot adequately be made on the positioning of the Llandovery/Wenlock boundary. Its setting at the base of the *centrifugus* Biozone is supported here. The suggestion (Teller 1994:9) that the *crenulata* Biozone be eliminated and replaced with the *tullbergi* zone also is supported here, basically because of the confusion surrounding the identification of *Mcl. crenulata* itself, and because it is felt that the concept of the *crenulata* biozone is invalid. It is doubtful

if the true *crenulata* zone has been fully recognised in many places as few correct identifications of the zone fossil have been made.
This debate will undoubtedly run for some time to come.

3.6 North Esk Inlier; Graptolite Biostratigraphy

3.6.1 Existing age data

The marine Silurian of the North Esk Inlier has traditionally been referred to the *Mcl. "crenulata"* Biozone (Uppermost Llandovery, C6, Telychian) on the basis of imprecisely identified graptolites, although the graptolite fauna has not previously been studied in any detail. Other biostratigraphically significant taxa are present in the Pentland Hills, including brachiopods, conodonts, acritarchs and corals, and it is possible in part to correlate these late Llandovery schemes (discussed below in section 3.7).

The accepted current stratigraphy for the sediments of the North Esk Inlier is detailed in Figure 3.6 (see also chapter 4). Important marker horizons are labelled, such as the Igneous Pebble and Quartzite conglomerates often used to correlate between the various Midland Valley inliers (Wellman and Richardson 1993:157). Robertson (1989:129, Fig. 5), gives a summary of the past stratigraphical subdivisions in the area.

The controversy regarding the age of the rocks of the North Esk Inlier, began when Brown and Henderson (1867), (the latter, regarded with scorn by the establishment within the Edinburgh Geological Society as of little importance as he was "self-educated" and "lowly" (Goodchild, 1900)), suggested that the rocks of the North Esk Inlier were entirely of Silurian age, contradicting the view proposed by the Geological Survey (Howell and Geikie 1861), that the upper beds (now known as the Henshaw Formation, see Fig. 3.6) were "Red Beds" of Old Red Sandstone age, lying above Ludlow age strata. Brown and Henderson (1867) believed that the sediments ranged in age from Wenlock to Ludlow. This view was based largely on brachiopods, a view supported by Davidson (1868), although Brown was clearly aware of the importance of the graptolites from the Pentland Hills as he had delivered a lecture to the Edinburgh Geological Society on the subject in 1866, the details of which were sadly not recorded. The first written account of graptolite biostratigraphical evidence is that of Peach and Horne (1899), based on graptolites found from the Gutterford Burn (Reservoir Formation, see Fig. 1).

Lamont (1947) was the first to suggest that the transition to Wenlock age sediments occurred at the base of the Henshaw Formation, and was coincident with the transition from marine to terrestrial sediments. Lamont (1952) proposed a new division of the Silurian, the Pentlandian, intermediate between the Upper Gala-Tarannon and the Wenlock, to account for the mass of palaeontological data from the Pentland Hills, and the apparent lack of correlation with faunas elsewhere. The correlation of the Gala-Tarannon with the Llandovery is now not questioned, and Lamont's "Pentlandian" has been rejected (Robertson 1989:138). However the work presented in this volume, with the recognition of further graptolite biozones at the top of the Llandovery, at least shows that Lamont's suggestions were not entirely misguided.

The Henshaw Formation has been dated from fish remains found in the Lyne Water Fish Bed (Figs 1 & 3.6), and this date has been further refined recently using plant microfossils (Wellman & Richardson 1993) to early Wenlock. All other biostratigraphical work on the North Esk Inlier (Mykura and Smith 1962; Tipper 1974, 1976; Robertson 1985, 1989), confirms a pre-Wenlock age for the underlying succession. In all of these studies, no clear taxonomic work was undertaken on the graptolites. They were assigned to the portmanteau species of *Monograptus spiralis*, *Monograptus priodon*, and *Monoclimacis vomerina (sensu lato)*. Due to the lack of preservation of diagnostic features of specimens studied, particularly proximal ends, graptolite biostratigraphical evidence remained inconclusive. Robertson (1989:138) suggested a crenulata Biozone age, with the possibility that the lowermost Reservoir Formation strata were deposited during the *griestoniensis* Biozone stage. He also noted that insufficient evidence exists to accurately define the Llandovery-Wenlock boundary in the Pentland Hills.

3.6.2 This Study

All available known graptolite specimens collected from the Pentland Hills were examined, including those from the Royal Scottish Museum, British Geological Survey, Grant Institute of Geology Edinburgh University (both existing collections, and research collections of Tipper (1974) and Robertson (1985)), and further new collections made by the author, during recent field work. Similarly specimens in the private collections of others including Dr E. N. K. Clarkson and Dr N. D. L. Clark were inspected. The extensive collections of the late Dr A. Lamont, are held in store by the Royal Scottish Museum but are currently not available for consultation.

Most of the material studied was collected from the Reservoir Formation, predominantly from the "Gutterford Burn Limestone Beds" Locality (Fig. 1B, Fig. 3.6). In this section the preservation potential of graptolite material is greater, but as the graptolites are mostly found in normal background sediment, rather than the highly fossiliferous coquina horizons, these specimens are considered representative of the Reservoir Formation generally. Rare graptolite specimens have however been discovered throughout the marine sediments of the North Esk Group. Recent sedimentary logging of the Reservoir Formation has produced the section in Figure 3.6A, the levels that have recently yielded the most biostratigraphically significant graptolite specimens (*Oktavites excentricus* (Bjerreskov, 1975) and *Monoclimacis geinitzi* (Boucek, 1932)) are marked (-G) on this section. The pattern of sediment deposition is consistent, without significant breaks. It is then reasonable to consider that the lowermost 250 metres of sediment, that have not so far yielded significant graptolite material, are not appreciably older than their overlying strata.

The following species are present (for references and taxonomic descriptions see Chapter 9): *Monoclimacis vomerina* ; *Monoclimacis geinitzi* ; *Monograptus priodon; Monograptus parapriodon ;Oktavites excentricus; Retiolites geinitzianus sensu lato.*

A great deal of the material available is broken or fragmentary, and consists largely of distal portions. However at least 10 specimens of most of the above species are confirmed, with many other specimens of some species. Illustrations of these species are given in section 7.8, included so that accurate comparisons can be made with material collected, illustrated or described from other areas.

Boucek (1953), Storch (pers. comm. 1993) and Loydell and Cave (1993), all record the incoming of *Monoclimacis geinitzi* in the middle part of the *spiralis* Biozone, prior to becoming prevalent (as the zone fossil of the *geinitzi* subzone) in the uppermost part of the *spiralis* interval. *Oktavites excentricus* was found by Bjerreskov (1975) to be confined to the middle of the *spiralis* interval. *Monograptus parapriodon* is characteristic of, and most common, in the lowermost part of the *spiralis* interval, but does occur in the middle part of the Biozone in Bohemia (P. Storch pers. comm). *Monograptus priodon* and *Monoclimacis vomerina* both have long time ranges and are characteristic of late Llandovery and early Wenlock sediments. *Retiolites geinitzianus sensu lato* Barrande 1850 and *Retiolites angustidens* Elles and Wood 1908, are known from the Reservoir Formation. Both have quite long time ranges through the late Llandovery and early Wenlock, and the presence of *R. angustidens* suggests a pre- *Cyrtograptus murchisoni* Biozone age. The Reservoir Formation of the North Esk Group can thus be assigned to the middle portion of the *spiralis interval* (see Figs. 3.2 & 3.4 for summary of correlation).

The overlying formations of the North Esk Group contain abundant fossil material generally, with a number of other taxa, including brachiopods, that are known to be pre-Wenlockian. Graptolite material from these formations is however much less common than shelly material, as these rocks were deposited in a much shallower water, higher energy environment. Rare specimens of the more robust forms of graptolite, particularly *Monograptus priodon* and *Retiolites geinitzianus sensu lato*, however, continue to be found in the Wether Law Linn Formation, possibly representing rocks of *grandis* and *insectus* Biozone age (Fig. 3.4). The Red Beds of the Henshaw Formation are thought to be predominantly of terrestrial origin (Robertson 1989), and have been dated independently as lower Wenlock by fish remains and plant microfossils preserved during rare marine incursions (Wellman and Richardson 1993).

3.7 Biostratigraphically significant fossils observed during this study.

3.7.1 Discussion

Most authors that have published directly on the NEI, have primarily been palaeontologists, and have therefore considered it important to give their opinion of the age of these rocks. Anomalies have crept in, as most authors have cited the presence of certain graptolites as

Sample	A	B	D	F	I	K	M	N
Conodonts present								
Panderodus unicostatus	0				0	0		
Pseudooneotodus sp.	0						0	
Distomodus sp. indet.	0	0						
Pterospathodus celloni	0				0			
Pterospathodus celloni (pennate)			0	0	0			
Oulodus sp. indet.					0			0
Carniodus carnulus					0	0		
Ozarkodina sp. indet.					0			
Pterospathodus amorphagnathoides						0		

Sample horizons	
SCRA =N	
930 =M	
920 =L	
860-875=K	*amorphognathoides Zone*
850-860=J	
B6 =I	
B6M24 =H	
B6M23 =G	
B5 =F	
550 =E	*celloni Zone*
B3 =D	
350 =C	
B3M6 =B	
M21B2 =A	

Figure 3.7
Conodonts obtained from samples from "Gutterford Burn Limestone Bed" locality
Analysed and identified by Dr. H Armstrong

being indicative of the age of the rocks, then from that information deducing that the trilobites (Clarkson and Howells 1981:509), or ostracods (Siveter and Vannier 1990:46), or brachiopods (e.g. *Pentlandella* Copper, 1977:296), or crinoids (Brower 1972), or echinoids (Kier 1973), are also of the same age. This has then led to these fossils, where they may be found independent of graptolites, being used to date rocks elsewhere, or to confirm the palaeoenvironment, because they are found in the Pentland Hills. This circular argument is of course perfectly reasonable and indeed accepted palaeontological practice, provided that the basic assumptions are correct. However, unless these fossils are independently dated from complete sequences of other biostratigraphically significant fossils, or otherwise corroborated, they cannot then be used as biostratigraphical indicators in the Pentland Hills.

As described below, the biozonal schemes of graptolites, conodonts and corals can now be correlated accurately by reference to the NEI, which should greatly improve future correlation in the uppermost Telychian.

3.7.2 Graptolites present

Monoclimacis vomerina (Nicholson, 1872); *Monoclimacis geinitzi* (Boucek, 1932); *Monograptus priodon* (Bronn, 1835); *Monograptus parapriodon* Boucek, 1931; *Oktavites excentricus* (Bjerreskov, 1975); *Retiolites geinitzianus* Barrande, 1850 *sensu lato*. and dendroids *Dictyonema pentlandica* Bull, 1987, *Thallograptus arborescens* Boucek, 1957; *T. inaequalis* Boucek, 1957; *Coremagraptus kalfusi* Boucek, 1957; *C. imperfectus* Kraft, 1982; *C. plexus* (Pocta, 1894); *Palaeodictyota pergracillis* (Hall and Whitfield, 1872).

3.7.3 Conodonts

The presence of P. *amorphognathoides* in sediments of the Reservoir Formation was noted by Robertson (1989); based upon identification of a small number of specimens by Dr. R. J. Aldridge. A larger number of blocks were selected on the criteria that they were not highly weathered; were still calcified; and contained some shelly fossil material or crinoid stems. These were sent to Dr. H. Armstrong in Durham, who kindly analysed them for their conodont content. The specimens were all from the logged section of the "Gutterford Burn Limestone Bed" locality. The results obtained are given in figure 3.7. The samples were sent in random order, and once sorted into stratigraphical order the results obtained are very convincing. (B3M6 is equivalent to the horizon found at 350 cm in the logged section, the sample being taken 6 metres along strike from the line of the logging; B6 is equivalent to 850-890 cm in the logged section).

All of the conodonts preserved suggest that the whole sequence is Upper Telychian, and pre-Wenlock. Samples D, F and I contain *"P. pennatus"* once thought to be a separate species but now shown to be the dextral element of *P. celloni*. This is most common from the upper part of the zone, and would suggest that the *P. celloni* Biozone specimens are from high within that zone. The lateral ledges around the Pa element in the *P. amorphognathoides* specimens from sample K, indicate *P. amorphognathoides* specimens from the lower part of that biozone.

The boundary between the *Pterospathodus celloni* and the *Pterospathodus amorphognathoides* conodont biozones appears to occur between 730 cm and 860 cm in the logged section. To be able to pinpoint accurately the boundary horizon to within 130 cm in a formation over 1100 m thick, is quite remarkable. It is also possible accurately to correlate the age of the graptolites from this same locality, with the age given by conodont data. The boundary between the *Pterospathodus celloni* and the *Pterospathodus amorphognathoides* conodont biozones is usually correlated with the middle of the uppermost graptolite biozone recognised in the Telychian, whatever each author may regard that to be (see fig. 3.2). To be able to actually tie in the two biozonal schemes to within hand specimen collecting distance,

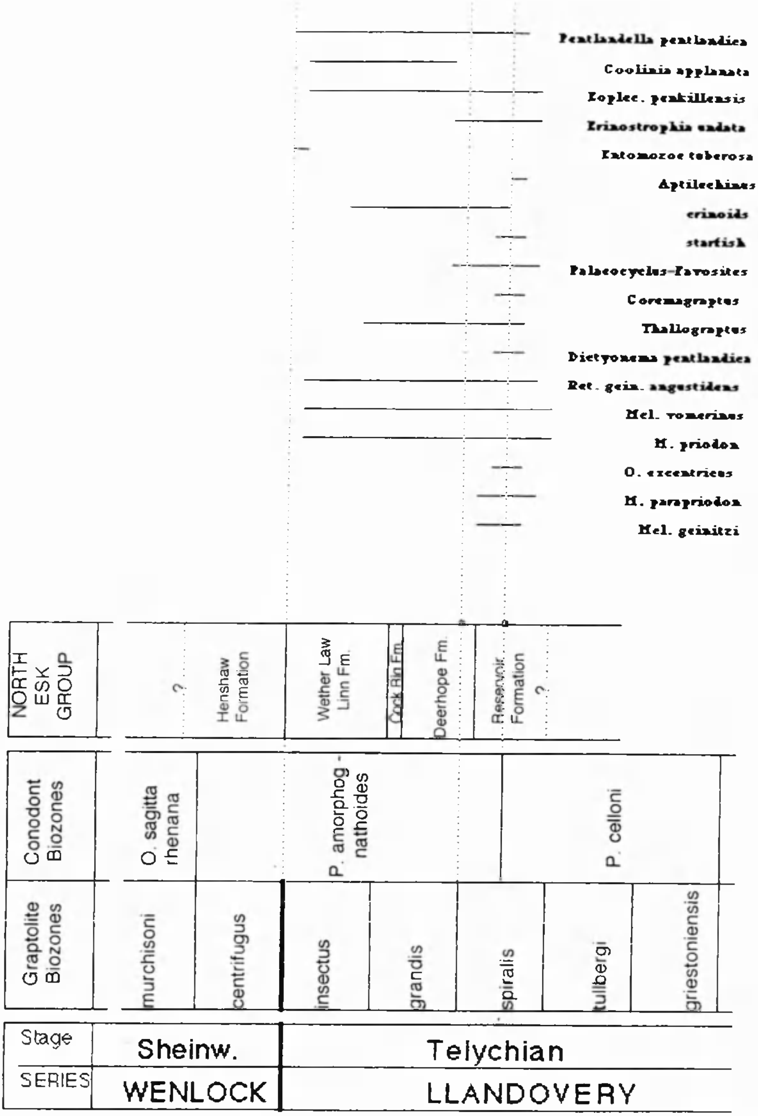


Figure 3.8: Range chart of selected elements of the North Esk inlier fossil fauna.

in an accessible rock section that readily yields well preserved specimens of both fossils, is very exciting and important.

Increasing resolution in conodont biozones is occurring for the Ordovician and attempts have been made to tie in the conodont biozones with the Ordovician graptolite biozones (Bergstrom 1986). This is, however, the first record of actual accurate correlation within the Telychian. The boundary between the *Pterospathodus celloni* and the *Pterospathodus amorphognathoides* conodont biozones can be shown to be equivalent to the middle of the *spiralis* graptolite biozone as represented in figure 3.8.

According to Dr. Armstrong's analysis, the minimum values of CAI of the specimens analysed are CAI 2. This indicates a temperature of 60°C and a depth of burial no greater than 2.5 km. The CAI's are recorded as variable, an effect of the proximity of the sediments to the series of intrusions observed in the Gutterford Burn.

3.7.4 Corals.

A number of the coral specimens present were examined by Dr. C. Scrutton, also of Durham University. There is enough good coral material, particularly in thin section (made by the author) to warrant further study, and a combined paper featuring the biostratigraphical details of the corals, conodonts and graptolites is planned.

Coral specimens are very common in the Deerhope Coral Bed (see fig 1, fig 3.4 and map for locality and stratigraphical position of this horizon). It must be stressed that the coral specimens mentioned below are from the "Gutterford Burn Limestone Bed" Locality only. The Deerhope Coral Bed is the subject of further study by Dr. ENK Clarkson and Ms. C Taylor (Clarkson and Taylor 1989).

The most common corals from the "GBLB" Locality, are *Palaeocyclus porpita (Linnaeus)*, and *Favosites multipora* Lonsdale. Other species identified are *Angopora hisingeri* Jones which is characteristic of the latest Telychian and earliest Wenlock, *Heliolites spongodes* Lindström, *Planocoenites* sp., *Phaulacus* sp., and rare *heliolitids* (3 species). Some of the species of *Heliolites* may be associated with those characteristic of the *Cystihalysites belledunensis* coral biozone as defined by Young and Noble (1990a), which ranges from the late Aeronian to the early *amorphognathoides* conodont Biozone. Notably absent from this fauna is *Aulopora* which is common from the Deerhope Coral Bed.

The co-occurence worldwide of two corals is so widely recognised now as to have become formally recognised as the *Palaeocyclus porpita - Favosites multipora* association. This association is widely accepted as restricted to horizons of late Telychian age (Bolton 1981; Curtis 1971; Eckert and Brett, 1989; Brett et al. 1989; Scrutton and Parkes 1992). The Palaeocyclus band was first identified as quite distinctive in the Tortworth inlier (Curtis 1971:16). The Tortworth beds are correlated with C6 beds of the Llandovery district by the

Crinoids were described by Brower (1975) from the "Gutterford Burn Limestone Bed" locality. The age range for the crinoids from the Gutterford Burn (Mid Fronian to early Telychian C2 to end C4) published by Donovan and Clark (1992:28), is entirely erroneous. It should be stressed that they are restricted to the spiralis graptolite Biozone in this area.

3.7.8 Brachiopods

The possibilities for accuracy in Llandovery brachiopod biostratigraphy are quite good, with evolving lineages of *pentameraceans*, *chonetaceans*, *Eocelia*, and *Stricklandia-Costistricklandia* having been recognised (Bassett 1989). From the Reservoir Formation, only 3 *stricklandiide* ventral valves are known, which are probably *Costistricklandia* (M. Bassett pers. comm. 1992). Late Telychian brachiopod faunas are quite distinctive (most of which are preserved in the NEI), with a number of species spanning the Llandovery Wenlock boundary (Bassett 1989:237). There is considerable potential for biostratigraphical control based on species of *Dicoelosia*. It is unclear as yet which species are present in the Reservoir Formation (see fig 10.19). Robertson (1989) recorded only *Dicoelosia* sp. There is currently not enough material of *Dicoelosia* collected to identify this to specific level, but this is a fault in collecting, as enough material has been identified at the "GBLB" locality, in the field to suggest this is worthy of further study (see fig 10.21). *Dicoelosia biloba* has been used to confirm Wenlock age (Holland 1988:357) in the Irish Silurian of the Dunquin Inlier.

The brachiopod *Megastrophia (Protomegastrophia) undata* M'Coy is relatively common in the Pentland Hills with 8? new specimens recorded (see fig 3.8, and fig.10.X). This species is only known from the NEI, the Charlestown Inlier in Ireland (Parkes 1992) and Gotland (Cocks and Worsley (1993), wherein the species was assigned to the new genus *Erinostrophia)*. This species is thought to be highly indicative that sediments are of late Telychian C6 *"crenulata"* Biozone age. It is found in the NEI in rocks from *spiralis* to *grandis* graptolite biozone age, and from celloni to lower *amorphognathoides* conodont biozone ages. A similar form *Erinostrophia walmstedti* occurs in the Lower Visby Formation of Gotland (Bassett and Cocks 1974).

Waterston (1979) mentioned the presence of *Eoplectodonta penkillensis* Reed 1917 as being characteristic of the uppermost Telychian and hence assigned a *"crenulata"* Biozone age to the sediments yielding eurypterid specimens. This species is now not thought to be so well restricted biostratigraphically. Another form, *Coolinia applanata*, does however seem to be restricted to the uppermost Telychian. This species is uncommon from the "GBLB" locality, and is much more common within the Wether Law Linn Formation above. This may suggest it to be characteristic of the *grandis* Biozone.

presence of *Costistricklandia lirata typica*.. Until now however, the *Palaeocyclus porpita - Favosites multipora* association has been described as of *crenulata* Graptolite Biozone age. Some correlation with conodont biozones has been possible. *Palaeocyclus porpita* is restricted to the *amorphognathoides* Biozone in Gotland (Scrutton & Parkes 1991:193). The Uggool Limestone Member of the Charlestown Inlier (Scrutton and Parkes 1991:195; Parkes 1993) has yielded specimens of *Pterospathodus celloni* along with a common *Palaeocyclus porpita - Favosites multipora* association fauna.

The *Palaeocyclus porpita - Favosites multipora* association in the NEI is recognised from a number of localities, and is common in both the "GBLB" Locality and the Deerhope Coral Bed. In particular, at the "GBLB" locality, *Palaeocyclus porpita* occurs both above and below the horizon now recognised as the *celloni-amorphognathoides* conodont Biozone boundary. In the past, the Deerhope Coral bed, considered as lying within the *crenulata* graptolite Biozone age has been used to date rocks with equivalent faunas in other areas (Scrutton and Parkes 1990:193). The stratigraphy outlined in this volume would place the Deerhope Coral Bed at the very end of the *spiralis* Graptolite Biozone or early in the *grandis* Biozone. The *Palaeocyclus porpita - Favosites multipora* association can thus be said to be equivalent to the mid-*spiralis* to *grandis* Graptolite Biozones, and of very late *celloni* to mid *amorphognathoides* Conodont Biozone age.

3.7.5 Starfish

A number of starfish are known from the Reservoir formation, and described in detail by Spencer (1914-1940). Spencer originally believed the sediments of the NEI to be Wenlock in age, and consequently named many of his new species accordingly, e.g. *Urastella gutterfordensis* Spencer 1918; *Protactis wenlockensis* (Spencer 1922); *Tæniactis wenlocki* Spencer, 1922; *Crepidosome wenlocki Spencer* ; and *Schuchertia wenlocki* Spencer .
However, by the time the final parts of the monograph were published, Spencer (1965) made reference to the more recent work on the area (Lamont 1947) and updated all of the Gutterford Burn Starfish Bed material to Llandovery age (Spencer 1965:571).

This has, however, caused others to refer their starfish finds to the Wenlock by comparison (Ward 1989:152). Many new specimens of starfish have been found from level 200 cm in the logged section of the "GBLB" locality, suggesting them to be *celloni* age, mid *spiralis* Biozone It is thought that some of Spencer's specimens also came from another Starfish horizon, above the *celloni-amorphognathoides* boundary (see fig 3.8 and map).

An exquisite fauna of echinoids has been discovered in the Reservoir Formation. Indeed a number of new specimens of *Aptilechinus* have been discovered, from level 200 cm in the logged section of the "Gutterford Burn Limestone Bed" locality, suggesting them to be *celloni* age, *mid spiralis* biozone. The new specimens of starfish, echinoid and crinoid are illustrated in figs 10.1-10.7.

Chapter 4

Geology.

4.1 Introduction

The North Esk inlier is not an ideal area for conducting research into sedimentology. Exposure is poor (fig 4.1), the rate of weathering is high and sedimentary structures are not visibly abundant. It is not an area likely to yield information initiating or confirming any theoretical principles. The sediments present can, however, be compared with others elsewhere and sufficient structures are preserved to warrant reasonably detailed interpretation. A model has been formulated that encompasses the sedimentary structures observed, in the light of the most recent research, rather than making broad generalisations.

Conclusions derived from this area, have implications for other areas and for interpretation of the tectonic history of the Midland Valley. The most recent model for the depositional history of the sediments of the NEI was given by Robertson (1985; 1989). Robertson's work focussed on the interpretation of the upper formations of the North Esk Group, and gave only a brief summary of the geology of the Reservoir Formation. This present study has focussed on the Reservoir Formation, and this is now interpreted quite differently. Robertson's conclusions regarding the deposition of the upper formations are not challenged, and actually enhanced by the conclusions made herein (see section 4.7 and diagrams therein). A summary of the depositional model for the whole group is given in section 1.6.

Reconstructions of the history of sedimentation in the area cannot be considered in isolation. Clearly a depositional model that disagreed with findings from other research must generate problems. Conversely any research findings should not be biased by preconceived ideas of what should be found. The importance of the maximum use of multiple palaeobathymetry indicators (Baarli 1988) is recognised, and an integrated approach is made here.

The palaeogeography of the Midland Valley during the Llandovery and Wenlock has received much attention recently, and the maps published by Cope *et al.* (1992) are followed here (fig 4.2). The Midland Valley of Scotland is now no longer considered in isolation. Correlation of depositional basins across the Midland Valley Terrane of Scotland, Ireland and into Newfoundland (recognised by Holland 1969), and possibly also Scandinavia (Pickering *et al.* 1988), is now well established (Doyle *et al.* 1991:440; Colman-Sadd *et al.* 1992:572).

When a palaeogeography has been established, it is possible to infer palaeobathymetry by considering the proximity of the depositional environment to the palaeocoastline. McKerrow (1979:137) suggested that interpretations of palaeobathymetry (being made at that time),

Figure 4.1: A: View of the Gutterford Burn and North Esk Reservoir looking south, showing poor exposure levels.
B: Small scale spheroidal weathering in shale horizons from east shore of Reservoir (lens cap 52 mm diameter)

C: Large scale spheroidal weathering in siltstones of Wether Law Linn Formation, Authors size 101/2 for scale.

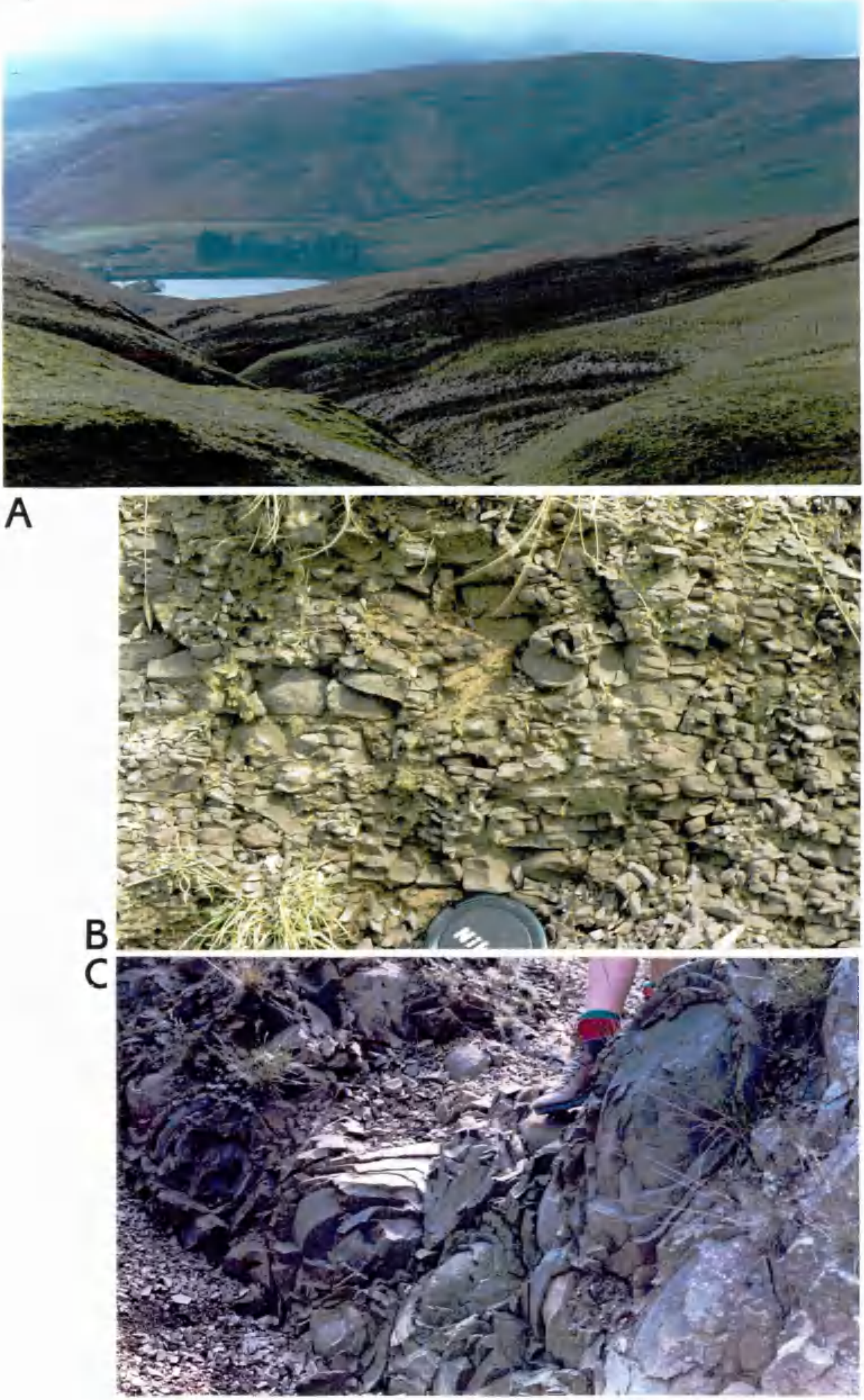
3.8 Chapter summary

A revised scheme of graptolite Biozones is presented. The concept of the *crenulata* biozone being the one biozone between the *greistonensis* biozone and the Lower Wenlockian *centrifugus* biozone, is replaced by four separate biozones.

The sediments of the NEI are suggested to have been deposited in the Llandovery, between the middle of the *spiralis* graptolite biozone and the base of Wenlockian *centrifugus* graptolite biozone.

The boundary between the *celloni* and *amorphognathoides* conodont biozones is identified within the Reservoir Formation, and corellated with the middle of the *spiralis* graptolite biozone. The *Palaeocyclus porpita* - *Favosites multipora* coral association is suggested also to indicate deposition during the period equivalent to the mid-*spiralis* to *grandis* Graptolite Biozones, and of very late *celloni* to mid *amorphognathoides* Conodont Biozone age.

Figure 4.1



were too dependent on models of palaeogeography, and furthered the use of fossil (brachiopod) communities to interpret water depth and hence improve palaeogeographical constructions. The argument is now thought to have come full circle. Palaeogeographical maps have improved greatly since 1979, and is in part due to such work as that of McKerrow (1979) being incorporated into the production of these maps. Recent palaeogeographical constructions are now becoming widely accepted. Although these maps will be subject to revision, this is likely to take the form of minor changes, rather than wholesale reconstruction. An important factor therefore, is that *there is not enough room in the (palaeo)geography, for the amount of topographic relief* required to suggest deposition as deep marine basinal-plain turbidites. Evidence is given below for the reinterpretation of these (Reservoir Formation) sediments as deposited by storm influenced processes in the equivalent of an outer shelf environment. A number of other Midland Valley Silurian sequences in Ireland have also recently been reinterpreted in this way (Doyle, 1994).

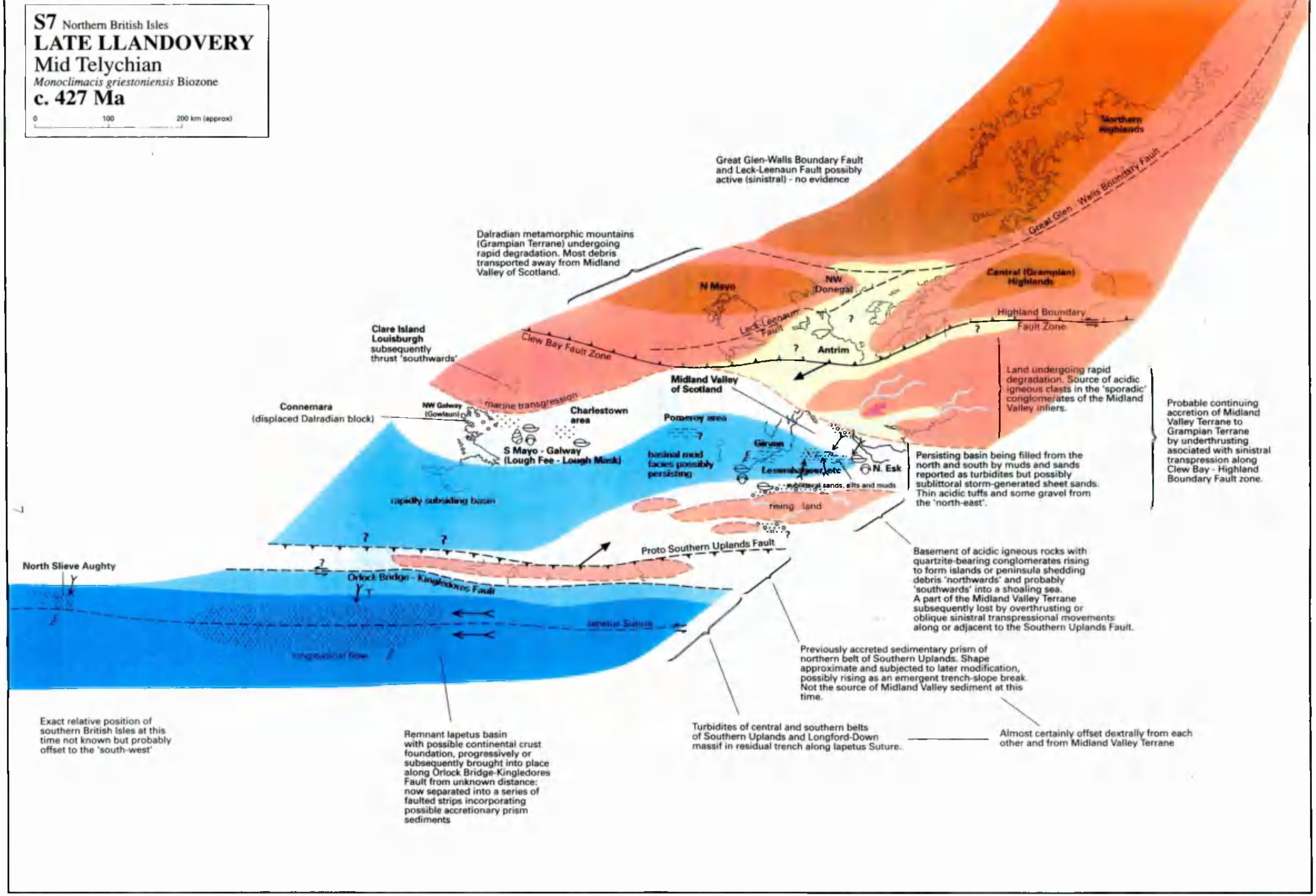
The late Telychian is interpreted as a time of global eustatic sea level rise (McKerrow, 1979), which has been recognised in North America, (Johnson 1987), Estonia (Johnson *et al.* 1991a), China (Johnson *et al.* 1985), Scandinavia (Baarli, 1990a:154; Baarli 1990; Johnson and Worsley 1982), Wales (Ziegler *et al.* 1968) and the West of Ireland (Williams and Harper 1988, Doyle 1994). The uppermost Telychian represents the maximum intensity of this extensive marine transgression (Doyle et al. 1990; Doyle 1994). Sea levels are thought to have fallen again in the early Wenlock (McKerrow 1979; Williams and O'Connor 1987). Therefore the unequivocal identification of a regressive sequence for the North Esk group, accurately dated as uppermost Telychian must be taken into consideration in the construction of any depositional model.

4.2 Overall pattern

The North Esk group records a regressive sequence, interpreted herein as being formed in water depths from outer shelf below storm wave base, gradually shallowing to nearer shore (figure 3.6 shows the currently accepted lithostratigraphy). Only the Reservoir Formation has been studied in detail here; further details of sedimentary structures, and fossil associations can be found in Robertson (1985; 1989) and are summarised below.

The alternating fine grained siltstones and mudstones of the Reservoir Formation are interpreted herein as distal storm deposits interbedded with finer offshore pelagic sediments (for comparative interpretation see Doyle 1994:200; Kreisa 1981). They can be compared with the sediments that Hurst and Pickerill (1986) described as deposited by storms on a muddy shelf. Previously these were considered to have been deposited as deep ocean plain distal turbidites, as is discussed in more detail in section 1.6 and 4.7. The Deerhope Formation is poorly exposed in its lower parts and is interpreted herein as overbank deposition of a fan. Robertson (1985:138) considered this to have been a deep ocean fan, with the Cock Rig Formation representing feeder channels within this, or possibly a canyon-fill deposit. The fan model is not disputed here, only its palaeobathymetry.

Figure 4.2. Proposed palaeogeography of the Midland Valley during the late Llandovery. From Cope *et al* 1992.



Great Glen-Walls Boundary Fault and Leck-Leenaun Fault possibly active (sinistral) - no evidence

Dalradian metamorphic mountains (Grampian Terrane) undergoing rapid degradation. Most debris transported away from Midland Valley of Scotland.

Land undergoing rapid degradation. Source of acidic igneous clasts in the 'sporadic' conglomerates of the Midland Valley inliers.

Probable continuing accretion of Midland Valley Terrane to Grampian Terrane by underthrusting associated with sinistral transpression along Clew Bay - Highland Boundary Fault zone.

Persisting basin being filled from the north and south by muds and sands reported as turbidites but possibly sublittoral storm-generated sheet sands. Thin acidic tuffs and some gravel from the 'north-east'.

Basement of acidic igneous rocks with quartzite-bearing conglomerates rising to form islands or peninsula shedding debris 'northwards' and probably 'southwards' into a shoaling sea. A part of the Midland Valley Terrane subsequently lost by overthrusting or oblique sinistral transpressional movements along or adjacent to the Southern Uplands Fault.

Previously accreted sedimentary prism of northern belt of Southern Uplands. Shape approximate and subjected to later modification, possibly rising as an emergent trench-slope break. Not the source of Midland Valley sediment at this time.

Exact relative position of southern British Isles at this time not known but probably offset to the 'south-west'

Remnant Iapetus basin with possible continental crust foundation, progressively or subsequently brought into place along Orlock Bridge-Kingledores Fault from unknown distance: now separated into a series of faulted strips incorporating possible accretionary prism sediments

Turbidites of central and southern belts of Southern Uplands and Longford-Down massif in residual trench along Iapetus Suture.

Almost certainly offset dextrally from each other and from Midland Valley Terrane

The Deerhope and Cock Rig Formations are considered herein to have been nearshore sediment accumulations, with periodic colonisation by unique communities, resulting in unique fossil assemblages (Clarkson and Taylor 1989). These deposits were possibly also affected by storm processes, and connected to alluvial deposits landwards. The Wether Law Linn Formation was the focus of Robertson's (1989) work, and he interpreted it as a shallow marine barrier complex, deposited and modified by (proximal) storm and fair weather processes (figure 4.3a). Fossil "associations", representing communities which repeatedly colonised these sands were recognised. The upper member of the Wether Law Linn Formation was interpreted (Robertson 1989) as deposited in a restricted lagoonal environment, protected by the barrier sands and silts, characterised by the Middle Member. The transition between the Wether Law Linn formation and the Henshaw Formation appears to represent a Silurian shoreline (Robertson 1989:139). The Henshaw Formation is interpreted as having been deposited in a terrestrial alluvial fan environment of Old Red Sandstone facies, with periodic marine incursions (Wellman and Richardson 1993).

The Reservoir Formation is about 1100m thick (the base is not seen) and consists predominantly of alternate thin beds of siltstone and shale. Cycles of sedimentation can be identified as mappable units, but most individual siltstone horizons are laterally persistent for only 10-20 m. The shales are fine grained mudstones containing thin stringers, rippled lenses, and lenticular laminations (Hurst and Pickerill 1986) of siltstone. The siltstones frequently show dewatering structures and loading. Bioturbation is common throughout. Rare fossils are found within the lowermost 900 m of sediment, mostly graptolites and *Dictyocaris* (interpreted here as of algal affinity (chapter 10) draping the sediment surface). There are also mud clasts, possibly bound by algae. The upper part of the formation is characterised by periodic deposition of lenses of biogenic material. Some are coquinas, containing reworked transported shell fragments, some are winnowed and *in situ* deposits, and partially colonised surfaces. Some lenses contain an undoubtedly *in situ* fauna of dendroids, echinoids, starfish or eurypterids (generally not together). The mica content of the sediments is high throughout.

4. 3 Sedimentology.

4. 3.1 Sedimentary structures.

Previous models for the depositional history of the Reservoir Formation (Robertson 1985), concentrated on the thin bedded silt-shale alternations, and recorded little in the way of internal sedimentary structures. Details of features observed during this study are described, illustrated, and interpreted below.

To consider these sediments as merely interbedded silt and shale (d-e Bouma cycle) is an oversimplification. Whilst the sedimentological evidence is not extensive, interpretation as distal outer fan basin plain turbidites ignores a wealth of information, and does not adequately explain all of the features present.

Figure 4.3
a) Summary diagram of the palaeoenvironmental setting, proposed by Robertson 1989:139.
b) Late Llandovery palaeogeographic reconstruction, taken from McKerrow *et al* 1991:171.

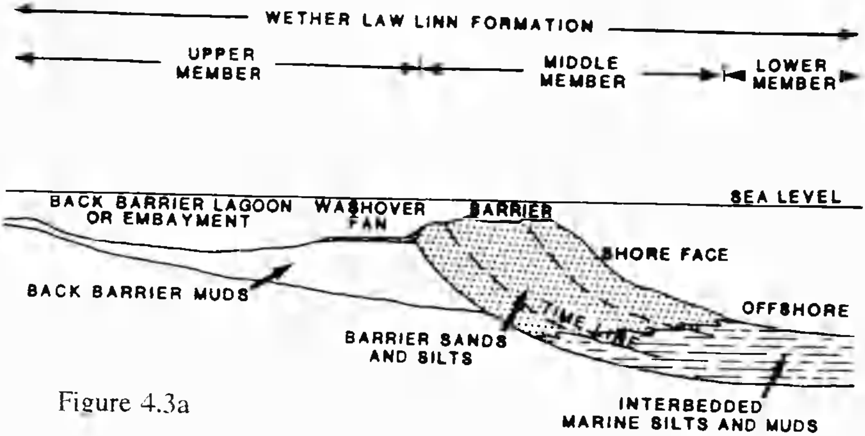


Figure 4.3a

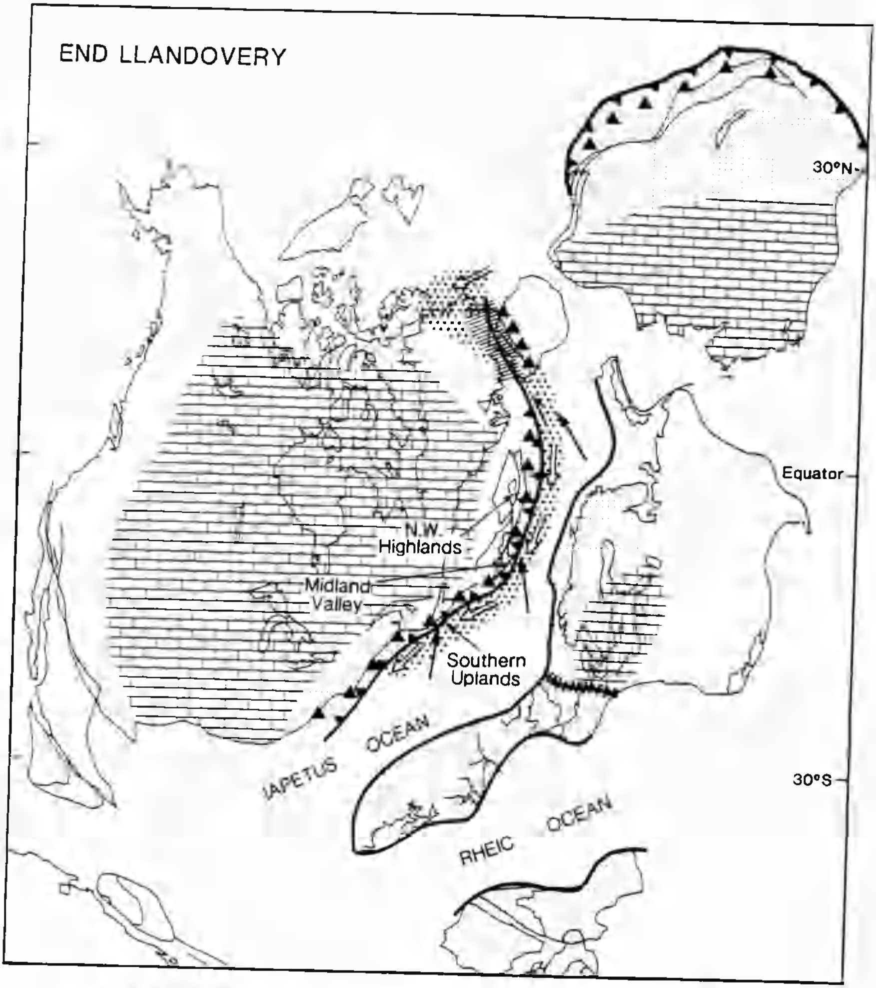


Figure 4.3b

Figure 4.3. a) summary diagram of the palaeoenvironmental setting for the Wether Law Linn Formation, proposed by Robertson (1989).
b) Late Llandovery palaeogeographic reconstruction. Taken from McKerrow *et al.* 1991 171.

Almost every thin section produced from this sequence contains large quantities of mica, sometimes with flakes over 1 mm long. The mica content is so ubiquitous that it is easy to overlook in thin section descriptions. Quite fresh clasts of redeposited rock particles are also common. Mica is susceptible to weathering and erosion, and rapidly disappears during sediment transport and deposition. Its presence is usually taken to imply proximal deposition quite close to source.

Overall, the Reservoir Formation sediments are fine grained, the largest particle sizes observed being of coarse silt grade and perhaps of a fine sand grade in the thickest beds exposed on the reservoir shore. The largest clast sizes are the biogenic particles and shell debris found in the coquinas (see later). This small particle size has been important to the previous interpretations of these sediments. Thin bedded alternations of mudstone and fine siltstone, not associated with thick, coarse grained beds, are classically interpreted as distal turbidites. Such fan fringe deposits are laterally persistent, showing uniformity over great distances and thicknesses (Mutti, 1977).

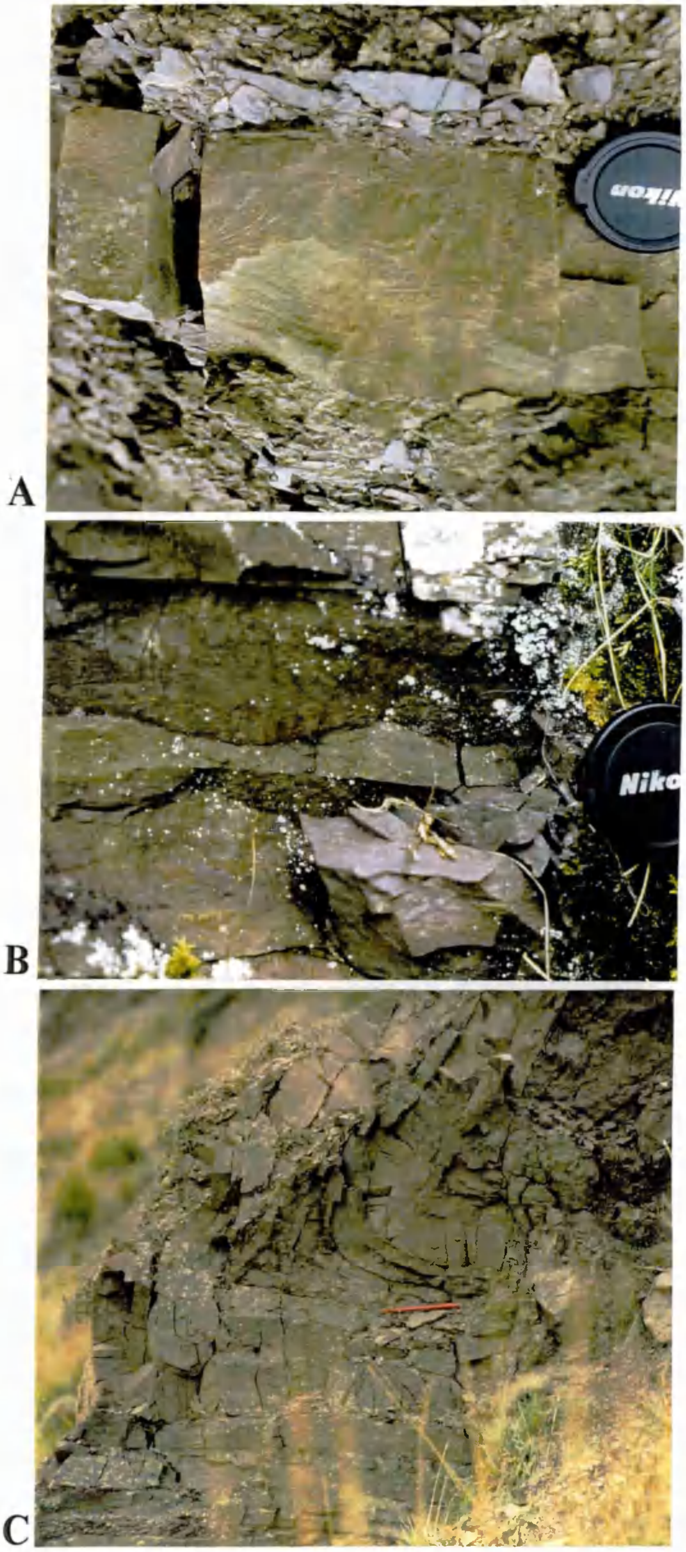
The fine grained nature of the sediments is herein interpreted not to imply distance from source, but to imply a fine grained source. Even the sediments of the Wether Law Linn Formation, interpreted as nearshore barrier sand bar and lagoonal sediments, are fine grained, the coarsest horizons being fine sands. It would therefore be unreasonable to suggest that sediments deposited by storm reworking of fine grained nearshore sediments, would deposit anything other than fine grained sediments offshore.

Doyle (1994:201) described storm generated horizons from the Irish Silurian as lacking in internal sedimentary structures and suggested an essentially unimodal grain size distribution as the cause. Generally, in the NEI, sedimentary structures can best be seen in loose weathered blocks. Also, the uniformity of particle size found in the NEI conceals internal structures. They can be highlighted when chemical differences cause unequal weathering rates, also resulting in different lichens growing. There is a problem in that if the rocks have been exposed for too long, they become obscured by lichen, and recently exposed rocks have insufficient weathering to make sedimentary structures visible. Therefore *in situ* sediments, are generally either too long exposed to show sedimentary structures as they have been exposed for many years, or too new when hit recently with a hammer. The best sedimentary structures are seen where the rocks are periodically scoured such as in a fairly new exposure along the reservoir shore.

Concretionary structures are rare. One horizon with nodules is known from within the logged section (section 4.5 and fig. 4.14). Such horizons may be more common but only found here due to the careful examination of freshly exposed material. Spheroidal weathering

Figure 4.4. Field photographs, lens cap 52 mm.
A: Hummocky cross stratification from grid reference NT 1601 5944.
B: Detached ripples of siltstone within mudstone, fron grid ref NT 1554 5757
C: Fold, possibly resulting from downslope slumping soon after deposition. Locality at mouth of Gutterford Burn, NT 1554 5838. Pencil 12 cm for scale.

Figure 4.4



is common (figs 4.1b &c) both in the siltstones and shales, and is due to the homogeneous nature of the sediments. This was examined by Haswell (1865:16)

> "Most of the hard and some of the soft beds have a peculiar concretionary structure; and in breaking them a prevailing form to lay open somewhat resembles in shape and appearance the carapace of a large crustacean; but this cannot be, as you sometimes get one ten inches in diameter enclosing one eight inches, which encloses another five, in the inside of which is another three inches, all having the same appearance and outline. They are not nodular concretions, with the matter arranged in circles but have the stratifications sometimes running straight through them, and the peeling seems to be caused entirely by the weathering. I have broken several thousand of these, and have failed to discover any markings which would lead to the belief that they are the carapace of a crustacean."

The Reservoir Formation is dominated by fine grained mudstone sometimes weathering to shale and sometimes remaining as massive mudstone. Although a few of the siltstone horizons are thicker, mud must have dominated the depositional environment. These mudstones are not structureless, and contain either:-

1) remains of intensive bioturbation, with abundant (silt or mudstone filled) *Chondrites* burrows (some horizons are structureless or mottled, the result of complete bioturbation),

or

2) thin stringers of siltstone within the muds, showing ripples, small scale lenses, some of which can be identified as small scale Hummocky Cross Stratification, lenticular bedding, or thin laminations of silt.

Parallel lamination is common within siltstone horizons as are ripples, with climbing ripples, asymmetrical and wave ripples, several varieties of cross laminations, undulating lenses of sediment, and foresets giving variable current directions. The only consistent factor readily obtained from these internal structures is the way up of the sediments. Many of the siltstone horizons have mudstone drapes within them and flaser lamination, and this is sometimes the only way that sedimentary structures can be observed within the siltstone, due to the otherwise unimodal grain size and type. Internal grading of siltstones is not common. A few examples of swaley and hummocky cross stratification (Yagishita *et al.* 1992) have been found, and some examples of detached ripples within shales (Broadhurst 1968). These features are illustrated in fig. 4.4.

The shale is not just simply the product of background sedimentation. The lenticular lamination within the shales, and flaser lamination within the siltstones (Hurst and Pickerill, 1986:705) are interpreted as the result of tidal current and wave reworking. According to Bourgeois (1980:684) laminated fine sands, and parallel laminated and burrowed facies are found on the outer shelf, beyond the region where storm waves are capable of erosion. Storm sands can have several features in common with turbidites as they are both deposited in a waning flow regime (Reading 1981).

Small scale thrusts and kink bands are discussed in chapter 5. It is possible that some of the folding and slumping structures (e.g. at the mouth of the Gutterford Burn fig 4.4c) are the

Figure 4.5 Field photographs. A: Possible mudcracks formed during subaerial exposure of deposition surface. from eastern shore of Reservoir. Specimen EEB 301, penny scale 12 mm diameter.
B: Sand volcano from eastern shore of Reservoir, formed during near surface wethering. Specimen EEB 302.
C: Cross section of above, lens cap 52 mm. D: Small scale HCS from eastern shore of Reservoir. Spec. EEB 313.

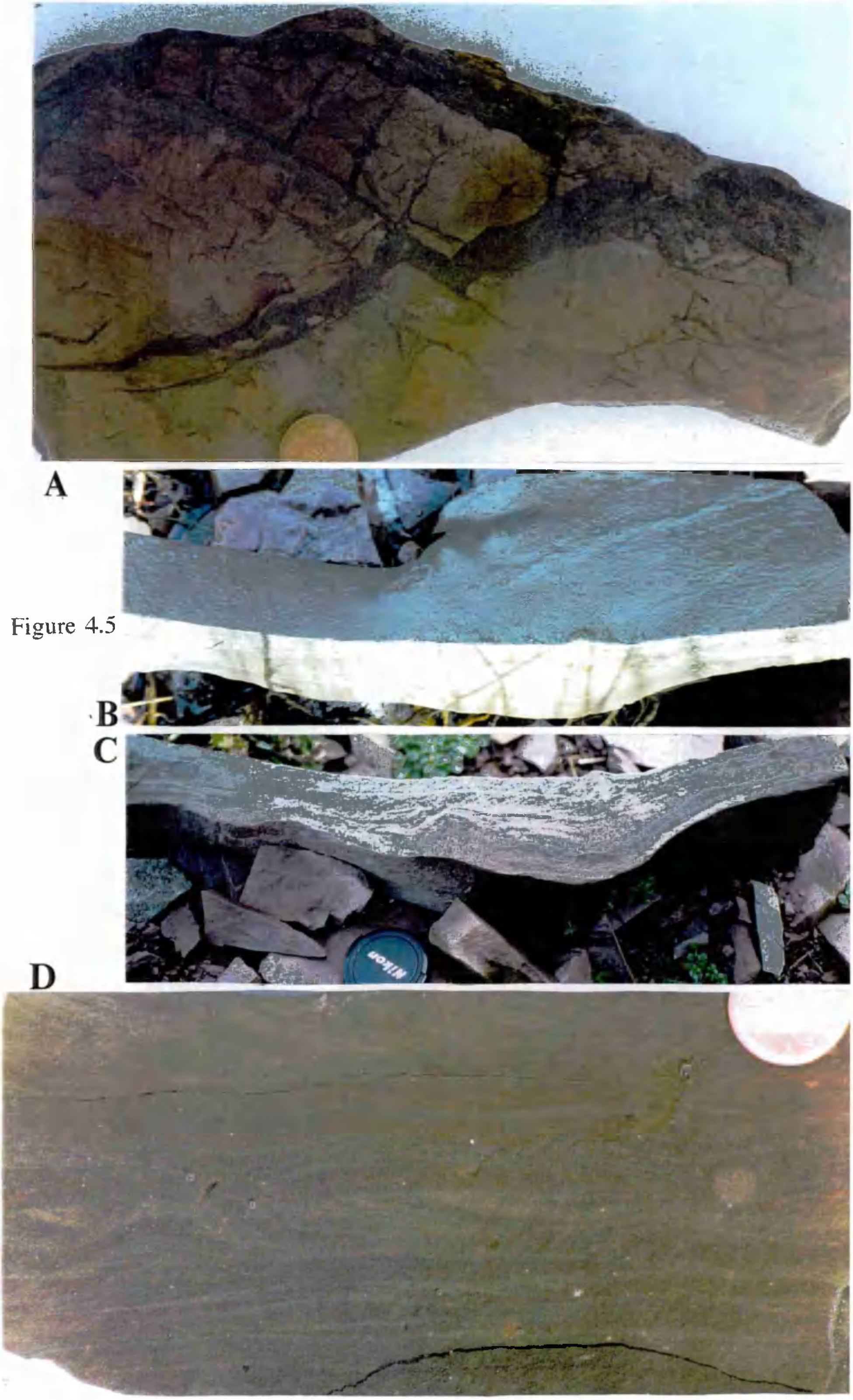


Figure 4.5

result of sediment slumping down a slope (Whitaker 1994:34). Slumping can occur on a continental slope (or basin margin) inclined at only 1° (Lewis 1971), may involve tens of metres thickness of sediment, and can be triggered by earthquakes. Such slumps have been analysed and used as palaeoslope indicators (Woodcock 1979b). However, pre-lithification slump folds can show considerable scatter and can record movement down the flanks of local basinal swells, rather than along the axis of any known trough or basin (Eva and Maltman 1994). Insufficient information exists here to pursue this issue.

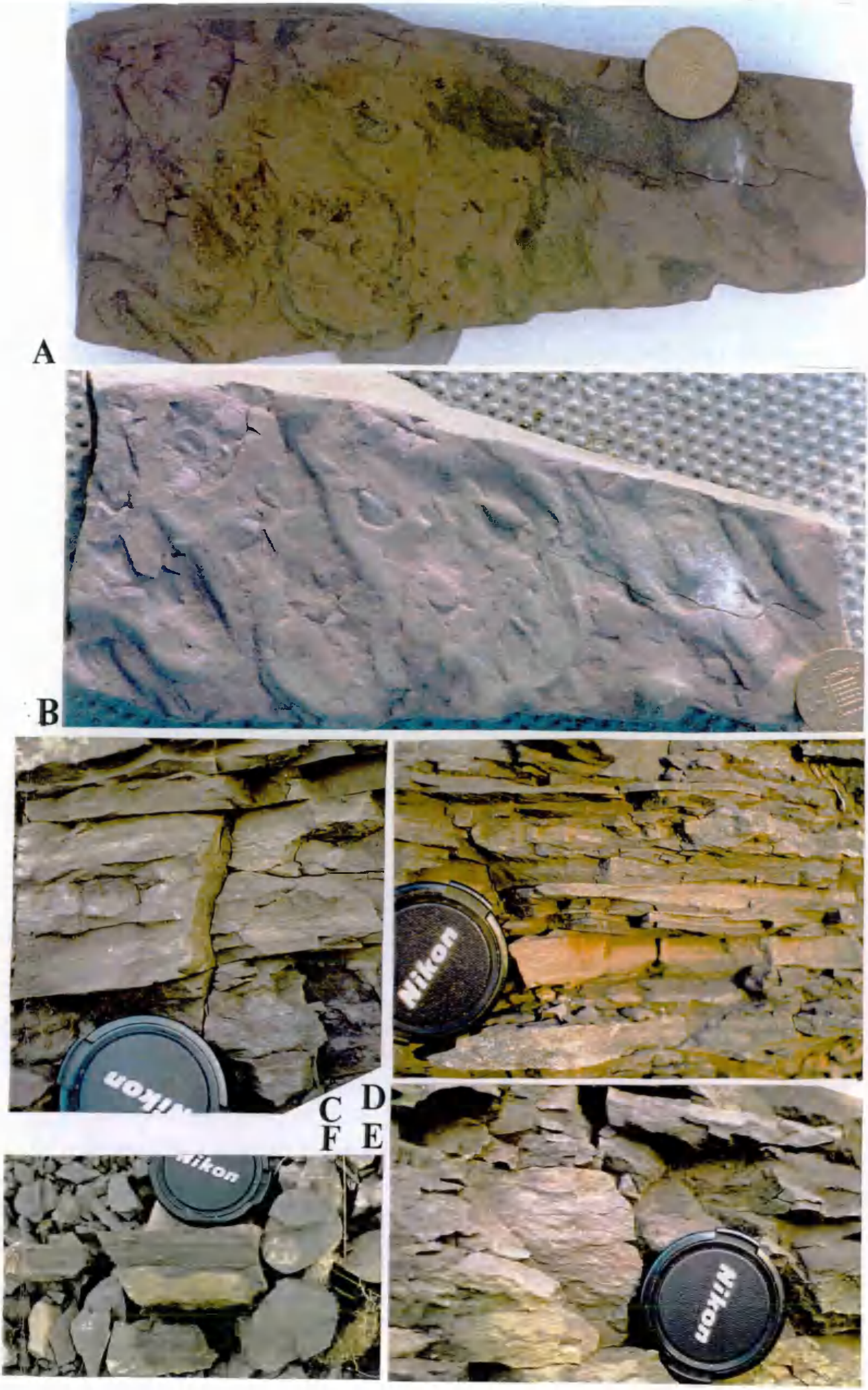
Hummocky Cross Stratification (HCS) is interpreted as being formed by wave action on the shoreface, continental shelf, and in shallow seas. It involves redeposition, below normal fair weather wave base, by fine sands and silts being delivered offshore by large waves and is associated with wave oscillation (Dott and Bourgeois 1982:663). Scarcity of HCS (the situation in the NEI) and abundance of parallel laminations tends to imply deposition below storm wave base (Nealon 1989:63). Palaeocurrent data from the Reservoir formation have proved inconclusive, which is the normal case with oscillating wave induced currents. Erosive channels and surface topography have been preserved by subsequent siltstone deposits.

Some siltstone horizons have rip-up clasts and rounded ‘pebbles’ of the underlying mudstone incorporated in their lower portions. The close proximity of the mudstone clasts to their position of origin suggests little transport. Some signs have been found that may be indicative of subaerial exposure. Features closely resembling mudcracks have been observed (fig 4.5a) (Dr. Terry Scoffin pers. comm. 1995), and whilst the possibility of these being syneresis cracks (Plummer and Gostin, 1981) is not ruled out, the angular nature and V shaped profile of the specimens considered, would imply a subaerial mode of origin. This would suggest at least temporary near shore exposure. Some of the bases of beds have prod and groove marks, but rain pits have not been positively identified yet. Also sand volcanoes are present. Today these (fig 4.5b&c) form close to the surface particularly where water is left lying on the shoreline in puddles, weighting down the surface and causing dewatering structures such as these to form in unconsolidated near surface layers as pore fluids escape. Large (5-20 cm. high) “sand volcanoes” are known as ‘monroes’ (after Marilyn Monroe) smaller ones are known as ‘twiggies’ (Reineck and Singh 1980:442). Dewatering structures tend to follow trends such as ripple crest orientation in underlying sediments, primary sedimentary fabric or local topography (King 1994:266).

Some mud clasts within this sequence form ‘mudflake conglomerates’. These are formed where flakes of mud are isolated by cracking of the surface during subaerial exposure. When water refloods the area, some of these flakes are lifted up into the base of the overlying siltstone. In later (e.g. Carboniferous onwards) deposits these mudflake conglomerates are

Figure 4.6 Bioturbation All from Reservoir Formation, eastern shore of Reservoir, *O.spiralis* Biozone age. A:B. Specimen EEB 303, Surface meandering *Planolites* (larger) and (smaller) *Chondrites* burrows, A, taken beneath water. C-E, Field photos. lend cap 52 mm diameter, *Chondrites* burrows are common within shales, where they often appear as green circles 3-5 mm diameter within reddish purple mudstones.

Figure 4.6



associated with tree and other vegetable debris. In the Silurian, little land plant material is available, but *Dictyocaris* is thought to have played this role in the Telychian.

Specimens with convincing Bouma sequences, particularly the d- e divisions typical of the supposed distal turbidites are not readily found, although sections with thin alternations of silt and shale are present (fig 1.5b). On closer inspection, these tend to be bioturbated and contain lenticular laminations of silt within the shale. It is possible that some of these siltstone horizons were deposited by turbidity flows triggered further (southwest) along the basin, or shores of the remnant ocean. The direction of flow of these currents may then have been directed (deflected) laterally along the basin. This would have caused sediment to be deposited by a turbidity current, distally from the source of the current, but actually not far off shore. Thus it is possible to be laterally distal without being at the distal margin of a fan fringe in deep water.

The shales vary in colour from red to olive green, pale grey to yellow. The colour of each sedimentary unit is not laterally persistent. Red shale implies that the depositional environment was oxygenating, not that there was a red soil present. The final colour of shale deposits is a result of depositional environment, compaction, diagenesis, weathering and combinations of all of these factors (Potter *et al.* 1980).

Attempts have been made to trace individual horizons laterally, but lateral continuity is not observed. Each siltstone horizon can generally only be traced the width of a single locality (up to 40m), and comparisons of sedimentary logs from neighbouring localities, although clearly exposing the same part of the sedimentary succession (see section 4.4) do not have exactly the same horizons. Similarly, on inspecting a single horizon, lateral variations are found. In one part of the same horizon, convolute bedding may be observed, and in another, parallel lamination at the same level within the bed. Most siltstone horizons have sharp bases and some have sharp tops. Some grading is observed. Thin (10-20 cm) proximal storm beds were identified in Western Ireland by Doyle (1994:198). Their thinness was attributed to restricted access to open sea and lack of adequate supply of sand.

The sediments of the NEI are thought to have been deposited rapidly, as indicated by the great thickness of sediment deposited within a relatively short period of time, and the prevalence of dewatering structures present (see above). 1500 m of (lithified) sediment was deposited in less than one graptolite biozone. Assuming one full Silurian graptolite biozone to have lasted 1 million years, then the NEI sequence represents approximately 3 mm of sediment for each year of deposition.

It should be noted that in present day oceans, significant quantities of mud cover the entire shelf only in association with major rivers. Large quantities of mud may also accumulate as a

Figure 4.7: From Reservoir Formation *O. spiralis* Biozone age, arthropod track locality (NT 1601 5944) Field photo. Surface trace fossil *Taphrhelminthopsis*. ring 21 mm diameter. Animal meandering across surface of sediement, 4.7b is detail of 4.7c showing possible footprints of animal.

Figure 4.7

result of tidal action. At the end of present day tidal current transport paths, sand patches (sheets) and substantial quantities of mud are deposited, particularly in water greater than 30m deep. Muds will accumulate at the end of tidal transport paths, where there are no large tidal currents to sweep the mud clear. This may be enhanced by ebb and flow currents taking mutually exclusive paths. The quantities of mud accumulating in the North Esk basin could have resulted from either of these mechanisms. It is impossible to tell what the tidal patterns would have been within the remnant Iapetus Ocean, and hard to estimate the size of rivers supplying sediment into the ocean at this time. It is thought likely however that major rivers were draining the land nearby, and these are shown on figure 4.2.

At the end of the Llandovery, the Midland Valley is thought to have been just south of the equator (fig 4.3b) (McKerrow *et al.* 1991:171). Climate has a major effect on the weathering rate on land, and temperature and precipitation control erosion and transport. The high sediment supply to the North Esk basin is consistent with the high weathering rates associated with equatorial climates, especially in the absence of a vegetation cover.

4.3.2 Bioturbation.

Wignall (1993:193) stated that "a declining oxygen gradient causes benthic diversity to decline to a zero point". This is supported by the observation that a superabundance of *Chondrites* burrows can be associated with anoxic conditions (McCann 1990:249). Colonisation of the substrate by only one animal, such as that forming *Chondrites* burrows, represents a very low faunal diversity. Wignall (1993:193) also noted that "a transition from firm to soft substrate is associated with a decline in overall benthic faunal diversity but, importantly, this has little effect on epibionts." Increasing substrate softness he associates with a reduction in the depth to which infaunal organisms can burrow (and still keep their burrow open), hence increasing substrate softness is linked with a decrease in faunal diversity. Wignall (1993:194) also suggests that soft substrates attract soft substrate specialists. The relative lack of benthic forms in the lower parts of the Reservoir Formation does not necessarily imply deep, or poorly oxygenated water. Because of the presence of relatively large quantities of animal burrows within the sediments, it is suggested that the substrate was soft and soupy, unsuitable for colonisation by benthic creatures. The majority of this bioturbation is of the *Chondrites/Planolites* association, which appear to be associated with softer sediment types.

Bruce (1992) stated that "The Reservoir Formation generally contains very occasional *Planolites*. within very dark mudstones, but no other trace fossils." This generalisation is not accepted here. *Chondrites* burrows are common within the shales, where they often appear as green circles 3-5 mm in diameter within reddish-purple mudstones. Surface meandering *Planolites* burrows have also been identified (fig 4.6). Very dark mudstones are uncommon in the NEI. The Reservoir Formation shales often have a mottled appearance due to complete bioturbation. Bioturbation does not occur in every horizon however, and whilst not absent, the *chondrites* burrows are not as common as their ubiquitous appearance

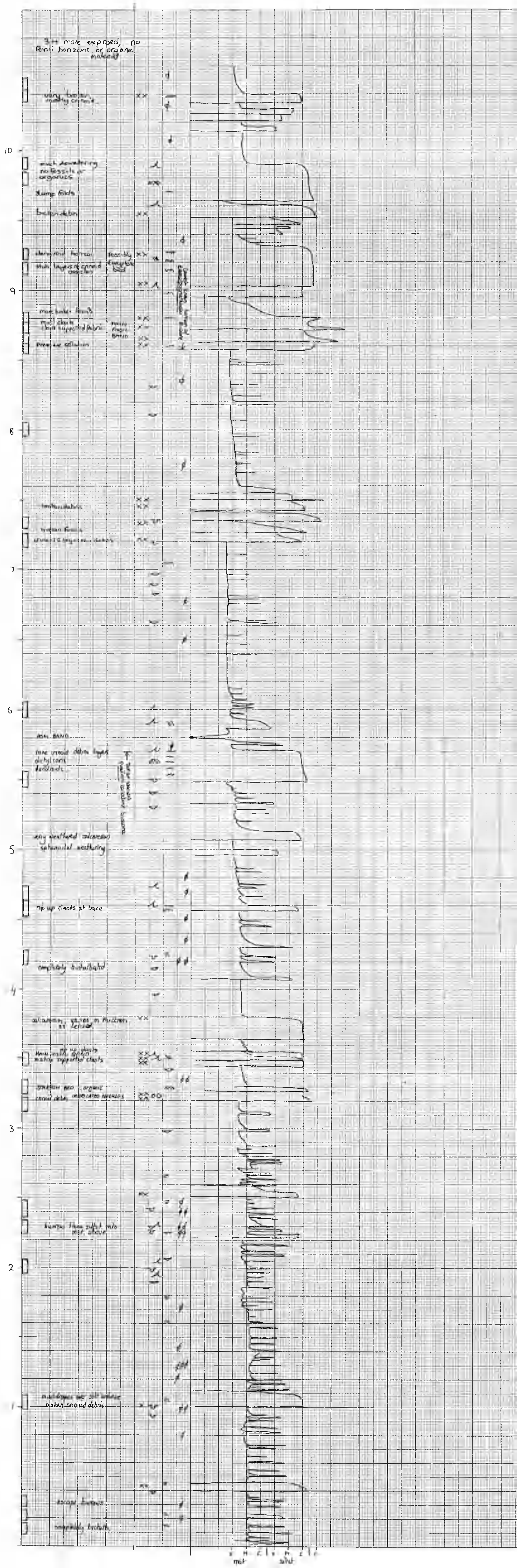

3+ more exposed, no fossil horizons or organic material
very broken, mostly crinoid
10
much dewatering no fossils or organics
slump folds
broken debris
crinoid horizon
possibly Eurypterid bed
thin layers of crinoid ossicles
9
more broken fossils
mud clasts clast supported fabric
many frags Brach
pressure solution
8
broken debris
broken fossils
crinoid & brach debris
7
6
ASH BAND
thin crinoid debris layers
dictyocaris
dendroids
very weathered calcareous spheroidal weathering
5
rip up clasts at base
completely bioturbated
4
calcareous, varies in thickness laterally
rip up clasts
matrix supported clasts
organic
crinoid debris
imbricated nodules
3
burrows through silt into mst. above
2
mudstones with silt laminae
broken crinoid debris
1
escape burrows
completely bioturb.
mst
silt

Figure 4.8

Sedimentary log of main trenched section of "Gutterford Burn Limestone Bed" Locality

Key to symbols used in log.

▯	Thin section made
ɸ	bioturbation
ɸɸ	lots of bioturbation
∽	loading of bed base
≡	parallel lamination
⫽	ripples
⌒	hummocky cross stratification
⅄	dewatering structure
⏑	lenticular lamination
∿∿	*Dictyocaris* bearing horizon
xx	fossil horizon
○	'nodule' horizon

throughout some shale sections elsewhere (Eckert and Brett 1989). This is thought to be because the fast depositional rate of the sediments periodically caused so great a thickness of accumulated sediment, that the organisms were unable to escape, and it took time (represented here by thickness of sediment) for the organisms to reestablish themselves.

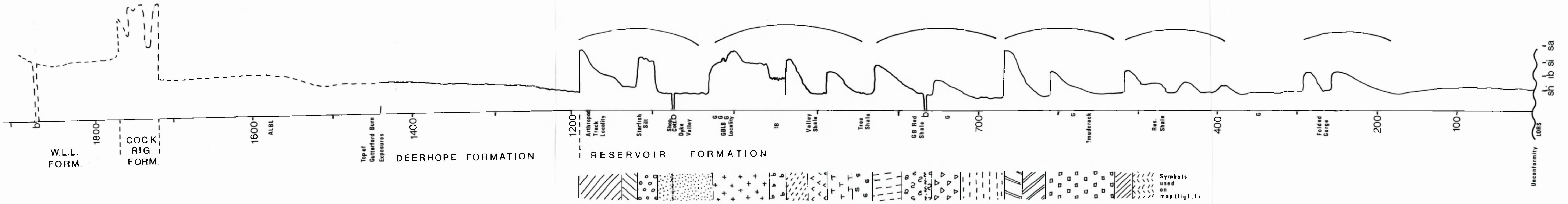
Chondrites burrows are commonly associated with the deeper (BA. 4) outer shelf environment (Eckert and Brett 1989:317), although they are thought to be produced by an environmentally tolerant animal, as they are found widely distributed in a number of facies and palaeo-environments (Bruce 1992:159). Bruce (1992:20) concluded that the Reservoir Formation was formed in deep water, based on the trace fossils present, a view not accepted here. Her identification of *Taphrhelminthopsis* (fig 4.7) is questioned in Chapter 10 of this thesis. Storm deposition commonly produces oxygenated conditions at deeper water depths than would normally be expected (Brett *et al.* 1993). The Reservoir Formation sediments are bioturbated, and although *Chondrites* burrows are present, they do not reach superabundant levels which would indicate anoxic conditions (McCann 1990:249). Storm generated density currents may have left deeper waters partially oxygenated, and therefore the ichnofossils present (fig 4.6) are not primary water depth indicators.

The accuracy of ichnogenera in indicating bathymetry has been questioned (McCann 1990), and they are now considered to be more related to substrate variations, a function of the type of sediment in which the organisms lived rather than large scale variations in water depth. The evidence from ichnofossils does not therefore contradict the outer shelf sediment depositional model proposed herein.

Horizons containing appreciable amounts of *Dictyocaris* do not appear to be fully bioturbated. It is thought possible that *Dictyocaris* represents the remains of primary vegetable matter upon which the burrowing organisms fed, and some specimens have characteristic holes through the sheets thought to be due to the passage of burrowing animals. This is discussed further in Chapter 10.

4.3.3 Fossil preservation/biogenic activity.

Fossils are rare throughout the Reservoir Formation (except at the “GBLB” locality, see section 4.6), with only a few individual specimens such as graptolites and brachiopods being recorded, and abundant *Dictyocaris* (see section 10.1). This is thought to be due to the predominance of mud in the water column, suggesting that the water would have remained fairly turbid. Doyle (1994:201) attributed the lack of brachiopods within Silurian shelf sediments in Ireland as possibly due to an extremely high proportion of storm sands (55%), and hence a high frequency of storm activity. This would have made the substrate extremely unstable, generating large amounts of fine grained material in suspension, and generally inhibiting colonisation by brachiopods. Alternatively the shoreface may have been exceptionally steep, so that the ‘appropriate’ depth for each brachiopod community was available only on a narrow strip of unstable shoreface. The combination of the two factors is



b
W.L.L. FORM.
1800
COCK RIG FORM.
1600
ALBL
Top of Gutterford Burn Exposures
1400
DEERHOPE FORMATION
1200
RESERVOIR FORMATION
Arthropod Track Locality
Starfish Silt
Shap. Cott.
b
Dyke Valley
G
G
G
GBLB Locality
!B
Valley Shale
Tree Shale
GB Red Shale
b
G
700
G
?mudcrack
Res. Shale
400
G
Folded Gorge
200
100
LORS
Unconformity
sh
ib
si
sa
Symbols used on map (fig1.1)

Figure 4.8 b

Schematic log of the Reservoir Formation of the North Esk group from the North Esk inlier.

Reproduced to the same scale as the map in figure 1.1. (see left hand column for key).

1mm = 3m.

Scale marked in metres from the base of the exposed succession beneath the LORS unconformity surface

Composite log with line showing overall composition of sediment at that point in the succession, as sediments are alternations on the millimetre scale of siltstone and shale.

Brackets show proposed cycles of sedimentation with an overall increase in both the amount of siltstone horizons and increase in grainsize within each cycle.

Main localities mentioned in text are identified.

b = metabentonite horizon

G = levels from which graptolites have been found suggested to have precluded the colonisation by brachiopods in Ireland, and in the NEI the high mud and storm input is thought to be responsible. Doyle (1994:201) noted that the absence of certain cosmopolitan genera such as Pentameroides and Costistricklandia underlines the importance of local conditions in determining which faunas are developed where. Brett *et al.* (1993) suggested that large quantities of mud deposition might cause Palaeozoic communities to occupy shallower than standard depths, as they were likely to be dependent on light penetrating to the ocean floor and the depth of the euphotic zone (Eckert and Brett 1989). The depth ranges of different benthic communities in different depositional environments is given by Brett *et al.* 1993. They also suggested that it is difficult to estimate absolute depths of epicontinental seas, as basin dimensions affect the wind fetch and surface area and hence the depths at which the effects of storms would be observed (Brett *et al.* 1993:28).

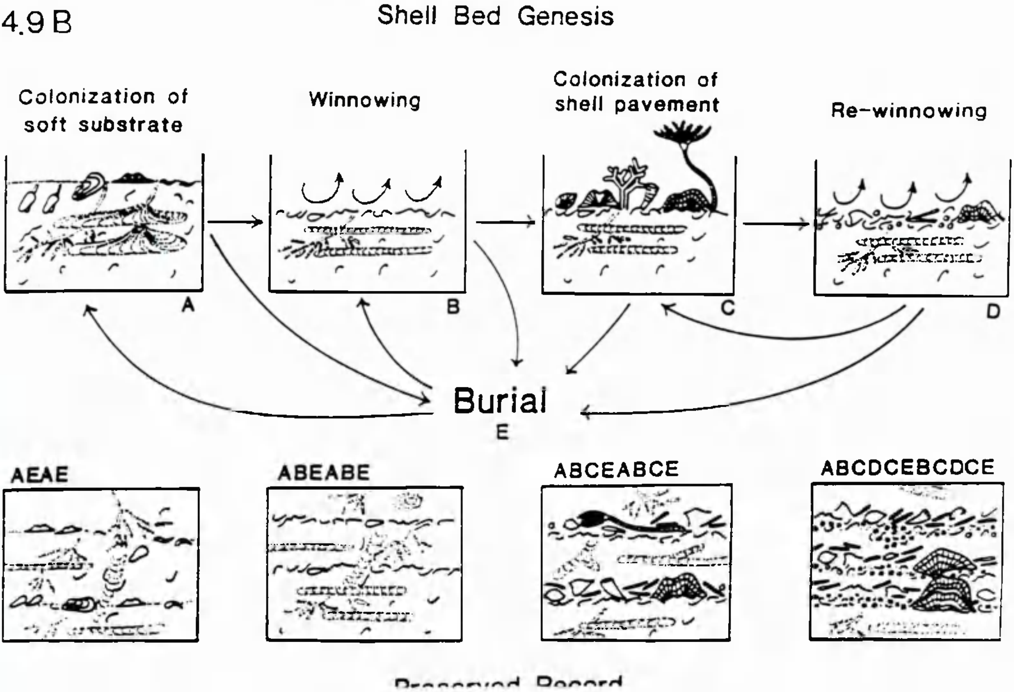
Higher up in the Reservoir Formation, beds preserved at the GBLB locality represent a period in the depositional history when colonisation by various animals was possible. It is known that organisms such as stromatoporoids took advantage of periods of reduced clastic supply to grow (Kershaw 1993), and the area appears to have periodically been extensively colonised. This colonisation appears to have been by a varied fauna, including starfish, dendroids and eurypterids, and also shelly faunas. Some of these are now preserved as coquinas (see below).

Most specimens of starfish, eurypterids and dendroids found in the Reservoir Formation are preserved almost totally intact, undisturbed and not having been appreciably current sorted. The positions and degree of preservation in which they are found (figs 10.1-7) suggests they have not been transported. The stylonuroid eurypterids, in particular, are fossilised with their appendages still articulated. These were described by Waterston (1979) as having been herbivorous, near-shore dwelling animals. Robertsons' (1985:181) model for the formation of the Reservoir Formation sediments, required all of the material deposited to have been transported downslope by turbidity currents, including the eurypterid remains. He cited the cushioning effect of transport within turbidity flows (Elmore *et al.*, 1979) as the method of transport, enabling articulated, undamaged animal remains to be transported offshore. Two factors preclude this, the non current sorted preservation of the starfish (undoubtedly inundated *in situ* see fig 3), and the fact that the majority of these specimens are found in lenses at the base of siltstone horizons. These horizons do not represent sediment reworking. The presence of complete starfish and echinoderms also indicates rapid burial, probably before death, as disarticulation occurs extremely rapidly in echinoderms (Donovan 1991). Schäfer (1972) has shown that complete disintegration of asteroids can occur in 17 days. Waterston (1979:315) concluded that the eurypterid specimens had not been transported far, if at all, and the Eurypterid Bed represents the life environment, or nearly so, of the community of animals and abundant plant life preserved in it. Such a view is supported here.

Figure 4.9. A) Continental shelf that surrounds the present day coast of the British Isles (from Reading 1991). B) Classification of shell bed genesis pathways, from Miller *et al* 1988.

Figure 4.9 A

4.9 B



The Eurypterid Bed, described by Waterston (1979) as one foot thick, was actually a lens of fossil remains, possibly representing a hollow in the sediment surface. Only the eurypterids that were feeding in, or were swept into the hollow, were preserved by sediment smothering. A similar situation is thought to have resulted in the deposition of the Starfish Beds. This suggests that, although no more starfish or eurypterids specimens are currently being found in the Gutterford Burn (except in loose blocks missed during the previous excavation), in the future, when further surface erosion has taken place, additional finds of starfish, eurypterid or dendroid beds may be made.

Preservation of a diverse and abundant stenohaline macrofauna indicates fully marine conditions with sufficient oxygen and nutrients present. Some of the coquinas in the Reservoir Formation may contain redeposited particles, but some are roughly *in situ* and covered by winnowed silt and mud. Storm lags are thin blankets, traced up to 10 m laterally of coquinoid limestone indicating a sudden change from low to high energy conditions. This wholesale transport of coarsely fragmented shelly debris, is triggered by storms periodically flushing channels of coarse debris (Brenner and Davies 1973:1693). Coquinas are not simple storm lags, but condensations of multiple storm-events including reoccurrences of winnowing, colonisation, and reburial processes. Where quasi-infaunal brachiopods such as *Eoplectodonta* and *Leptaena* (i.e. in the NEI) are involved, coquinites cannot be simple ablation lags, as they cannot simply represent shell accumulation on the sea floor in the absence of sedimentation (Brett 1991:335).

A classification scheme exists for coquinas and shell beds deposited as a result of or during the action of storm processes (Miller *et al.* 1988, fig 6), and it is now established that coquinas are not all transported (Brett 1991:334). Comparison of the GBLB locality shell beds, can be made with the scheme of Miller *et al.* (1988:40). This suggests that some beds represent winnowing and redeposition of shelly material from elsewhere, probably communities developed nearer shore. However, some of these beds are the remains of *in situ* communities which colonised the substrate, and then recolonised on top of the shell bed after periodic storm events disturbed the community. A complex history of repeated colonisation, winnowing and deposition events is therefore indicated. Furthermore, shell bed types have been identified elsewhere, that are indicative of different palaeobathymetries (Fursich and Oschmann 1993), and this is an area for possible further study in the NEI.

It is possible that shelly horizons may be more common within the lower portions of the Reservoir Formation but are too weathered at the surface to be exposed. The high weathering rate of these sediments has been discussed above. Also this one ("GBLB") locality has been extensively excavated, including the removal of many tons of specimens by Laurie (1892a-c), leaving the fresher material closer to the surface. Throughout the sedimentary environment represented by the Reservoir Formation it is possible to imagine eurypterids wandering over a mud blanketed surface, infaunal species colonising these mud blankets, and epifaunal suspension feeders colonising shell pavements and the surfaces of coquinas (Miller *et al.* 1988).

An increase in the abundance and concentration of skeletal accumulations, depends on both a reduction in the sedimentation rate and increase in the amount of benthic productivity (Kidwell 1993). Also, shell beds within basin environments with high subsidence rates, tend to be limited geographically and laterally impersistant (Kidwell 1993:166). Both of these factors are thought herein to apply to deposits within the upper Reservoir Formation.

4.3.4 Comparison with other areas and conclusions.

Some of the coquinas found in the "GBLB" locality, are similar to those described by Nealon and Williams (1988) as being deposited by wave action in shallow water shelf deposits from Ireland. Nealon and Williams (1988) also note that beds are not laterally continuous, contain large individuals of certain brachiopods and are associated with other shallow water sedimentary structures.

Doyle (1994:197, Facies C), interpreted coquinas from Ireland, associated with mudstone layers heavily bioturbated with *Chondrites* burrows, as more proximal storm deposits. Similar sequences are found in the upper parts of the Reservoir Formation, which are herein interpreted as more proximal storm deposits. Clarkson and Taylor (1989:38) note that corals deposited *in situ* within the Deerhope Formation, need not to have been living in deep water if light penetration was attenuated by suspended sediment. Corals are not found again above the volcanic ash capping the Coral bed.

The Reservoir Formation sediments have been interpreted as deposited in a deep marine environment (Robertson 1985; Bruce 1992). Finney (1986a) interpreted the sediments of the Womble Shale and Bigfork Chert of the Middle to Upper Ordovician of the Ouachita Mountains of Arkansas, as deep marine. His reasons were:- (1) beds are laterally continuous for distances in excess of 300 km. (2) they are composed of fine grained clastics and cherts. (3) except as allochthonous clasts, benthic fossils are absent and planktonic forms are abundant. (4) shallow water sedimentary structures and bioturbation are missing. (5) graded calc-arenites and conglomerates suggest deposition by turbidity currents and debris flows. The above therefore shows that few of the criteria used by Finney (1986a) to determine deep marine sedimentation can be used for interpreting the Reservoir Formation sediments as having been formed in a deep marine environment.

A number of sequences within the Irish Silurian have been recently reinterpreted as being deposited in shallow storm influenced rather than deep marine turbidite conditions (Nealon 1988; Williams and O'Connor 1987; Williams and Nealon 1987). Factors cited as indicative of storm deposits (Nealon 1988) include the presence of small scale HCS (heights from 0.005 to 0.01 m.); laminations are found within sandstones horizons having mud drapes over them, with laterally varying internal structures; that sharp contacts are observed at the base and top of individual horizons. Turbidite deposits are characterised by more continuous deposits. The Glencraff Formation in Ireland, which has been reinterpreted (Nealon 1989:63) as having been formed by mid to outer shelf storm deposition, is underlain by the Lettergesh Formation, which has coarser grain size and thicker beds, and its interpretation as distal turbidites has been maintained. The situation in the NEI is slightly different. The lowermost parts of the Reservoir Formation, exposed to the south of the reservoir, although being generally thinner with less bioturbation, are interpreted as having been deposited slightly further away from the shore, on the equivalent of the outermost shelf, or the deepest part of the shallow sea basin; they are not basinal plain distal turbidites. Basin-filling sequences have been observed elsewhere. For example, King (1994) described the migration and filling of the Upper Silurian foreland basin of Northwest England as a transition from turbidite deposits to sediments deposited by storm dominated processes.

Based on the above, the Reservoir Formation sequence is interpreted as deposited by distal to intermediate storm currents on a low energy, mud dominated shelf (Reading 1981:252) or shallow marginal-basin sea.

4.4 Sedimentary cycles

In the Reservoir Formation, a number of sedimentary cycles, or trends, have been observed, which are illustrated on the sedimentary log (fig. 4.8). These cycles are recognisable as mappable units in the field. Within each cycle, there is a gradual increase in bed thickness and grain size upwards. This is followed, in the next cycle, by a return to thin bedded units with a fine grain size. The thickest clastic beds have the coarsest grain size. This is at most only equivalent to a fine sandstone grade. The NEI regressive sequence was deposited at a time of almost worldwide transgression. This implies that the sediment supply in this area was considerably greater than the subsidence rate. Cycles of sedimentation must therefore represent variations in either sediment supply, subsidence rate, or eustatic sea level.

Sections where storm generated silt, or sandstone, horizons, become coarser and thicker higher up the sedimentary sucession, have been identified as sequences representing “proximality trends” by Baarli (1988). She stated that ‘the effects of storms and the presence of tempestites decrease gradually as distance from shore and water depth increases’ (Baarli 1988:577). She also identified a transition zone between nearshore and offshore, and concluded that:-

-the percentage of storm layers deposited decreases gradually from the shoreface through the transition zone and further offshore

-storm layer frequency reaches a maximum in the transition zone

-mean bed thickness decreases strongly from the shoreface into the transition zone and then gradually decreases offshore

-maximum bed thickness decreases gradually offshore

-percentage of cross lamination present, shows a strong maximum in the transition zone.

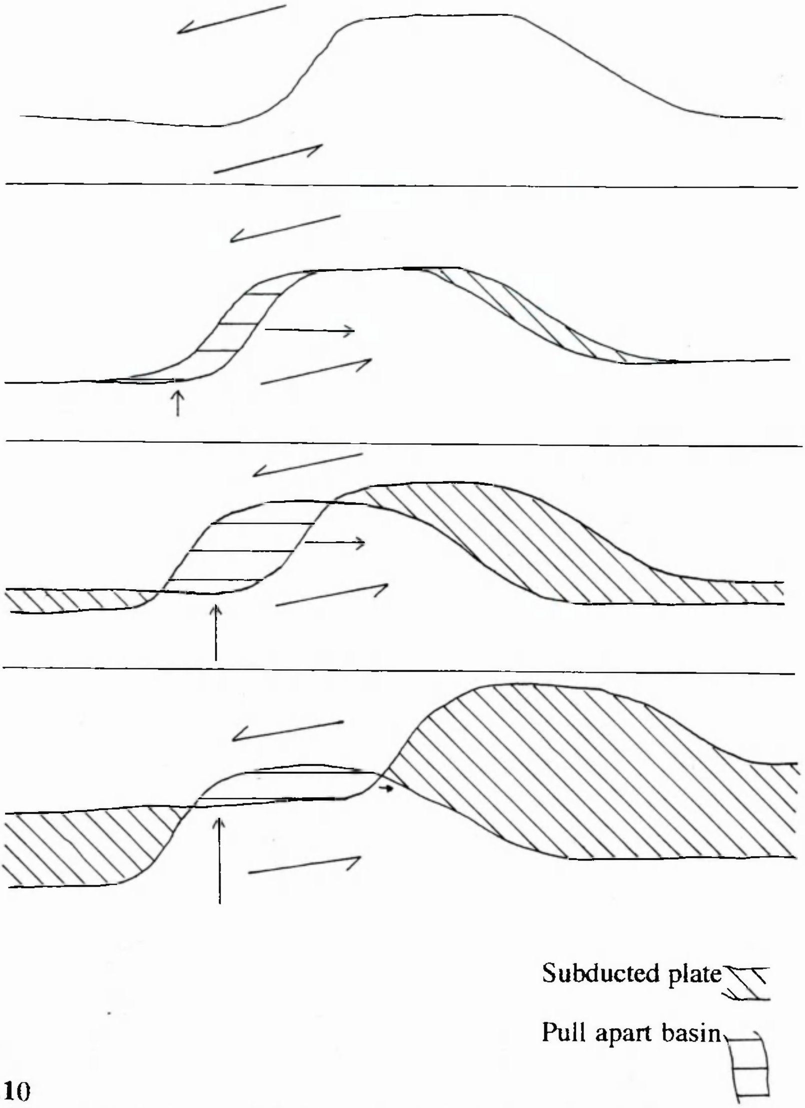


Figure 4.10
Result of oblique subduction, subduction related to strike- slip motion
A: Irregularity in continental margin
B: Pull apart basin begins to open (trans tension) with some subduction
C: Pull apart basin increasing in width (trans tension) and begins to reduce in length (trans pressure increases)
D: Pull apart basin nearly closed, width of basin now greater than length (trans pressure greater than trans tension)

Miller *et al.* (1988) suggest that benthic communities tracked depth limited environments as they migrated in response to cyclic changes in relative sea level. They also observed that both bed thickness and amount of mud-blanketing increased, and degree of winnowing decreased with depth of water (Miller *et al.* 1988). Storm deposits can therefore be used as palaeobathymetrical indicators, as the average thickness of a storm generated layer decreases from shallow to deeper water. As a result, storm generated deposits can help to estimate transgressive and regressive events (Kreisa 1980:840). Cycles (or sub-sequences) of sedimentation within storm generated sequences were recognised by Brett *et al.* (1990) in the Silurian of the Appalachian Foreland Basin. They suggested that these cycles were related to sea-level drop and local tectonic uplift, and introduced the concept of relative sea level curves in a local area.

Bed thickness and grain size have long been linked, particularly for turbidite deposits (Potter and Scheidegger 1966). This is due to currents of higher energy being able to carry more sediment and larger particles, with current strength thought to be related to proximality. Upward thickening of beds within a turbidite sequence was observed by Collinson *et al.* (1991) in Western Ireland, and interpreted as indicating an outward progradation of the deltaic sediment supply. Bed thickness Megasequences (cycles of thinning upwards and thickening upwards) are often recorded in turbidite successions, and a statistical analysis of these cycles was made by Lowey (1992). He concluded that the most informative way of identifying such cycles was by accurate plotting of thickness against bed number, and then visually identifying cycles of thin bedded and thick bedded deposition from the prepared charts. This is then checked by Fourier analysis. A similar technique can be applied to the patterns of sedimentation observed in the NEI. Accurate measurements of bed thickness have been made, and visually inspected to identify thickening upwards, and thinning upwards phases of deposition. Further rigorous statistical analysis using the methods of Lowey (1992) would need to be applied before these could be formally identified as (storm) Megasequences.

The overall trend within each of the cycles identified in the Reservoir Formation, is of thickening and coarsening up. From the above, this can be seen to imply increasing proximality or water shallowing. Current strengths were strong, but probably not exceptionally so, as few erosional features are preserved. Minor fluctuations in eustatic sea level are difficult to identify, but within a transgressive sequence, we at least know that the sea level was changing and may have contributed to these cycles. The overall trend within the North Esk group is of emergence or coastline progradation. The cycles observed during this study were probably related to periodic tectonic events within this active strike-slip regime. These tectonic events could cause the episodic raising of the basin floor, or result in increased sediment supply causing shoreline progradation.

4.5 Basin dimensions.

The evidence from the sediments of the NEI concerning the shape and dynamics of the basin of deposition is sparse and two-dimensional. A few conclusions and suggestions can be made however, the most important being that the basin of deposition of the sediemnts of the NEI is thought herein to have been a nearshore marginal basin of limited size and depth. If a comparison is made with the width of continental shelf that surrounds the present day coast of the British Isles (fig 4.9), the position of the basin of deposition of the NEI, would have been within this halo and not extending out into the (deep) open ocean from off the edge of the continental shelf as suggested by Robertson (1985). Lamont (1952) envisaged a basin infilling model for the deposition of the sediments of the NEI. Brower (1975) suggested quiet and relatively shallow conditions for the deposition of the crinoids, and followed Lamont's basinal model. The model supported here for the deposition of the NEI sediments is the infilling of a shallow marginal marine basin. The possible mechanisms for creating such a basin are discussed below.

Tectonic activity undoubtedly influenced the formation, and subsequent moulding, of the basin into which these sediments were deposited. In the Oslo region, the Silurian sediments are considered to have been deposited in a nearshore basin formed by isostatic subsidence of the continental shelf as a result of emplacement of nappes. Normal shelf deposition resumed in the Oslo region once the basin had been filled (Baarli 1990b). Similarly, separate fault controlled basins of deposition have been described for the Silurian of Newfoundland (Arnott 1983). Tectonic models by no means all agree on the position of the basin of deposition for the Midland Valley inliers either at time of deposition or throughout the subsequent emplacement history. This is discussed further in chapter 5. Certain factors are, however, relevant .

Some present day small enclosed seas are weakly tidal and some have intricate tidal patterns. The present day North Sea, for example, receives a progressive tidal wave from the Atlantic. This results in complex tidal patterns, with some of the world's largest tidal ranges (up to 15 m), and highest tidal velocities. The more open the shelf, or sea, is to the prevailing winds and the open ocean, the more intense the tidal activity (Reading 1981:215). Pickering *et al.* (1988:370) note that the distribution of Silurian sediment facies which occurred in the remaining marine basins of the remnant Iapetus ocean was related to the reorganisation of global oceanic circulation patterns, which followed the partial closure of the "open and wide ocean", from the late Ordovician to early Silurian times.

Williams and Harper (1988) suggested that the Midland Valley basin of deposition was 300-350 km wide at its widest part. In the model envisaged by Bluck (1983:130) for the evolution of the Silurian Midland Valley, the overall width of the arc-interarc, arc-forearc and accretionary prism regions together, would be about 100 km. If the Midland Valley basin were this small and completely enclosed, then it would have been microtidal (Doyle 1994). The presence of wavy, lenticular and flaser bedding in alternating sequences of sand and silt, is commonly indicative of tidal action. In the Reservoir Formation, such sedimentary structures are interpreted herein to be indicative of (low energy) tidal reworking. It is thought herein, that there was still a connection to the much reduced, but still extant, Iapetus ocean during the late Llandovery. Also, the basin of deposition of the NEI is not thought to have been completely enclosed, and was exposed to some tidal influence.

When two parallel faults in a wrench fault system are off set, a basin can form between them, which is known as pull-apart basin. These basins are common in strike-slip fault related settings, which is consistent with models for the formation of the Midland Valley of Scotland (see chapter 5). Pull apart basins are characterised by rapid infilling, and this could explain, in part, how an apparently regressive sequence could be deposited during a time of overall transgression, as pull-apart basins are characterised by very fast deposition rates. It is possible that the enormous thickness of sediment described here, was deposited during the infilling a pull-apart basin. Present day examples of pull-apart basins are the Dead Sea, basins associated with faults parallelling the San Andreas Fault and the Alpine fault zone of New Zealand. Pull-apart basins are usually about 30 km. wide and long, and their depths are almost equal to their widths. In present day cover rocks, en-echelon folds (see chapter 5) are valuable indicators of the presence of strike slip faults and pull apart basins at depth (Reading 1981:461).

The post-Silurian tectonic history of the Midland Valley terrane, makes it difficult to be certain if this basin was formed by pull-apart processes, and if so, what its dimensions were. The processes of trans-tension and trans-pressure, which operate during and after the opening of a pull-apart basin as the transcurrent motion continues (fig 4.10), tend to be associated with thrusting and faulting rather than plain faulting. This could have been partially responsible for the upending of the sediments into their current sub-vertical position, with the thrusts currently seen at the surface (chapter 5) mimicking those at depth. Pull apart basins are floored by thinner crust, allowing the basin to be more easily underthrust and uplifted. The continuation of this thrusting motion may have caused the updoming of the overlying LORS sediments which are now draped over the top of the NEI in a gentle anticline.

4.6 Gutterford Burn Limestone Bed Locality

4.6.1 Introduction

The "Gutterford Burn Limestone Bed" Locality was studied in detail during this project for a number of reasons.

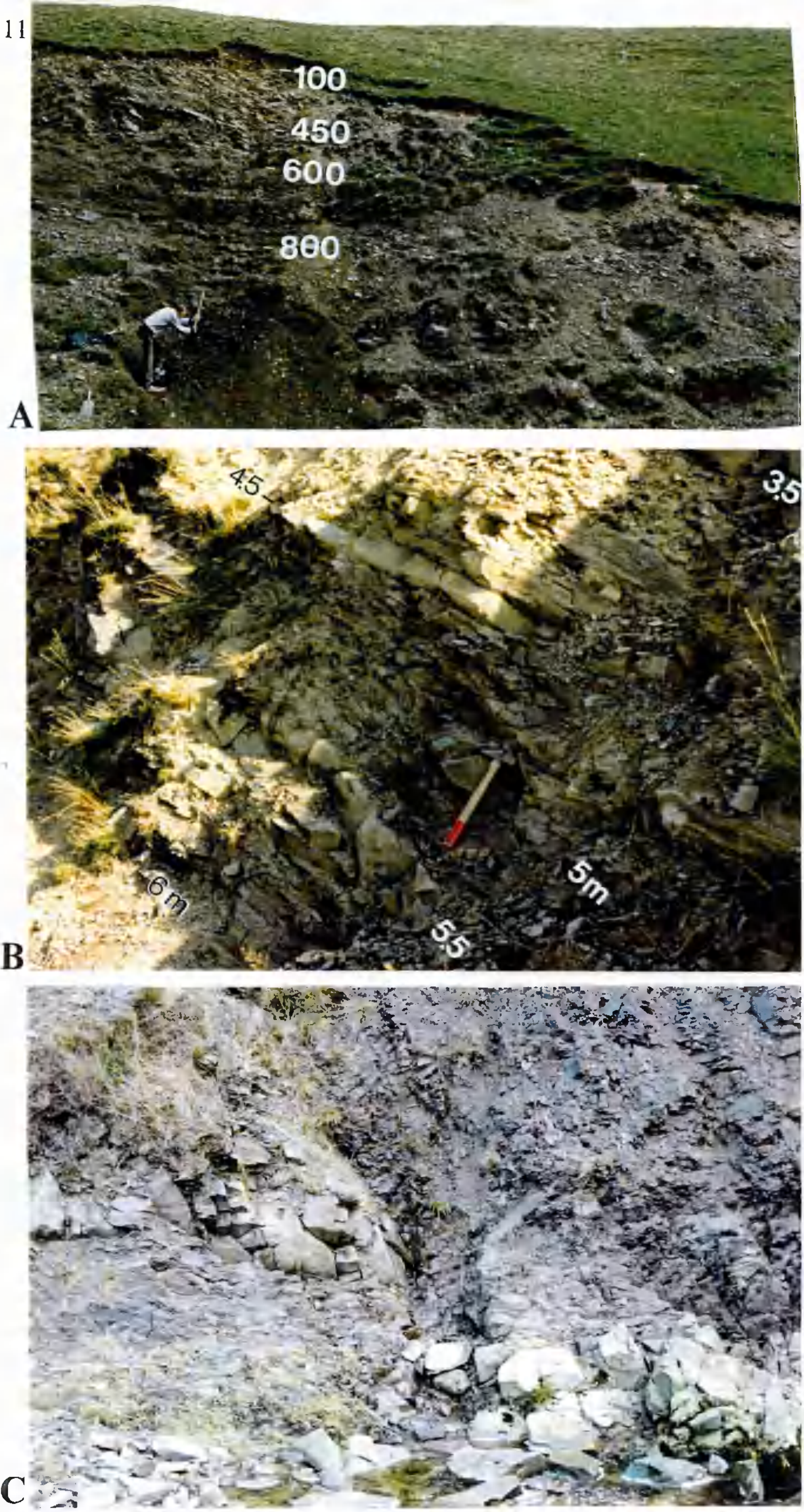
1) It is the most interesting and informative section (from a palaeontological point of view) within the Reservoir Formation.

2) To collect fresh material in order to consider the exact nature, number, size and composition of the 'Limestone Beds', and to consider the mode of origin of the fossiliferous horizons known as the "Limestone Beds".

3) The sedimentary patterns occurring between the "Limestone Beds" could be considered representative of the normal Reservoir Formation sedimentation patterns and could be

Figure 4.11 Gutterford Burn Limestone Bed Locality grid ref. NT 1589 5918. *O spiralis* Biozone age.
A: Whole locality with levels in logged section marked in cm. Taken durnig excavation work, my father for scale.
B: Part of logged section in detail, marked in metres. Hammer 32 cm long.
C: Fault cutting southern end of locality, downthrow to south 1.2 m

Figure 4.11



logged, thin sectioned and studied in millimetre scale detail. This process is not a realistic one for the whole of the Formation, but this section could be considered indicative of the Formation as a whole, and the results from it extrapolated.

As noted by Robertson (1985) the "Gutterford Burn Limestone Bed" is not one, but a series of highly fossiliferous horizons, that are in fact not limestones but highly fossiliferous and calcareous siltstones. Henderson (1880) first described this as a limestone bed, and the name "Gutterford Burn Limestone Bed" Locality (or "GBLB" Locality) has been retained here to maintain a link with the past and for ease of identification in the field. Different thesis field mapping projects (Robertson, 1985; Tipper, 1976) and field guides to the area, had created numbering or naming systems for each locality, so that they could be referred to later. The most recent locality numbering system of Robertson was used, but this proved difficult, as the more detailed study undertaken here, considered more localities. The name "GBLB" was retained to avoid any ambiguity over which locality was being referred to (see fig 4.11). The physical top of the "GBLB" locality is the stratigraphic base of this section. The sediments are partially overturned, lying at a steep angle dipping 60- 80 ° to the South East, whereas the younging direction remains to the North West.

It is at this one locality ("GBLB") that almost all of the known fossiliferous horizons within the Reservoir Formation are found. One of the Starfish beds and the Eurypterid Bed are from this part of the banks of the Gutterford Burn, and all of the fossiliferous horizons, as detailed below. At least two faults are known to cut almost perpendicular to the bedding at this locality (fig 4.11), displacing the sequence. This sequence is not known to be repeated elsewhere in the Gutterford Burn.

The GBLB locality exposes strata that are quite high up in the Reservoir Formation. This formation is described elsewhere (section 4.3) as having been deposited in gradually shallowing water and in increasingly proximal conditions.The influence of storm deposition, and the high mud input into this basin have also been recognised. By this stage of the infilling of the basin, the sea floor was within the range of the effects of storm waves, although probably not above fair-weather wave-base. Wave reworking caused sediment transport, formed shell coquinas and periodically buried the *in situ* benthic community. Infaunal organisms created escape burrows, although some were unable to escape.The high mud input into the basin, probably resulted in fairly turbid conditions, and therefore low light levels at relatively shallow water depths. Deposition of these sediments probably coincided with the first time that this part of the sea floor was properly within the photic zone. This allowed colonisation for the first time by pioneering communities of crinoids, dendroids and starfish. Some of these communities may have already been established in nearby shallower water and migrated out.

Figure 4.12. : Photomicrographs of thin sections. All slides taken from logged section of GBLB locality.
A: EEB 91.4 X15. Loading of siltstone into underlying mudstone and dewatering of lower siltstone layers.
B: EEB 91.5 X70. Cross section through burrow with clay lining.
C. EEB 91.5 X10. Loading and bioturbation. o= cross section through burrow,*=longditudinal section, x= loading

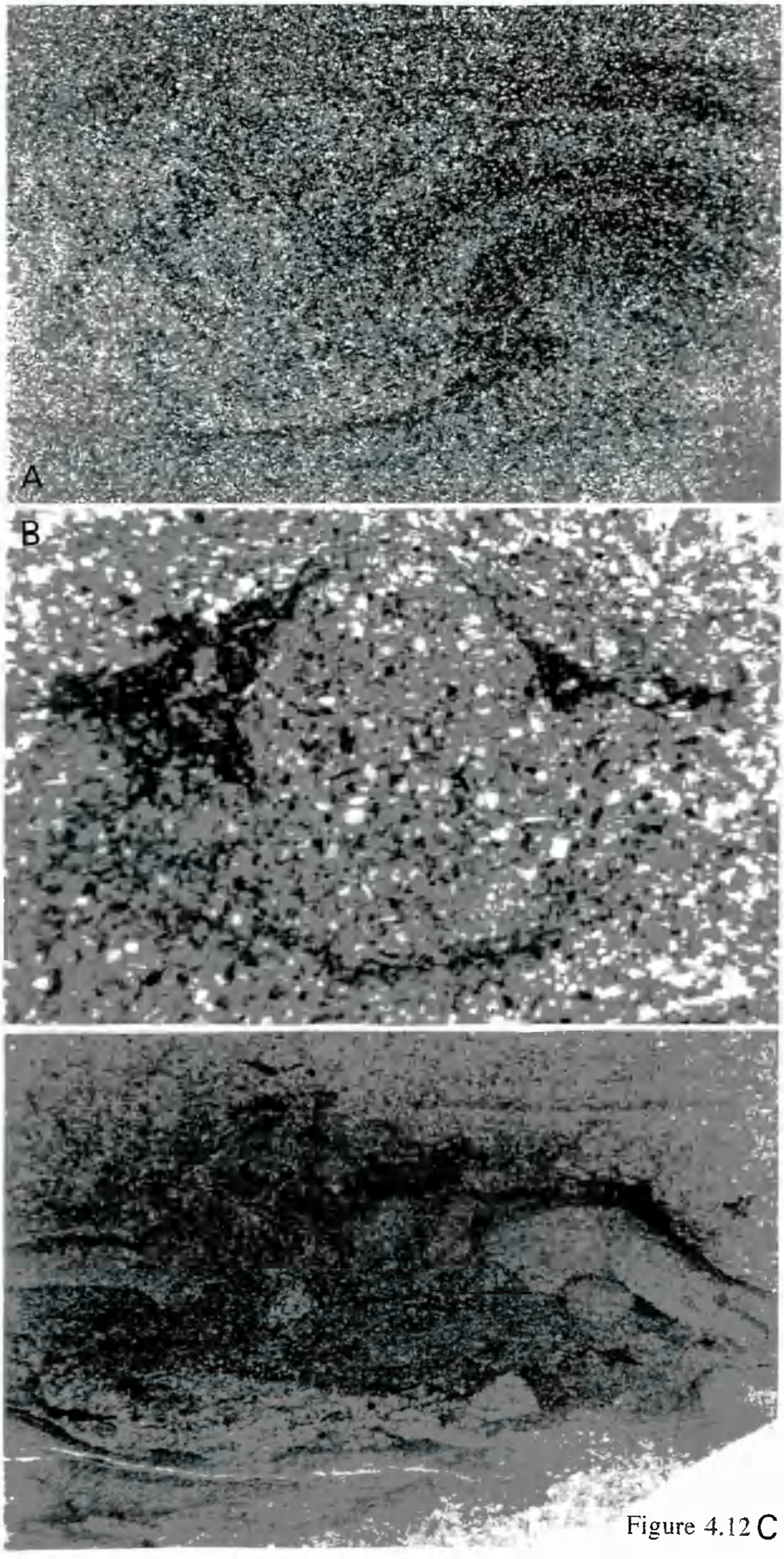


Figure 4.12

Prior to the start of this project, only one 'Limestone bed' was visible. An excavation was conducted to remove the scree and weathered material to exposed fresh sediment. One sub-vertical trench about 20 metres long and perpendicular to the bedding was excavated. A shorter, parallel trench 5 metres away was also exposed. The main section was logged in detail, hand specimens were collected at regular intervals and from informative horizons. These blocks were later cut and polished, and thin sections were made. Fossil bands were sampled, where appropriate, further along strike (see Chapter 10 for charts of specimen collection points, thin sections and logs).

Once the locality was properly exposed, it became clear that there were three main phases of fossil coquina deposition, and that fifteen separate fossil bands could be identified. These fossiliferous horizons are not laterally persistent. Indeed, one band consists of one cm. of finely broken shell sand (with abundant crinoid ossicles) at one point, and becomes further along strike, a 10 cm thick shell debris band, with fragments up to 1 cm diameter, including abundant trilobite sections and brachiopod debris. Good fossil specimens were collected and samples of the more calcareous material were sent to Dr H Armstrong for analysis of the conodont fauna, the results of which are contained in section 3.7.3.

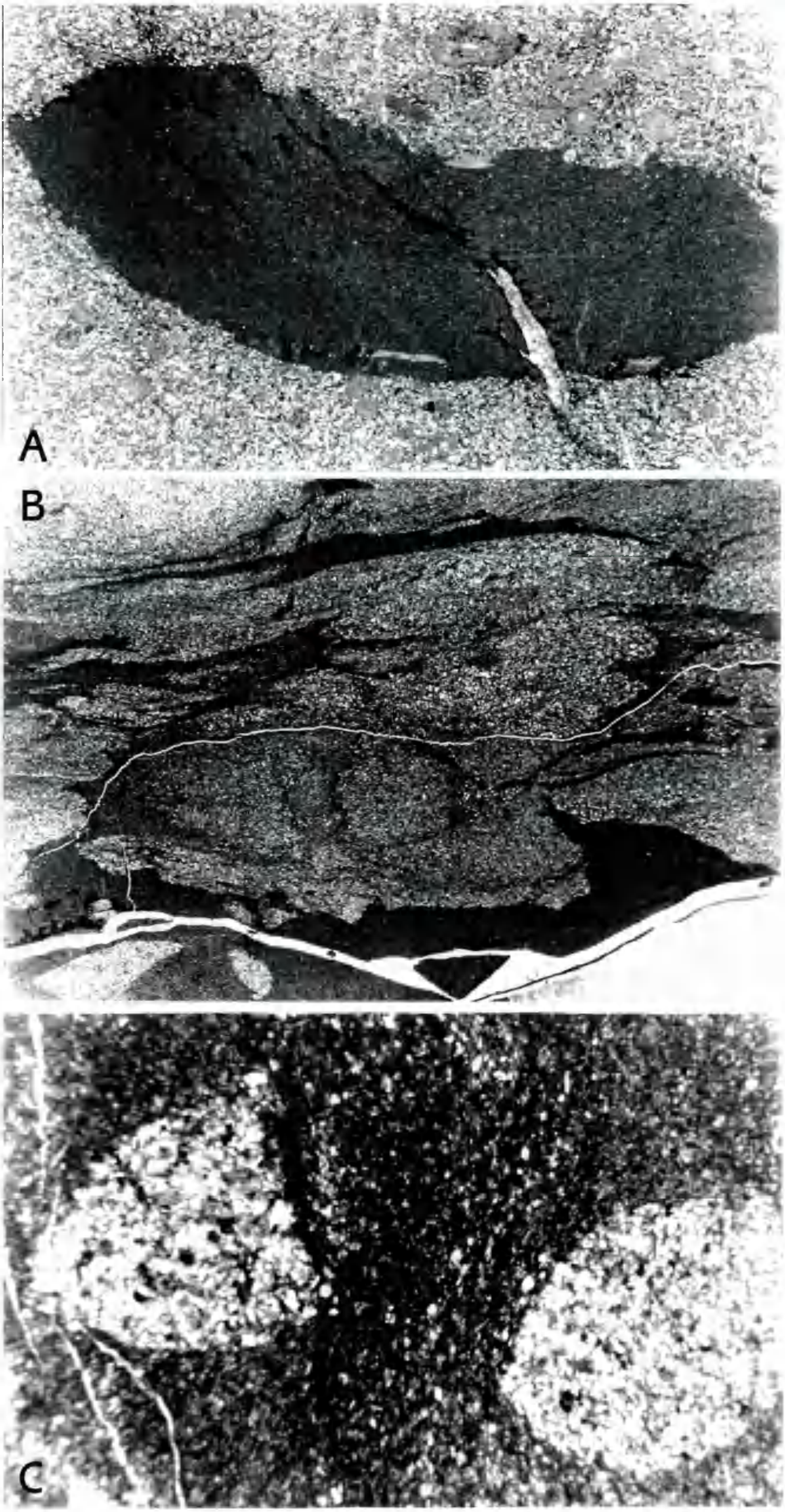
4.6.2 Sedimentary structures

The "GBLB" locality is an exposure of interbedded fine grained siltstones (fine grained lithic-arenite) and fine shales, with fossiliferous horizons (bioclastic-arenites) within the section. The nature, composition and structure of these sediments was analysed by accurate bed by bed recording (logging) in the field (fig 4.8). This was supplemented by a laboratory study of thin sections and hand specimens, analysing both rock type and fossil specimens. A thin section and sample layout diagram, and annotated logs are included in fig 4.8 and Chapter 10. Throughout the measured section, grain sizes and bed thicknesses are small, ranging from fine mudstones to coarse siltstones and rare fine sandstone. Structures observed are illustrated in figs 4.12 and 4.13.

During the analysis of thin sections from the GBLB locality, laminations were observed in detail. In some sections it was possible to identify individual siltstone horizons of only a few millimetres thickness, but nonetheless with distinctive loaded bases, disturbed tops (due to dewatering) and internal lamination or grading. Thin sections from this sequence (see figs 4.12 and 4.13) show evidence of dewatering. Particularly common are 'flame structures', which form where sections of the siltstone from which the water is escaping are dragged up by the pressure of the water escaping into the mudstone above. The loading of siltstone into the underlying soft sediment surface of mudstone is common, as are rollover foresets, which are due to small scale slumping and dewatering. Ripples, burrows with mica flake surrounds, parallel and wave formed lamination (HCS), are all delineated by the alignment

Figure 4.13. : Photomicrographs of thin sections. All slides taken from logged section of GBLB locality.
A: EEB 91.6 X15. Large mudclast in siltstone, surrounded by crinoid debris.
B: EEB 91.7 X15. Cross section through burrow with clay lining in middle and small burrows at base of photo. Flame dewatering structures and siltstone loading into mud matrix
C. EEB 91.7 X 70. Quartz rich siltstone infilling burrows through mudstone.

Figure 4.13



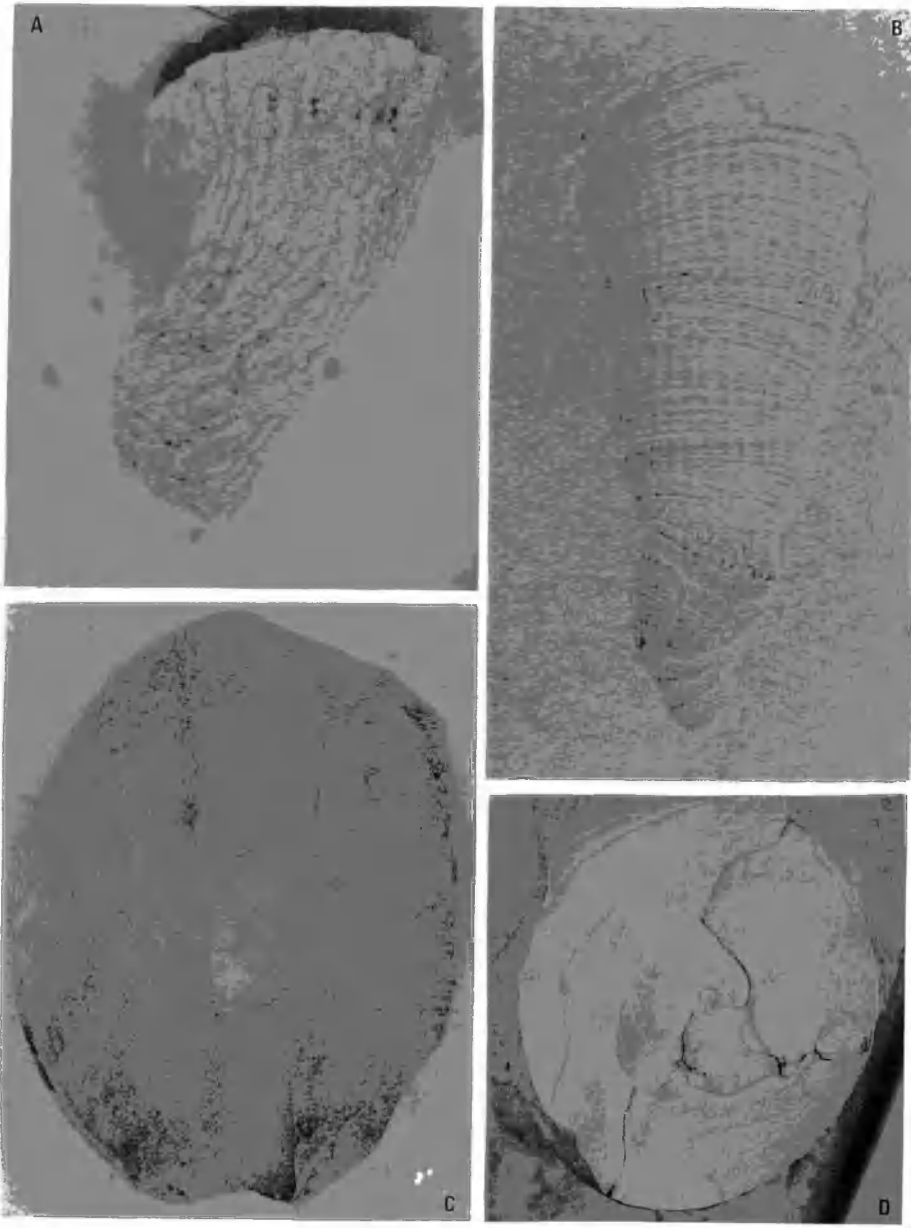
of mica flakes. Specimens of *Dictyocaris* and graptolites in cross section are rarely found. Some grading up and down is seen, although most commonly fining upwards. Some mud flakes and rip up clasts are also observed. The most fossiliferous and least weathered material often has a calcareous matrix approaching a muddy limestone, which is more properly referred to as a calc-arenite.

Point counting of these sections was attempted but not pursued, as the sediment layers are so thin that the figures obtained would at best be averages. As stated by Ward (1989:110), such point counts can be shown by Cathodoluminescence to be inaccurate. The fine grain size of these sediments also inhibits the calculation of percentages of constituent grains. These sediments are generally fairly immature. Clasts are dominantly angular and some are elongate. Some biogenic clasts are quite rounded, and show signs of having been partially lithified prior to deposition, such as geopetal infills, not lying parallel to bedding. No major differences occur throughout the logged section in grain roundness, sphericity or composition, other than on a local scale. These mudstones and shales contain predominantly quartz clasts, with a high percentage of both biotite and muscovite micas, including some flakes up to 0.5 mm long. The presence of feldspar in these sections also implies immaturity. The clay content of the siltstone matrix and of the mudstones, is thought herein to be related to the high background mud input to the basin at the time of deposition. There is also a relatively high proportion of rock fragments. The coarser sediments are a fairly good example of what might have been called a "greywacke" but are referred to here as Fine Grained Lithic Arenite.

The immaturity of the sediments implies that the particles did not travel far prior to deposition. Immature sediments are commonly formed at times of crustal unrest (Tucker 1981:76). The sediment immaturity is probably also a function of the original sediment supply. This could have been from either the north or south of the basin, eroding the greywackes of the Southern Uplands "accretionary prism" or eroding an arc (Bluck 1984), or most likely eroding the emergent land mass to the north, the present day Scottish Highlands. Palaeocurrent indicators are unequivocal due to poor exposure and to contemporaneous wave reworking of the sediments. The quartz clasts may have originated from preexisting sediments. There are a few concentrations of heavy minerals delineating sedimentary laminae, this could also imply winnowing and reworking of the sediment. The rounding of the biogenic clasts suggests that the animal remains were winnowed prior to fossilisation. There is some pressure solution between calcareous fossil fragments in the more tightly packed fossiliferous horizons. The calcareous nature of the matrix of some of the more fossiliferous horizons was probably formed during diagenesis. The feldspar content may have been effected by the humid conditions on land at the time of erosion from the source rock, thus accelerating the decay of feldspar grains prior to deposition.

Figure 4.14. : All specimens from GBLB locality *O spiralis* age. A: EEB4 X 10, B EEB2 X10. C EEB11 X 2. D EEB 15 X 2 A&B. Effect of periodic sub-lethal storms on solitary corals, recording several generation of toppling and renewed growth. C, D. Nodules from 320 cm in logged section. C Orthocone, D, cephalon of *Acernaspis eskaspis sufferta* and gastropod *Gyronema*

Figure 4.14



The high mica content of these sediments suggests that one of the source rocks may have been a mica schist. There are small quantities of chlorite present. This has previously been thought to imply metamorphic grade, but the grains are considered here to be detrital. Some of the quartz grains may have originated from preexisting sediments, and possibly from reworking of sediment, trapped by barriers in nearshore facies. Many of the sands in present day shallow seas are relict and represent reworking of those deposited initially after the last ice age. At the time of deposition, the North Esk Basin was a new geographical feature, with little relict sediment available for reworking.

One bed containing nodules has been found, and some of these contain fossil fragments (fig 4.14). These nodules probably grew at, or close to, the sediment surface at the time of deposition and were later reworked, as they now appear to be imbricated. One clay band is present within the logged section. Unfortunately both horizons are too highly weathered to warrant further chemical analysis.

4.6.3 Shell Beds (Coquinas)

An excellent study of distal storm "event" deposits by Miller *et al.* (1988) is an important work which contains a description of the method of formation of the shelly horizons, with which the formation of shelly horizons within the Reservoir Formation can be compared. The classification of shell bed genesis pathways from Miller *et al.* (1988) is given in figure 4.9. Further work would have been necessary during this study to classify each fossiliferous horizon found in the GBLB Locality, but some interesting analogies can be drawn.

Miller *et al.* (1988:35) note the significance of the formation of winnowed shell lags, with material probably transported from nearshore facies. These formed a firm, stable substrate which permitted colonisation by attached epifaunal suspension feeders. These would otherwise have been excluded from colonising this area by the fluid, muddy substrate (fig 10.7). Miller *et al.* (1988) also note the effect of periodic sub-lethal storms on certain animals, with some broadly conical rugose corals being flipped up and dying, and some corals recording several generations of toppling and renewed growth (fig 4.14). They also suggest that not all shell beds or coquinas are greatly transported, although some material may be transported out by storms from contemporaneous nearshore facies. Most shell beds record periodic winnowing, colonisation, and deposition events, more or less *in situ*.

By comparison with the classification of Miller *et al.* (1988:35; fig 4.9 herein) the shell beds of the Reservoir Formation (particularly the horizons containing more broken material) may be reworked, winnowed shell bed. These shells may have originated from the nearer shore community association (Weather Law Linn Formation) as described by Robertson (1989). They may have been trapped by low lying coastal plain, lagoon or barrier island, and then transported to the outer shelf environment. The presence of undamaged, datable graptolites between these shell beds, implies that the graptolites were contemporaneous. Whilst some of the horizons were reworked and winnowed, some of the shells are clearly in life position, and most of the shell beds represent inundated *in situ* communities. The quantities of mica incorporated in the sediments, even within the shell beds, implies that re-working has not been great.

It is therefore concluded that the shell beds in the Reservoir Formation were formed and modified by repeated intermediate to distal storm events, formed below normal fair weather wave base. Patterns of storm winnowing, rapid deposition, and periods of non deposition controlled and modified the benthic fauna. Storm events caused environmental stress to individual organisms, such as dendroids (see chapter 7) and corals (fig 4.14). Some storm events were non survivable, causing all of the organisms to be buried. Sometimes the sediment was recolonised by epifaunal deposit feeders where the sediment surface was too unstable to support suspension feeding organisms. It is possible that more shell beds occur throughout the Reservoir Formation, but that the high degree of present day surface weathering precludes their observation in the field.

4.6.4 Exceptional preservation horizons

The Gutterford burn is renowned for the presence of certain highly fossiliferous horizons. The Gutterford Burn Eurypterid Bed, the Starfish Bed, and the dendroid bearing horizons, contain exceptionally well preserved fossils. A number of fully articulated crinoid specimens have also been found. The site of the GBLB locality is where most of these beds are found. The preservation is indeed exceptional with many specimens preserved fully articulated and undisturbed. With the exception of eurypterids, a number of new specimens of each of these fossils have been found during this study and are illustrated in Chapter 10.

In the Gutterford Burn, these "exceptional preservation" horizons are in fact non-laterally continuous lenses. They probably represent slight hollows in the original sediment surface. This allowed removal, and transport away, of those members of the community positioned on the sediment surface topographic highs, whilst burying *in situ* those caught in the hollows. Additionally it could have been that, within these hollows, the amount of sediment dumped on top of the animals was thicker, and only those on the topographic highs managed to escape.

All of these beds are associated with abundant reticulate structure and plain sheet vegetable or algal matter (and *Dictyocaris*). Starfish are not found in the Eurypterid Bed, eurypterids are not found in the Starfish Beds, but dendroids are found in both other beds, and in horizons thought to have preserved "Dendroid Meadows", without associated eurypterids or starfish. The Starfish Beds could be termed "echinoderm-rich" beds as they contain, along with the exquisitely preserved starfish specimens and crinoids, a number of new specimens (Chapter 10) of the Lower Palaeozoic echinoid Aptilechinus caledonensis Kier 1973. Some of these new ecinoids may yield details of the structure of the apical disc, not seen in previous studies (Kier 1973). The dendroids preserved have been studied in detail and are discussed in chapters 6-9.

The starfish from the Gutterford Burn, require thorough taxonomic revision, and whilst Spencer's (1914-1964) monograph is excellent, further updating is required. For this reason the starfish found have been identified to generic level only (figs 10.2-7). It is tempting to assign these specimens to a species such as Crepidosome wenlocki which was erected by Spencer for the Gutterford Burn starfish specimens, but it is thought here that this should await further taxonomic revision.

Some starfish species from the NEI, such as Furcaster sp. appear to be relatively small. Brower (1975:633) suggested that specimens of the crinoid Pisocrinus campana from the Gutterford Burn also appear dwarfed. The specimens could either be juveniles, or be dwarfed due to the high sediment input, or other non-ideal conditions. Brower (1975:633) also commented that the crinoid fauna was of low taxonomic diversity when compared with starfish beds of the same age found in other areas. He suggested that the conditions were marginal for the establishment of crinoid colonies. This is corroborated by the work on the regrowth structures of dendroids detailed herein, which suggests fairly harsh conditions for the colonisation and survival of delicate benthic faunas. Other work on the sedimentology has confirmed the relative harshness of the environment. It is not thought, however, that the dwarfing was due to low benthic oxygen levels, as not all of the benthic community was affected, and the amounts of vegetable matter preserved would not have developed if oxygen conditions had been low.

The lensar nature of the "remarkable-preservation" horizons can make it difficult to ascertain if one particular element within the fauna is dominant. One collecting episode (field season) may result in the collection of many echinoid specimens; the next, a great number of dendroids; and the next, perhaps many specimens of one species of starfish. This collecting and specimen yield bias, precludes an accurate or meaningful faunal analysis. It is thought however that these remarkable horizons are life assemblages, and slight variations are due to variations across the original benthic environment.

The presence of the reticulate structure material (fig 10.28) and of *Dictyocaris*, is fundamental to the interpretation of the benthic environment. Both are thought to have been of algal origin, and to have formed surface sheets (see chapter 10). The growth of surface algal mats suggests a time of low sedimentation and reduced suspended sediment load. The presence of algal mats meant that there was sufficient supply of vegetable matter to attract grazers such as the eurypterids (Waterston 1979:316), and possibly some of the asteroids. The reticular structure of some of the sheet material probably mimicked a primary structure within the algal mat. The fossilised structures probably resulted from post depositional/pre lithification drying out of the algal mats within the sediment, by a process possibly similar to syneresis.

Figure 4.15. Summary diagram of palaeoenvironmental interpretation. Formations of the North Esk Group: Hen. == Henshaw formation, WLL= Wether Law Linn Formation, CR=Cock Rig Formation, DH= Deerhope Formation, Res.= Reservoir Formation. NWB=Normal Wave Base, SWB= Storm Wave Base.

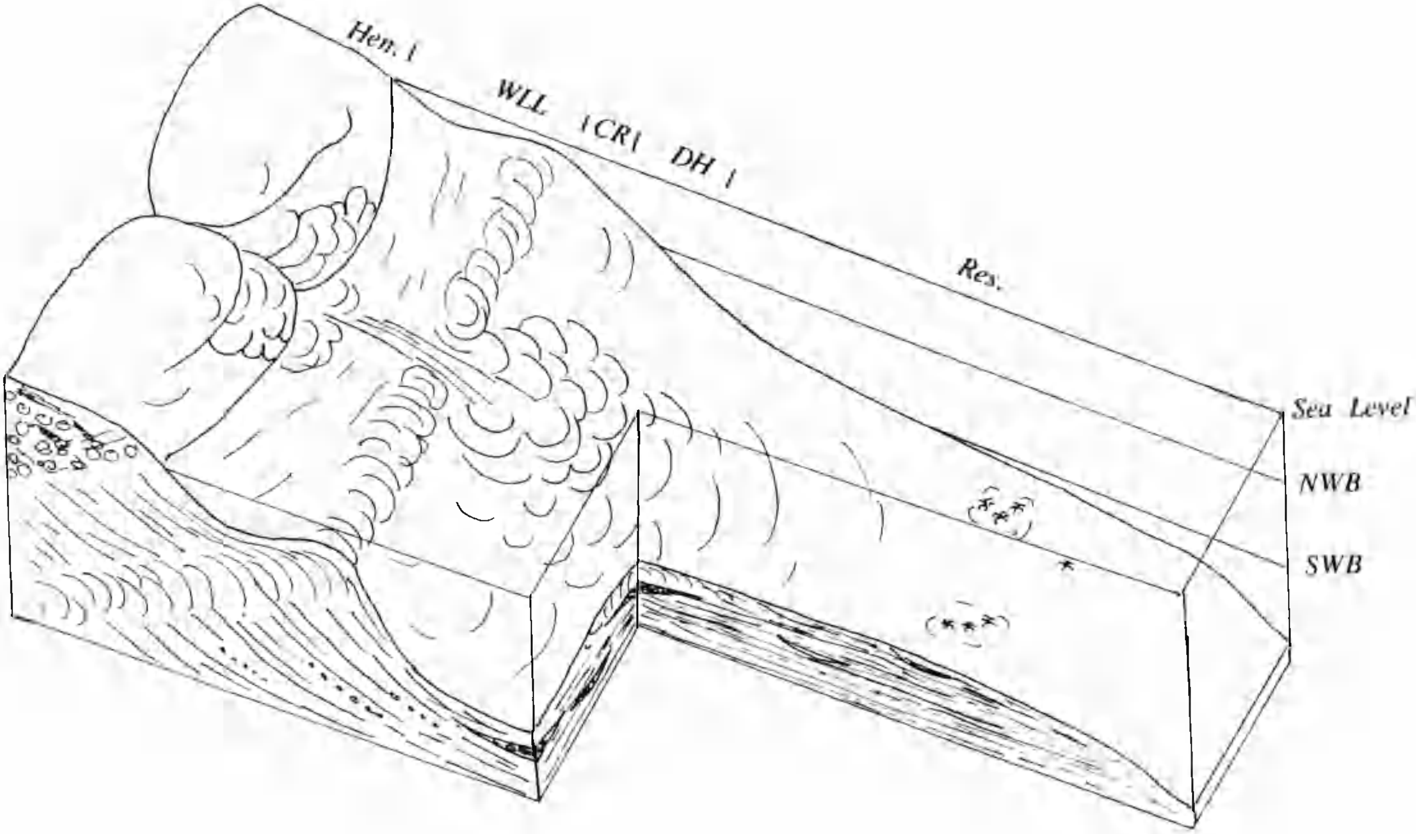


Figure 4.15

Gale (1987:129) suggested that Lower Palaeozoic asteroids were rather inflexible animals, incapable of complex arm movements. The apparently flexible arms (see fig 10.3C) of some of these species appears to disagree with Gale's hypothesis. The starfish specimens also provide the best evidence for *in situ* deposition, as there are only minor signs of current alignment, with two specimens preserved facing one another (fig 10.4E).

These exceptionally preserved horizons are thought to preserve close to the life assemblage. As there are no bivalves or accumulations of shelly material associated with these beds, we can assume that the echinoderms did not inhabit areas with abundant shelly animals. This also partially confirms Gale's (1987:129) hypothesis that Lower Palaeozoic asteroids lived on soft substrates by direct ingestion of food, rather than extraorally preying on bivalves as their modern descendants do today.

4.7 Overall Interpretation of sediments.

Previously the Reservoir Formation sediments were considered to have been deposited as deep ocean plain distal turbidites (Robertson 1985; 1989). The problem with this model is that the sedimentary sequence is conformable, without appreciable break, and the Robertson (1985; 1989) model did not satisfactorily explain the transition from deep marine to relatively shallow nearshore facies, without a break. A more transitional model is given here.

The sediments of the Reservoir Formation are interpreted herein as having been deposited rapidly by distal to intermediate storm sands on a low energy, mud dominated shelf, or by the infilling of a shallow marginal basin sea. Cycles of sedimentation have been observed, and interpreted as the result of periodic fluctuations in relative sea level. This basin was not enclosed and connection still existed during the late Llandovery with the remnant Iapetus Ocean.

The fine grained nature of the Reservoir Formation sediments is herein interpreted not to indicate distance from source, but to imply a fine grained source. Bioturbated mudstone layers and siltstones with common dewatering structures are identified. Higher up in the Reservoir Formation, the presence of coquinas associated with beds containing exceptionally preserved fossils, are interpreted as more proximal storm deposits, indicating a decrease in water depths.

The North Esk Group records a regressive sequence in a time of overall transgression. This is interpreted herein as being a succession of water depths from outer shelf, below storm wave base; gradually shallowing to nearer shore deposits; followed by terrestrial deposit sedimentation. The alternating fine grained siltstones and mudstones of the Reservoir Formation are here interpreted as distal storm shelf deposits interbedded with finer pelagic sediments (fig 4.15). These are overlain by marine fan facies sediments of the Deerhope Formation, representing overbank deposits. The sediments of the Cock Rig Formation are thought to represent fan feeder channels. This was overlain by the Wether Law Linn

Formation, which was formed by a repeatedly colonised shallow marine barrier complex, deposited and modified by (proximal) storm and fair weather processes. The upper member of the Wether Law Linn Formation is interpreted as a restricted lagoonal environment overlain by the Henshaw Formation terrestrial alluvial fan facies (Robertson 1985; 1989).

4.8 Igneous activity

Volcanic ash bands (or metabentonites) from the Wether Law Linn Formation were identified by Tipper (1974), discussed by Robertson (1985:42) and studied by Batchelor and Clarkson (1992). Further details of analysis of metabentonites from the Reservoir Formation are given below (Section 4.9; Fig 4.17).

One 3.5 m to 10.0 m thick igneous body is exposed in the Fairliehope Burn, the North Esk River and the Gutterford Burn. This intrusion runs sub-parallel with the strike but cuts across the stratigraphy locally. Fresh samples of the intrusion are difficult to obtain as it is very heavily weathered. It is best located by identification of the heavily baked sediments at the margins. The composition of this intrusion is a fine grained dolerite and is very similar to that of the many thin (0.1 m to 1.0 m thick) intrusions that cut the overlying Lower Old Red Sandstone sediments (Cockburn 1952), and virtually parallel the trend of the intrusion cutting through the Silurian sediments. These also roughly parallel Caledonian Orogenic trends.

Robertson described the intrusion as being folded by f1 and f2 folds in the Gutterford Burn, referring to two phases of deformation he envisaged affecting the whole area. Close inspection during this project suggests that the intrusion bifurcates and follows weaknesses in the sedimentary layers. It is thought that the locality exposed in the Gutterford Burn, is the site of a line of en-echelon folding (see chapter 5), and that the intrusion appears to be folded as it follows flexures within the host rock.

Robertson (1989) suggested that the folding of the intrusion along 'Silurian' trends implies that the igneous body would appear to be Silurian in age. The LORS sediments are probably underlain throughout by Silurian sediments. To form intrusions in the LORS sediments, the igneous material must first have passed through the underlying Silurian sediments. It is thought here that the single main intrusion passing through the NEI sediments was typical of the bodies feeding the intrusions in the LORS. They exploited the near vertical bedding of the Silurian to rise, and when they met flexures within the Silurian sediments, they bifurcated, so that when incident on the overlying LORS sediments, the one initial feeder intrusion had become many smaller intrusions. This would then date the time of intrusion to post LORS deposition, and pre UORS deposition. These intrusions are not seen to cut the UORS sediments and are therefore thought to have been emplaced during the mid-Devonian.

4.9. Metabentonite analysis.

At a number of localities within the Reservoir Formation, the presence of pale streaks of clay rich horizons was recognised (fig 1.5c). These beds have been subjected to considerable surface weathering, but it was thought that they were similar to units identified elsewhere within the NEI as metabentonites, and therefore considered worthy of further study.

The original reasons for conducting analysis on these specimens were:-

1) to try and confirm that they are indeed metabentonite horizons
2) to determine if there was some sort of chemical signature enabling a particular bentonite horizon to be correlated and
3) if the localities sampled represented one or more horizons.

It was clear from fieldwork mapping, that either at least two bentonite horizons are present, or if only one horizon is present, then there must be an unexposed major fault zone causing the bentonite horizon to be offset. The specimens were gathered from three main localities, and at all but one of the localities, two or more sampling opportunities were available, as detailed on the map (Fig. 1), and specimen number list (table 4.16).

All of the clay bands appear to vary from 2-5 cm thick along strike. Colour variations within the horizons sampled are apparent, and bands from dark red to cream or grey coloured are seen, although the majority of the beds are soft pliable cream coloured clay. Horizons were excavated and sampled using a brush to clear away the shale, and a "Swiss Army" knife to slice out the specimens.

Table 4.16: BENTONITE LOCALITIES

Spec.	Locality.	Sample comment.
1	Reservoir.	Bulk sample
2	S. G.B.	Stratigraphic base of bed (bit in between red clays)
3	S. G.B.	Red clay near stratigraphic top of bed
4	N. G.B.	(consists of two discrete horizons) Strat. base bent., fresh material from bed top (1)
5	N. G.B.	Strat. base bent., weathered material
6	N. G.B.	Strat. base bent., fresh material from bed top (2)
7	N. G.B.	Strat. base bent., cream coloured material
8	N. G.B.	Strat. base bent., grey coloured material
9	N. G.B.	Strat. base bent. strat. base, bulk sample
10	N. G.B.	Strat. top bent. weathered material
11	N. G.B.	Strat. top bent., fresher material
12	S. Shep. Cott	Weathered end of bulk sample
13	S. Shep. Cott	Fresh material, stratigraphic base of bed
14	S. Shep. Cott	Fresh material, stratigraphic top of bed
15	S. Shep. Cott	Fresh material, bulk sample
16	South of N. Shep. Cott	Bulk sample
17	North of N. Shep. Cott	Stratigraphic top
18	North of N. Shep. Cott	Stratigraphic base
19	North of N. Shep. Cott	Bulk sample

Grid references of localities

S Shep. Cott.	NT 1602 5937	Arthropod track Loc.	NT 1601 5944
N Shep. Cott.	NT 1603 5940	GBLB Locality	NT 1589 5908
N. G. B.	NT 1579 5866	Folded Gorge	NT 1554 5757
S. G. B.	NT 1576 5859		
Res.	NT 1536 5825		

Figure 4.17. Major elements in weight %. Trace elements in ppm. Trace element ratios.

BENTONITE SAMPLE ANALYSIS

	EB1	EB2	EB3	EB4	EB5	EB6	EB7	EB8	EB9	EB10	EB11	EB12	EB13	EB14	EB15	EB16	EB17	EB18	EB19
SiO_2	56.94	56.46	55.24	56.74	54.74	53.63	61.62	58.57	57.68	55.36	56	57.37	53.38	59.51	56.9	58.89	58.87	59.75	58.77
Al_2O_3	22.25	23.24	24.2	27.22	26	25.45	27.29	23.21	24.3	23.09	23.3	25.28	24.32	23.73	25.6	24.5	24.57	26.68	25.91
Fe_2O_3	5.09	4.99	6.89	5.06	2.69	5.55	2.76	5.07	3.82	7.29	7.42	5.18	4.1	4.75	4.75	5.05	3.22	3.92	3.34
MgO	3.52	4.41	3.77	2.62	2.63	2.59	2.46	3.57	3.06	4.55	4.45	3.49	4.39	4.25	3.44	4.13	2.89	4.25	3.09
CaO	0.75	4.02	0.63	1	2.78	1.24	4.9	1.07	1.62	0.64	0.66	0.5	0.58	0.65	0.81	0.84	1.05	0.97	1.01
Na_2O	0.96	0.75	0.66	1.14	1.27	1.19	2.19	1.31	1.59	0.67	0.77	0.71	1.06	0.6	0.75	0.9	1.09	0.81	1.02
K_2O	5.42	6.53	6.73	7.41	6.72	6.79	6.36	5.59	5.89	5.04	5.77	6.4	6.03	6.08	6.47	5.88	5.55	6.39	6.16
TiO_2	0.83	0.92	1.16	1.09	1.07	1.08	1.12	0.9	1.01	1.39	1.39	0.93	1.02	0.84	0.8	0.96	0.8	0.81	0.9
MnO	0.06	0.05	0.03	0.02	0.01	0.03	0.11	0.05	0.07	0.1	0.1	0.05	0.03	0.03	0.03	0.33	0.16	0.11	0.21
P_2O_5	0.05	0.13	0.15	0.16	0.16	0.17	0.19	0.11	0.16	0.28	0.26	0.16	0.16	0.13	0.14	0.16	0.17	0.13	0.13
TOTAL	99.68	99.49	99.46	100.47	98.06	97.68	100.19	99.45	99.79	99.21	100.11	100.36	99.57	99.58	99.8	100.60	99.78	100.57	99.92
LOI	5.6	7.7	5.4	5.5	6.5	5.5	7.4	5.4	5.6	5.8	5.7	6.1	6	5.6	6.1	5.7	5.8	6.1	5.9
Ni	30	11	20	11	12	14	16	42	28	48	51	52	27	30	28	50	36	20	24
Cr	112	83	64	2	2	4	7	67	36	205	205	38	23	41	28	34	7	6	1
V	140	110	113	65	67	65	63	111	84	191	191	104	92	105	94	106	47	61	58
Sc	22	20	24	16	14	15	15	20	20	41	40	19	18	17	18	17	12	13	13
Cu	41	14	4	71	221	92	157	290	182	70	83	54	39	45	52	35	57	60	58
Zn	66	71	71	35	34	34	40	84	61	78	82	55	56	59	56	62	48	46	45
Sr	75	102	117	145	100	105	267	87	154	126	120	84	109	53	77	99	143	114	127
Rb	207	240	277	238	212	224	210	197	201	218	220	236	210	218	226	208	182	222	208
Zr	705	600	780	1015	927	941	937	533	742	287	286	771	846	623	735	724	780	779	765
Nb	18	32	40	47	42	44	42	31	37	20	21	39	42	34	38	39	38	39	38
Ba	547	326	641	6085	4550	6201	861	507	514	496	564	362	440	293	362	552	725	271	476
Pb	14	12	15	11	11	11	13	10	13	12	14	29	25	21	28	44	39	24	27
Th	20	30	40	45	40	41	37	30	35	23	25	42	45	35	40	41	39	40	39
La	140	160	344	156	108	160	146	28	87	847	772	225	170	117	103	120	144	77	83
Ce	295	355	736	376	774	369	340	46	204	1615	1465	360	261	150	164	308	417	177	258
Nd	102	135	267	150	110	148	137	36	61	609	554	164	133	94	78	94	113	61	72
Y	89	94	123	147	130	137	130	81	110	78	77	106	109	60	94	105	94	91	92
Zr/Nb	11.4	18.0	19.5	21.6	22.1	21.4	22.3	17.2	20.1	14.4	13.2	19.8	20.1	18.3	19.5	18.6	20	20	20.1
Nb/Y	0.46	0.34	0.33	0.32	0.32	0.32	0.32	0.38	0.34	0.26	0.27	0.37	0.29	0.39	0.4	0.37	0.4	0.43	0.41
Zr/TiO_2	24.7	65.2	67.2	93.1	86.6	87.1	83.7	59.2	73.5	20.6	20.6	77.9	82.4	74.2	82.1	75.4	95	96.2	95.0
Ti/V	35.4	50.2	61.6	100.6	95.83	99.7	106.7	48.6	72.1	43.7	43.7	57.1	66.5	48	57.5	53.5	102.1	79.7	92.8
Ti/Th	249	276	348	327	321	324	336	270	303	417	417	297	306	252	270	288	240	248	240
Zr/Y	5.25	6.38	6.34	6.9	7.13	6.87	7.21	6.58	6.75	3.68	3.71	7.27	7.76	7.08	7.86	6.96	8.09	8.56	8.29
La/Y	1.58	1.7	2.79	1.06	0.83	1.17	1.14	0.34	0.79	10.86	10.02	2.12	1.56	1.37	1.09	1.23	1.53	0.85	0.91
SiO_2/Al_2O_3	2.53	2.43	2.28	2.08	2.11	2.11	2.26	2.52	2.39	2.4	2.4	2.27	2.19	2.51	2.22	2.4	2.44	2.24	2.25
K_2O/Al_2O_3	0.24	0.28	0.27	0.27	0.26	0.27	0.23	0.24	0.24	0.25	0.25	0.25	0.25	0.26	0.25	0.24	0.23	0.24	0.24

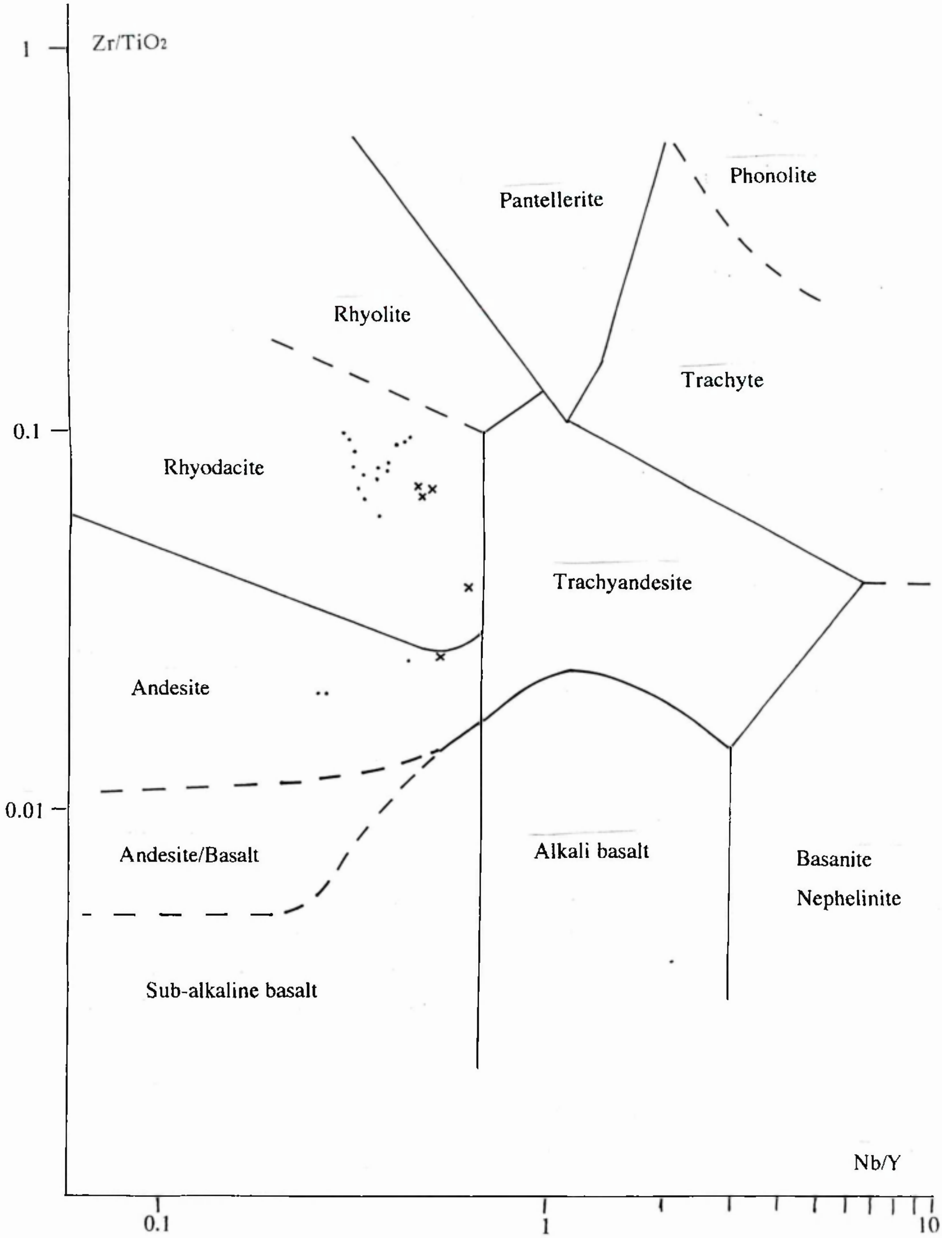
The colour variations did not seem to appear as differences in geochemistry. Samples were collected after considerable excavation to remove surrounding (contaminating) shales, and reveal fresher material, also to gauge the lateral continuity and variations in thickness of each band within each locality. Only part of each specimen collected was analysed (part remains should further analyses be required). Sections were cut from each sample, and made into pressed glass discs, and then analysed for their major and trace element content by X-ray fluorescence methods. It is believed that specimen EB 7 was possibly contaminated during preparation. Results are given in figure 4.18.

The field work and mapping suggested that it should be possible to correlate the "Reservoir" locality metabentonite with the "Shepherds Cottage" locality bed. The north and south Gutterford Burn localities should also be along strike from one another, and are physically separated by one bend in the burn (about 20 metres) and associated hillock. these two localities do not line up perfectly, and this is thought to be due to local small scale faulting (see fig 1). At least one of the "Gutterford Burn" horizons considered herein to be a bentonite (S. G.B. locality), was described by Robertson (1985:42) as resulting from "A small thrust along a thin white clay band." It was hoped that this chemical analysis might confirm the nature of the clay band.

Element ratios are compared as this is the most meaningful way of eliminating the unquantifiable contributions from sea water and clastic input (Batchelor and Weir, 1988:21). Plots commonly used in the study of metabentonites, such as Zr/Y against Nb/Y, K2O/Al2O3 against SiO2/Al2O3, and La/Y against Zr/Y, were prepared to find if the samples from this study plotted within the same fields as other metabentonites (fig 4.19). It was thought that any anomalies would point to these horizons not being of volcanic ash fall origin. The results were entirely consistent with those obtained for metabentonites elsewhere (Merriman and Roberts, 1990), leading to the tentative conclusion that these samples are indeed metabentonites. Further confirmation could be obtained by analysis of clay content.

The specimen collected from the North Gutterford burn locality (samples EB 10 and 11), appears to have a 2-3 cm. layer of sediment separating two distinct clay bands of up to 5 cm thickness (mostly 2 cm). This could imply that these metabentonites were deposited by a major eruptive event, followed by a minor one, similar to the interpretation by Batchelor and Clarkson (1993:124) for the later Deerhope Burn ash band. Samples EB1 and EB 10 and 11 plot significantly outside the range occupied by the other samples on two of the ratio plots, the Zr/Y against Nb/Y plot and the Zr/TiO2 against Nb/Y plot, and on the latter much closer to the two samples of adjacent siltstone analysed by Batchelor and Clarkson (1993). On inspection of the results it is thought probable that the two samples EB10 and EB11 taken from this second "minor event" actually represent reworking (and contamination by sedimentary input) of part of the material from the initial eruptive event. No evidence for a "minor event' or secondary reworking of the ash band is seen at the NGB locality. Sample

4.18 : Classification diagram (after Winchester and Floyd 1977). Dots = Reservoir Formation samples, crosses = Wether Law Linn samples (Batchelor and Clarkson 1993).



EB1 was difficult to obtain as it is highly weathered, and is thought to have been contaminated by the surrounding shales.

"Bentonites are smectite rich clays formed when silicic vitric ash is altered by prolonged contact with sea water in conditions of low silica activity. During diagenesis and low grade

> metamorphism, bentonites are transformed to mudstones, rich in mixed layer illite-smectite, referred to as K-bentonites or metabentonites." (Merriman and Roberts, 1990:259).

Comparison with other geochemical analyses of metabentonites, leads to the tentative conclusion that the clay bands from the Reservoir Formation, are actually metabentonites. Further analysis of the clay content by the methods described by Batchelor and Clarkson (1993:125), and further collection of certain horizons would be possible extensions of this preliminary study. This could possibly also include the ash band occurring in the GBLB locality logged section which is almost coincident with the *celloni/amorphognathoides* conodont Biozone boundary.

The clay bands known from the other formations of the North Esk inlier have been analysed elsewhere (Tipper, 1976; Batchelor and Clarkson, 1993). The results from samples analysed here were compared with these published results, and also with published metabentonite analyses from other areas such as Ireland (Cameron and Anderson 1980; Sloan and Bennett 1990) and Dob's Linn (Batchelor and Weir, 1988; Merriman and Roberts, 1990).

The emplacement of the Midland Valley inliers and the possible tectonic regime that existed at the time of deposition, particularly with respect to the presence or absence of a subduction related volcanic arc (Bluck 1985), has been a subject of recent controversy. Any information on, or indicators of, the possible volcanic source of these bentonites is potentially important to late Llandovery tectonic models.

Cameron and Anderson (1980), working on metabentonite deposits of lower Silurian age from Northern Ireland, discussed the process of confirmation that these claystones were indeed of volcanic origin. They noted that evidence from all over Britain suggested that substantial volcanic activity was occurring throughout the Llandovery and possibly into the Wenlock, this despite few rocks of volcanic origin, such as lavas or intrusions, being preserved. Studies of Silurian (late Wenlock) volcanism in Ireland have been made (Sloan and Bennett, 1990), and record subalkaline rocks, intermediate between tholeiitic and calc-alkaline, generated at a destructive continental margin. Sloan and Bennett (1990) suggest that subduction may, however, have ceased before eruption of these lavas and pyroclastic rocks. The Silurian rocks of the Midland Valley are probably related to the same subduction zone and hence the same phase of volcanicity. Analysis of the possible source of the Irish metabentonites (Cameron and Anderson, 1980)) has not yet been published, and it is thought that these may yield much information about the proposed Midland Valley volcanic arc.

The results of analysis of the Reservoir Formation clay bands, showed no distinctive pattern of enrichment that could be used to differentiate between separate ash fall events, nor whether these samples were formed by the same event and later faulted into their current offset position. Winchester and Floyd (1977) introduced the use of the ratios Nb/Y (index of alkalinity) and Zr/TiO2 (differentiation index), to plot a geochemical grid to discriminate between volcanic rock types. The most interesting relationship, for the Reservoir Formation

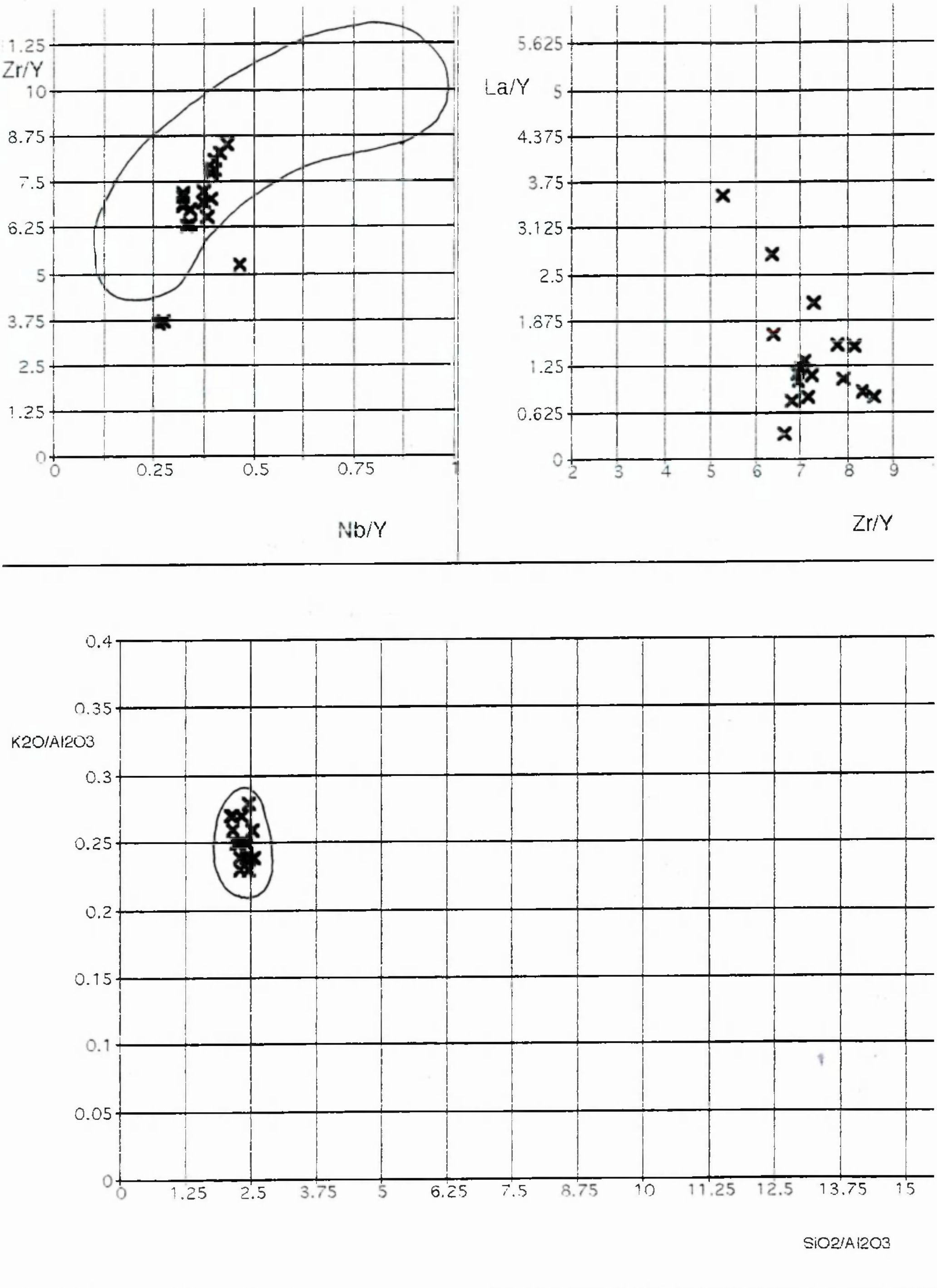


Figure 4.19 : Element ratio plots of metabentonite samples. Marked area shows range of values for metabentonite samples from other areas.

samples, came from comparing the plots on such a geochemical grid (fig 4.20), with the samples of Batchelor and Clarkson (1993) from the Wether Law Linn (NEI), and the samples from Dob's Linn (Batchelor and Weir, 1988; Merriman and Roberts, 1990).

Results from within this study suggest that the proposed stratigraphically higher Shepherds Cottage locality samples (EB12-19) have slightly higher Nb/Y ratios than the remainder of the Gutterford Burn samples (EB 4-15), and according to the geochemical grid, are possibly derived from a slightly more alkaline source. The samples of Batchelor and Clarkson (1993) from the Wether Law Linn Formation ash band (which is even higher in the stratigraphic column), also suggest a slightly more alkaline source. The samples from Dob's Linn, are from older horizons (from the Ordovician onwards). Almost all of the Dob's Linn samples plot as less alkaline than those from the Reservoir Formation. An increasing alkalinity trend within the parent magma is suggested.

The metabentonite analysis results presented by Merriman and Roberts (1990) was considered entirely consistent with the model of a (now missing) volcanic back-arc across this plate boundary (Stone *et al.* 1987), and that the arc, of calc alkaline character, was founded on continental crust. The evidence presented here is also entirely consistent with this model, and possibly indicates increasing alkalinity of the source with time.

4.10 Chapter summary

The Reservoir Formation sediments consist of alternating siltstones and shales and were deposited by distal to intermediate storm currents on a low energy mud dominated shelf or in a shallow marginal-basin sea. There is evidence of cycles of sedimentation, probably associated with fluctuations in sea level, and the depositional basin may have been formed by pull apart processes. The GBLB locality sediments show patterns of storm deposition such as repeated winnowing, rapid deposition and periods of non deposition. This controlled and modified the benthic fauna. (sedimentary processes are further summarised in section 4.7). Minor igneous intrusions of probably Middle ORS age, that follow flexures and weaknesses in the Silurian sediments are described. White clay bands are identified as metabentonite horizons, with probably two such horizons cutting through the Reservoir formation, although no descrete chemical signature could be identified for either horizon. The source for these metabentonites was calk-alkaline in character, and comparison with metabentonites from higher up in the North Esk Group, suggests an increasing alkalinity of the source with time.

Chapter 5

Structure and Tectonic History

5.1 Introduction.

The sediments of the North Esk inlier have a relatively simple structure, even though the beds are vertical and one might have expected a greater yield of structural geological information. However, this thesis does not contain a detailed account of structural geology, since any extrapolation from small local scale features described here, to large scale tectonic movements, can be no more than tentative. Given the limited exposure of Silurian rocks in the Midland Valley, any structures or trends identified may have considerable bearing on the various tectonic models which have recently been postulated for the formation of the Southern Uplands and the Lower Palaeozoic rocks of Southern Scotland generally (Lee *et al.* 1990; Soper and Woodcock 1990; Stone *et al.* 1987).

The Silurian rocks of the North Esk inlier consist essentially of a conformable suite of sediments, currently in a sub- vertical position, with a constant younging direction towards the North West. These rocks have been affected by faulting, folding and thrusting on a local scale which is discussed below. In the field, these rocks map essentially as straight lines, which would be expected for vertical rocks. Structural complexities are not generally thought to cause correlation difficulties in this area. This has been partially confirmed by use of the chemical signature of metabentonites, to correlate the same horizon exposed in two separate localities (see section 4.9). The possibility of repetition of small parts of the sequence due to unexposed faults and thrusts cannot, however, be ignored.

5.2 Previous models.

The first authors to present a structural model for the sediments of the North Esk Inlier were Henderson and Brown (1869, Pl.VIII, section 1). Their section across the Reservoir is simple and idealised. It suggests that all the strata are conformable, dipping slightly to the south east, with one overfold above the reservoir, which is much the same picture as we envisage now. Peach and Horne (1899, figs. 120, 121) suggested a more complicated structural history, involving repeated isoclinal folding with vertical axial-planes, up-ending the strata into their current sub vertical position. Their fig 120 (1899:592) involves such great shortening that one bed in their section is repeated up to nine times in the figure as presented.

Lamont (1954) suggested a more conformable and less structurally complex sequence, although without clear illustration. Lamont also recognised the presence of major crush belts, particularly cutting across the north shore of the Reservoir. Mykura and Smith (1962:11) produced an excellent map, noted that the sequence formed a regularly ascending group, and mentioned only minor folds. Tipper (1974) indicated that insufficient data about reversals in younging directions were available to him at that time, to alter the "existing" model of isoclinal folding. He did describe the local dip variations of the rocks from the vertical, and concluded that this was entirely due to hill creep (discussed in section 5.3).

A non-isoclinal folding model was given by Robertson (1985:41) who recognised constant younging to the north-west. This model described two folding episodes, *f1* and *f2*. Robertson's *f1* series of folds are reported to be restricted to the Reservoir Formation. They form laterally impersistent groups of anticline-syncline pairs of isoclinal or sub-isoclinal folds. Robertsons later folding episode *f2* (which he notes as refolding *f1*) is described as open kink folds with fold axes plunging to both the north-east and south-west. It is to the *f2* folding episode that Robertson (1985) ascribes the variation of dips from the vertical; these include some that Tipper (1976) described as hill creep.

Robertson (1985:42) was also the first to suggest that tectonic thrusting has affected the sediments of the NEI, although the field evidence for the single thrust belt that he describes is not clear (see section 4.3.4). Neither did Robertson discuss the emplacement of the Silurian strata in their current vertical attitude, or the relationship between the NEI, (which represents the oldest rocks at the core of a regional anticline), and the formation of the anticline itself.

The structure and emplacement of the Midland Valley inliers have been mentioned directly and indirectly by other authors, particularly those working on the Southern Uplands, this will be discussed further in section 5.4.

5.3 Local Structure.

5.3.1 Overall patterns.

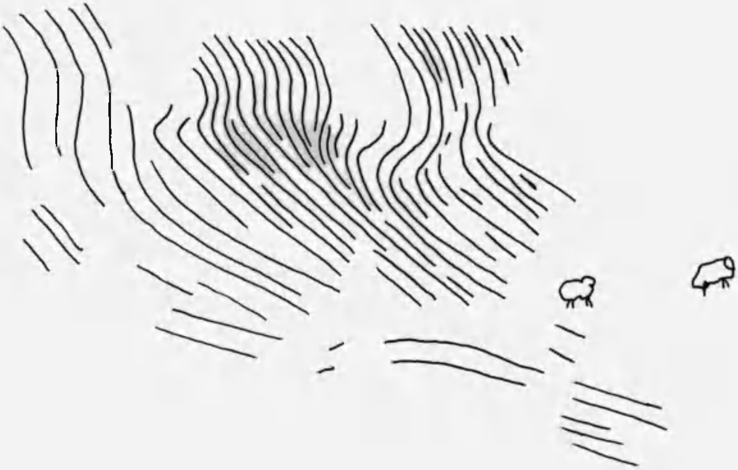
The North Esk inlier is an outcrop of Silurian strata that have been exposed by the erosion of a “window” through the overlying Devonian sediments. The Silurian strata lie at the core of an apparent regional antiform. The overlying Devonian sediments to the south of the inlier dip gently (30°) to the south-east, and to the north , they dip gently to the north-west.

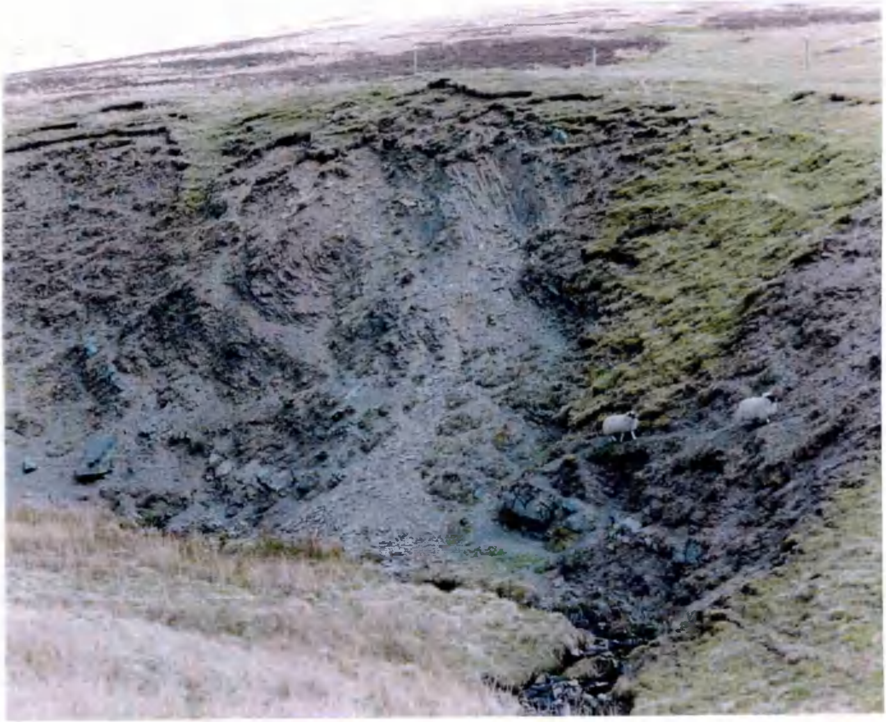
The rocks exposed in the North Esk Inlier are close to vertical, striking roughly north-east to south-west with dips decreasing to, at the most, 30 degrees in either direction. For most sedimentological and palaeontological purposes, all changes in dip can be thought of as minor variations from the vertical. Large tracts of outcrop are inclined in a similar direction. For example, almost all of the rocks exposed on the east shore of the reservoir dip gently to the south-east, whilst those on the north shore dip gently to the north-west. The streams such as the Gutterford Burn, tend to exploit the areas where the strata are most inclined, the vertical strata, and areas of weakness associated with folds.

The younging direction within the inlier remains constant. At individual localities the strata may be inverted (e.g. GBLB Locality). These beds young constantly to the north-west, therefore no large scale repetition by folding is envisaged. The inversion of the beds at some localities, is merely a variation from the overall vertical trend.

> It is possible that small scale slumping involving a few metres thickness of sediment, slipping a few metres down slope, may have occurred. This could have occurred either at the time of deposition (see section 4.5), or recently. The latter could cause local variations in dip of near surface strata, as a result of hill creep (arrowed in fig 5.4C). This possibility cannot be ignored, but should not be confused with strata folded at or near the surface (fig 5.4D), which in the example given, could clearly not be hill creep as it folds the wrong way (up-hill). At other localities where folding is in the downslope direction, this could be described as hill creep (Euan Clarkson Pers comm.). Hill creep is considered here to have only minor

Figure 5.1 a . Intensively folded locality. The "arthropod track" locality (Reservoir formation, North Esk inlier), grid reference NT 1601 5944. Overlay highlights the most important structural features. Sheep for scale.





effect on the strata, and that most of the variations in dip observed, are directly related to the tectonic structures described below.

5.3.2 Folding.

There are three separate localities (in the "folded gorge", grid reference NT 1554 5757; in the Gutterford Burn, grid reference NT 1591 5928; and the "arthropod track" locality, grid reference NT 1601 5944) where the outcrop of folding on a more intense scale is exposed (fig 5.1). If exposure were better overall, then it is thought that more examples of intense folding would probably be found. At the existing localities, isolated, laterally impersistent, antiform-synform pairs are exposed. The shale horizons are thickened and bulbous in the hinge area. In the siltstones, either weak axial-planar cleavages developed, or brittle failure of more substantial units occurred.

Robertson (1985) considered the large scale variations in dip to be open folds, and he suggested that these, and the isolated examples of intense folding, resulted from two distinct folding episodes, *f2* and *f1* respectively. It is here considered more likely, however, that only one folding episode is involved. Cross-sections through the Reservoir Formation across the valley of the Gutterford Burn (fig. 5.3B,C) show that the burn runs along a narrow band of vertically oriented rocks in the base of the valley, surrounded by blocks of strata dipping in different directions. It is thought here, that these represent kink bands or kink zones (see fig 5.3A). The exposures of more intense folding described by Robertson as fold episode f1 are thought to be Chevron Folds (Ramsay and Huber 1987) formed at the intersection of two conjugate kink zones (Hobbs *et al.* 1976:173 and 211) (see fig 5.3A). Kink band geometry has been used in Wales to produce models of Lower Palaeozoic dextral strike-slip movements (Pratt 1992).

The nature of ideal kink bands is discussed by Dewey (1965); these are symmetrical and possible, although difficult, to analyse mathematically. The folding described here can be considered as compressional kink folding, developed in a body departing from ideal behaviour (Paterson and Weiss 1966:371). Also, loading may not have been perpendicular to the bedding. The fold asymmetry of Reservoir Formation strata suggests that loading was at a slight angle to foliation, and that this loading caused a shortening up to 30% (Paterson and Weiss 1966:361). The shearing out of the folds along their axial planes in areas of Chevron folding (fig 5.4A) is common for such fold mechanisms and is known as Hinge Collapse (Ramsay and Huber 1987:428). Departure from the ideal, and lack of examples, means that the structures cannot be further studied mathematically. The recognition of the fold mechanism as kink fold formation however, allows comparisons with other folded regions such as that described by Kimura *et al.* (1989) between the Mariana and Yap trenches.

Variations of the dips of Reservoir formation strata have been plotted on stereonets, both in areas of chevron folding and exposures away from intense folding. These confirm that only one clear phase of deformation affected the inlier, as all data confirm that folding occurred around a single axial-plane, which dipped 10-20° south west, towards 225° (fig. 5.5). This implies that almost all of the large scale folding is tectonic, from one phase of deformation and not syn-sedimentary. The pole to such an axial plane should indicate the direction of

Figure 5.1 b.
Intensively folded locality.
The "Folded gorge" locality (Reservoir formation, North Esk inlier),
grid reference NT 1554 5757. Overlay highlights most important structural features. Car parts in water for scale.

loading. In this case the loading is consistent with Caledonian trends and roughly parallells the line of the terrane boundary, the Southern Uplands Fault (Floyd 1994).

Chevron folds are only exposed in the Reservoir formation of the NEI. Rocks of similar age in other Pentland Hills Silurian inliers (Bavelaw and Loganlee) show signs (dip variations) of the same process having affected the rocks, but no direct evidence of folding due to lack of exposure. The different response of rocks higher up in the Silurian succession to the same compressional deformation is related to the decreasing fissility of the rocks up section. The alternation of siltstone and shale characteristic of Reservoir formation rocks, are well suited to the formation of kink bands. They exhibit a high ductility contrast, without a high ratio of competent to incompetent layers (Ramsay and Huber 1987:427). Rocks of the upper formations of the North Esk Group are more uniform throughout, without regular changes in competency. These are less likely to form kink bands, and may have been more prone to the formation of thrusts roughly parallel to the bedding as a result of the application of the same stresses that formed the kink bands in the Reservoir Formation sediments.

5.3.3 Thrusting.

Robertson (1985:42) was the first to propose that thrusting may be involved in the tectonic history of the North Esk Inlier, although when Lamont (1954) suggested the presence of a major crush belt passing through the North Esk Reservoir, he was probably considering the sort of bed-parallel displacement that we now associate with thrust motion. Lamont's crush belt (grid ref. NT 1545 5833) is marked only by poorly exposed fractured sediment, depressions in the hillside and difficulties he experienced with correlation between the sediments exposed to the east and west of the Reservoir. A study of the air photos and of strata exposed within the Reservoir when the water levels have been lowered, shows no evidence for a laterally persistent 'crush belt', only of possible faulting along normal regional trends.

Robertson (1985:42) described thrusting at only one locality within all of the Pentland Hills inliers. He described only "small-scale" movement (unquantified), along a plane marked by a "thin white clay band" (grid reference NT 1576 5859). This clay band has been collected and studied by the author, and is thought not to represent a thrust melange, but to be one of the suite of metabentonites discussed in section 4.9. The possibility however, that such a soft horizon acted as a glide plane, facilitating some lateral movement, cannot be ruled out.

Despite these two false starts in the description of thrusting in the area, thrust motion has indeed been involved in the history of the Silurian inliers of the Pentland Hills. Examples of the small scale thrust episodes observed, in particular in the lower formations of the North Esk and Loganlee Inliers, can be observed in the field (fig. 5.2). In these examples, motion was bedding parallel and only on a small scale, with displacements of up to one metre. It is possible that these are local indications of larger scale displacements of tens of metres or more.

Different manifestations of the affects of deformation are observed for different lithologies. Shale horizons, for example, buckle, fracture and are bunched up (fig 5.2). The more competent and homogeneous siltstone horizons (particularly those over 10 cm thick) exhibit more coherent patterns; it is these that show the more informative patterns. The shales lacked

Figure 5.

Examples of the small scale thrusts observed in the field. C: View due south, "folded gorge" North Esk inlier, grid reference NT 1551 5757 and A: from Loganlee inlier, view due south,. Note bunched up shale horizons and siltstone horizons forming thrust wedges and ramping of beds over themselves

B: Weathering of limestone bed material, newly exposed calcified sediment leaches out considerably within a few months. Within 6 months the specimen becomes mould material, in a further 6 months the rock matrix will crumble away and within two years the specimen will resemble muddy clay.

the tensile strength to remain coherent and the shear stress was dissipated through the softer horizons (Hobbs *et al* 1976:199). Thrust wedges were formed in more competent layers, and shortening caused the ramping up of some beds over themselves (fig 5.2).

The thrust motion recorded in the Pentland Hills Silurian inliers suggests pressure from the south or south-east, caused blocks to ramp up over those to the north. Within the Pentland Hills Inliers the sense of fault displacement is sinistral. When the existing dip is restored for each example of thrust motion, the best approximation to the average thrust motion is towards 282°.

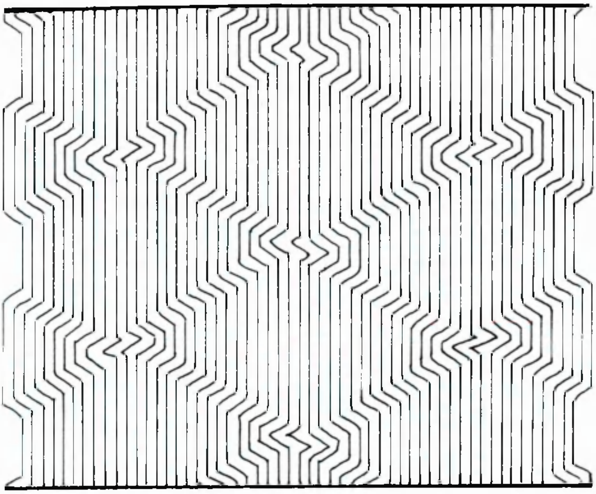
5.3.4 Faulting.

All of the Pentland Hills inliers are cut by many sub-vertical faults trending roughly perpendicular to the strike of the rocks at approximately 135°. Locally, some of the fractures have slicken-sides or are infilled with calcite and quartz. These may be associated with the trend of some of the igneous intrusions cutting through the unconformably overlying LORS sediments. This implies that the faulting may be associated with the same phase of tectonism as that which caused the igneous activity. The timing of the igneous activity is discussed in chapter 4, and it is suggested to have been active in the Mid Devonian.

The throw on the faults within the NEI is usually about one metre (rarely up to 6m) with down-throw usually to the north-east. Where exposure is good, such as along the east shore of the reservoir, the lateral displacement of the strata caused by these faults can clearly be assessed. Each fault is not always laterally persistent, or even clearly exposed. Unknown fault displacement factors add further difficulties to correlating and drawing up maps across areas of poor exposure.

The whole of the Pentland Hills currently forms a block standing proud of the flat lying Midland Valley of the Edinburgh area (fig 5.4 B). The Pentland Fault which forms the southern boundary the Pentland Hills, runs parallel with the Southern Uplands Fault. Indeed the north-easterly extension of the Pentland Hills Fault, the Firth of Forth Fault, is considered to be an ancient deep crustal lineament representing the offshore extension of the combined Pentland Fault and Southern Uplands Fault (Floyd 1994:58). To the south of the NEI the Pentland Fault, running through the village of Carlops, forms a clear boundary with the surrounding Carboniferous age deposits. To the north the boundary is more diverse with strata dipping gradually away from the hills and down to the flat lying Carboniferous deposits, forming one limb of the regional antiform. The boundary between the Silurian and UORS at the northern edge of the inlier has always been accepted as a fault which followed regional trends. Following recent mapping, no evidence has been found for this fault, particularly no lateral continuity further along the line of the Pentland Hills. Stratum contours produced on this boundary coincide with the "fault" line from field evidence. The Upper Devonian or Upper Old Red Sandstone facies Devonian to Carboniferous age deposits (UORS), are known to unconformably overlie the LORS sediments throughout the Midland Valley of Scotland (Cameron and Stevenson, 1985:28), it is thought more reasonable to suggest this northern boundary to be the regional unconformity surface at the base of the UORS in this area. Large scale "faults" such as this, can become entrenched in the literature. The derivation and definition of Midland Valley fault patterns, are currently being reconsidered (Floyd 1994).

A.



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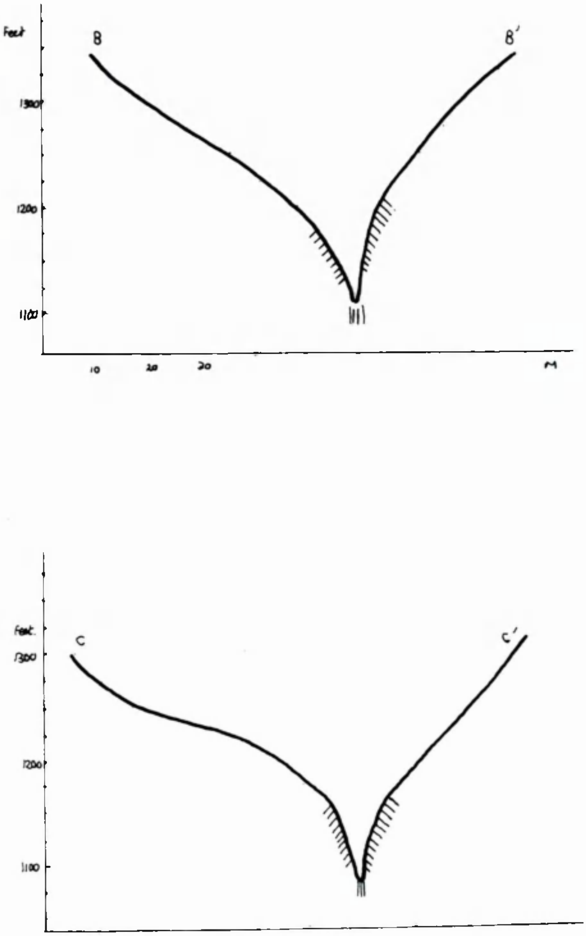

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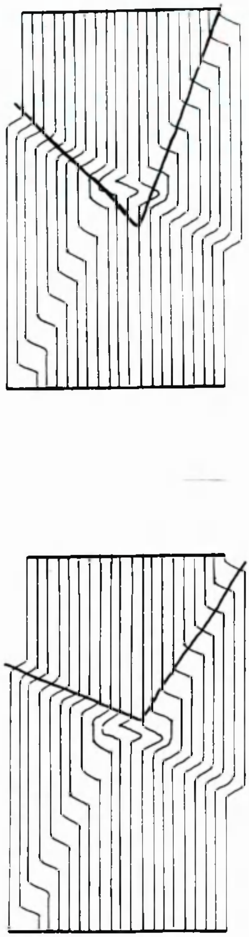


Figure 5.3 A: Formation of conjugate kink zones, and where these intersect, formation of Chevron Folds (after Ramsay and Huber 1987:369). 10 % compression.

B: Cross-sections through the Reservoir Formation across the lower section of the Gutterford Burn

C: Possible cross section through kink bands cut by Gutterford burn, and the increased angle of kink band of east bank of burn

5.4 Implications.

5.4.1 Midland Valley.

It has long been known that a chain of interrelated inliers of Silurian age are exposed along the south of the Midland Valley of Scotland. These run from The Pentland Hills Inliers, (North Esk, Bavelaw and Loganlee) in the North East (Robertson 1985), to the Girvan (Cocks and Toghill 1973) and Craighead (Ward 1989) inliers in the Southwest, via the Carmichael (Rolfe 1960), Hagshaw Hills (Rolfe 1961), and Lesmahagow (Jennings 1961; Walton and Oliver, 1991) inliers. This discontinuous chain, all record an early Silurian regressive sequence from fully marine to terrestrial deposits and give us a tantalising insight into the prevailing conditions in the Midland Valley at time of deposition, during the Llandovery and Wenlock (although the Craighead inlier also records Ordovician strata (Ward 1989)). In recent years, further information has been added to the Midland Valley model from the realisation that the chain extends to the similar aged rocks of the Pomeroy, Lisbellaw and Charlestown Inliers of Ireland. This comparable regressive sequence at the western end of the chain, is recorded in slightly younger rocks than in the east. An account of the basin model for the formation of the Scottish and Irish inliers of the Midland Valley is given by Williams and Harper (1988).

It is accepted that by Devonian times the Midland Valley acted as a graben structure receiving sediment pouring in from both the north and south (Dewey 1971, Haughton 1988), tapping unrelated sediment sources on the northern and southern continental margins. What is as yet uncertain, is what role the Midland Valley played earlier on in the Caledonian Orogeny. Most of the information available concerning the Ordovician and Silurian history of the Midland Valley, is from these inliers. A picture is emerging of what position the Midland Valley occupied relative to both the remnant Iapetus Ocean, and the Southern Uplands, at the time of deposition of the Silurian sediments of the Midland Valley inliers. This is linked to the problems of interpretation of models for the formation of the Southern Uplands (Murphy and Hutton 1986), the closure of Iapetus (Pickering *et al.* 1988; Soper, 1986; Soper and Woodcock 1990), and subsequent terrane accretion (Hutton 1987, Max *et al.* 1990) around which much interest and controversy has centred in the literature of recent years (Pickering Bassett and Siveter 1992; Woodcock and Soper 1992).

The Midland Valley inliers were deposited in a crucial position, at a crucial time for our understanding of the tectonic history of the whole area. It is thought that the sediments of the Midland Valley inliers were deposited in marginal basins, along the southern continental margin of the Supercontinent Laurentia, at a time when it formed the northern boundary of the remnant Iapetus ocean (fig 4.3 B).

A three plate collision is envisaged between Laurentia, Baltica and Avalonia (McKerrow *et al.* 1988; McKerrow *et al.* 1991; Soper 1986; *Soper et al.* 1992; Soper and Woodcock 1990; Vaughan and Johnston 1992), which by the end of the Llandovery times had isolated a section of the remnant Iapetus ocean (4.3 B). The presence of an accretionary prism development (Leggett 1980; Leggett et al. 1979) or imbricately thrust successor or back arc basin infill (Stone *et al.* 1987; Murphy and Hutton 1986) at some point along this continental

Figure 5.4 A: Hinge Collapse: from "folded gorge", grid reference NT 1554 5757. B: The present day Pentland Hills forming a block standing proud of the flat lying Carboniferous sediments of the Midland Valley of the Edinburgh area. C: Local variations in dip of near surface strata possibly caused by hill creep (arrowed)D: Strata folded at or near the surface, from grid reference NT 1561 5828, mouth of Gutterford Burn, looking north.


d


b


a


c

margin may also have further separated the Midland Valley from the open ocean. The present day distribution of these terranes, with the Southern Uplands separating the Midland Valley from the final suture line may be a result of later strike-slip movement bringing together terranes that were originally unconnected (Hutton 1987; Max *et al.* 1990; McKerrow and Elders 1989; Soper *et al.* 1989; Storetvedt 1987; Trench and Haughton 1990; Williams and Harper 1991). The nature of the basement beneath both the Midland Valley and the Southern Uplands is not well known, but approximations from seismic data are being made (Soper *et al.* 1992; Soper *et al* 1989; Lee *et al.* 1990).

5.4.2 Southern Uplands.

The Caledonian Orogeny affected almost the whole of Scotland, particularly the area now from the north of the Great Glen Fault, to the Iapetus suture line, which is probably south of the Southern Uplands. To the east, the effects of the orogeny extended to the present day coastline, and on into the contemporaneous Finnmark Orogenic Zone in Scandinavia. Similarly westwards, the orogenic zone extended through Ireland to the westward (pre-Atlantic) extension the Appalachian Orogenic Zone in Newfoundland (see Pickering *et al.* 1988:362 fig 1).

Bluck (1985:437) noted that "Rocks belonging to the Caledonian and associated events in Scotland are amongst the most studied in the world". Since that time there has been a further blossoming of papers on the area (see above). In particular, this has focussed on two controversial issues, the formation of the Southern Uplands and the closure of the Iapetus Ocean.

Early models for the formation of the Southern Uplands were abandoned when something of a breakthrough in thinking occurred with the recognition of the Southern Uplands as an accretionary prism (Leggett 1980, McKerrow *et al.* 1977), suggested to have been formed as a result of the northward subduction of the Iapetus ocean. This model finally made sense of the many complex structural and stratigraphic problems that had previously existed. There was a place for the Midland Valley Inliers in this model, as an upper trench slope break. The emerging "Cockburnland" (the top of the imbricate pile stack), is thought herein to have acted as a barrier to N-S faunal migration, whilst allowing open lateral marine connection and acting as a source of sediment. As this model so neatly encompassed the details of the geology of the Southern Uplands known at the time, it became widely accepted. However, many aspects of this model have been widely discussed and each detail subjected to rigorous examination, so with time, the model has evolved.

The first main change to the Leggett (1980) accretionary prism model was postulated by Bluck (1984, 1985) who recognised that a major element of strike-slip motion may have been involved in the collision. He also suggested that the volcanic-arc normally associated with a subduction zone (of which there is little direct evidence remaining), may none the less have existed, but was subsequently translated laterally by strike-slip motion. Possible evidence for this arc is given by the presence of metabentonite horizons (described in section 4.9) which imply calc-alkaline volcanism to have occurred within the radius of a few hundred kilometres of the basin of deposition of the NEI sediments (see also Teale & Spears 1986). Volcanic clasts derived from the erosion of such an arc, are expected to be found in the sediments, particularly the conglomerates, of the inliers, which have to date not all been

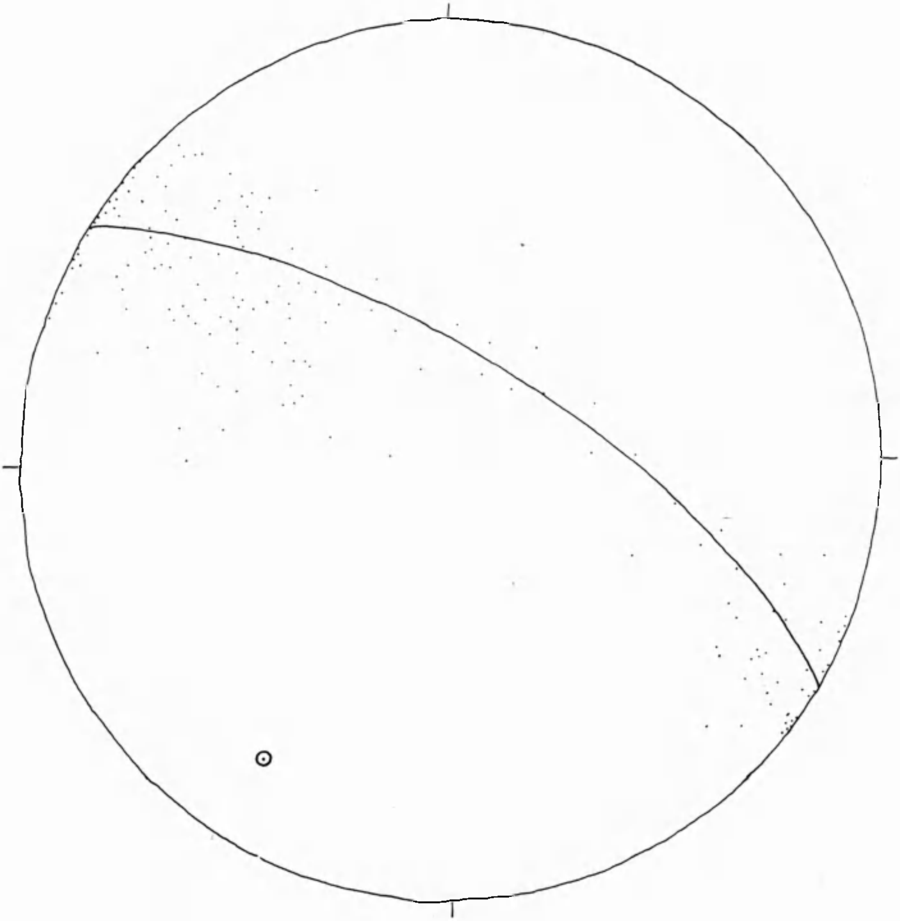


Figure 5.5 Stereographic projections of dip measurements.

A: Plot of poles to bedding
from Gutterford Burn exposures away from intense folding
Key to sympols;
=pole to bedding
=pole to pi-pole girdle
Axial plane dips 22° towards 232°

adequately analysed (Ward 1989). As the Southern Uplands have been considered in more detail, more problems have been identified and a more complex history considered. The current models are summarised in a review by McKerrow (1987) and in papers by Soper and Woodcock (1990), and Stone *et al.* (1987).

5.4.3 Iapetus Closure

Since Dewey (1969) first discussed the nature of the closure of the Iapetus Ocean, and throughout all of the "Southern Uplands" controversy, the Midland Valley of Scotland (and Ireland) has often been considered as attached to the Southern Uplands (Leggett 1980). We can now consider each area of geological outcrop separately, and not, as in the case of the Midland Valley inliers, as a consequence of events in the Southern Uplands. As outlined above, the Midland Valley is not necessarily part of the accretionary prism but probably one of many fragmented basins, stretching right across to what is now Western Ireland. Recent studies such as those by Pickering *et al.* (1988) and Soper *et al.* (1989) describe the Iapetus closure itself, as more complex and diffuse.

"Terrane accretion by oblique docking under sinistral transpression in Newfoundland and Britain was complex and clearly occurred over a considerable time" (Pickering *et al.* 1988:366). It is now widely accepted that during the closure of the Iapetus Ocean in the late Palaeozoic, Britain lay close to a triple collisional junction between two major continental masses, Laurentia and Baltica, and a microcontinental terrane, Eastern Avalonia. The earliest time for which there is evidence that the continental margins of Eastern Avalonia and Laurentia were juxtaposed is the Wenlock (Soper and Woodcock, 1990:527). A three plate destructive margin is considered, with the northward subduction of Iapetus beneath Laurentia. It is suggested that East Avalonia and Baltica approached Laurentia obliquely, gradually cutting off a section of Iapetus as they began to dock with one another by early Llandovery times (Pickering *et al.* 1992). Some authors suggest Avalonia and Baltica collided first, and hence closed the Törnquist sea before closing the Iapetus Ocean (McKerrow *et al.* 1991), or possibly Avalonia docked with Laurentia first, and Baltica then collided and the remnant Iapetus was closed over (Soper and Woodcock 1990; Pickering *et al.* 1988).

From the early Llandovery, strike-slip motion was probably already occurring along the fractured Southern margin of Laurentia and through the Llandovery and Wenlock this continued as the Iapetus remnant was consumed. It is at this time that the Midland Valley Inliers were deposited somewhere along the continental margin. The terrane boundaries are unclear, but the Midland Valley has such an internal continuity of geology (Williams and Harper 1988) it could be considered to have been deposited on one terrane, although the possibility that each of the inliers record the sediments deposited on separate terranes cannot be ruled out. From present day cross strike sections, it is not clear what the original spatial relationship of these terranes was (Soper *et al.* 1989). Strike-slip motion continued until much later, possibly until late Devonian. It has been suggested that up to 600 km of sinistral displacement took place, as late as middle Devonian times, along the Great Glen Fault (Storetvedt 1987). Comparable (dextral) movement of terranes transported from the south along the the west coast of North America has been described (Soper *et al.* 1989). These were rotated clockwise as they were dispersed along the continental margin. The strike of the NEI sediments does not quite parallel the regional structural trend or the southern Uplands

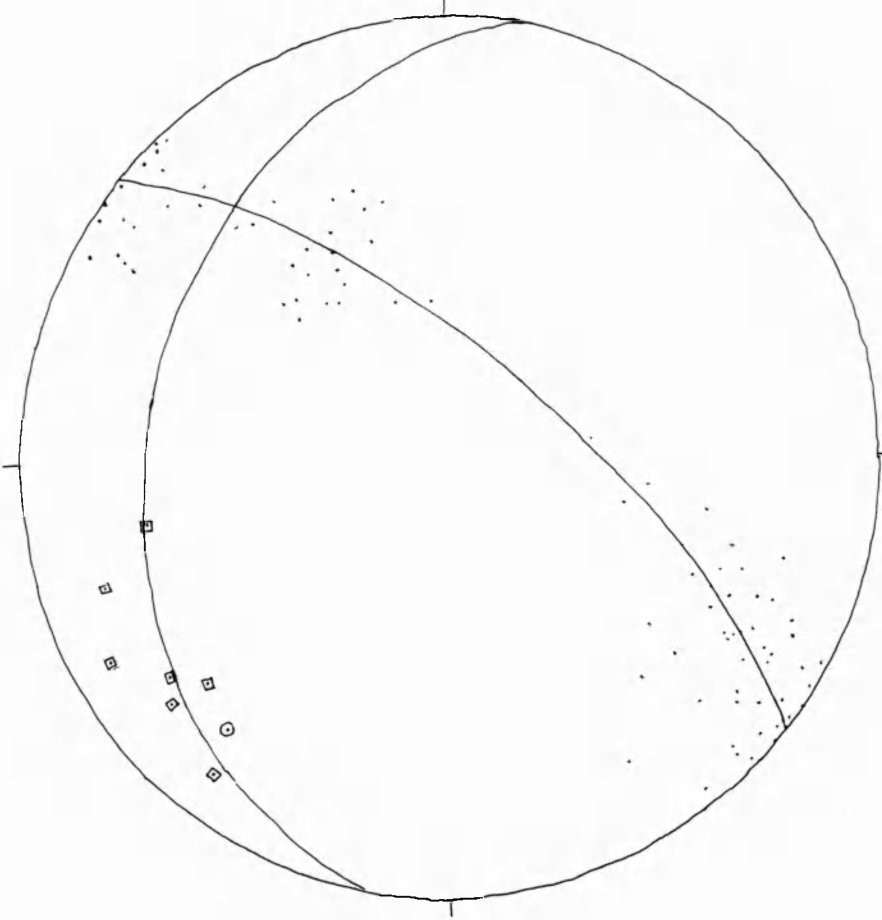


Figure 5.5 Stereographic projections of dip measurements.

B: In areas of chevron folding at Arthropod Track Locality, grid reference NT 1601 5944.
Key to sympols:
=pole to bedding
=small fold hinges
=pole to pi-pole girdle
Axial plane dips 23° towards 292°

Fault, which may be attributed to a similar terrane rotation during emplacement, only in this case anticlockwise motion, as the strike slip motion was sinistral. A model of strike-slip motion along the southern edge of the Midland Valley, south of the Southern Uplands, is supported by observations of sinistral (left-lateral) Caledonian (mid Devonian) shear and dextral (right -lateral) Hercynian (Permo-Carboniferous) shear along the Great Glen fault zone (Storetvedt 1987; Storeveldt *et al.* 1990). Although not all authors agree with such complex models, or that strike slip motion took place at all (Trench and Haughton 1990:255).

Closure is thought to have been "soft collision", not marked by the onset of slaty cleavage but by more subtle markers such as changes in structural style (Pickering *et al.* 1988). An important marker of the first stages of docking seems to be the change from marine to terrestrial deposition. This seems to have become the settled condition in Newfoundland by middle Ordovician (Pickering *et al.* 1988). Unroofing of blocks that supplied ORS facies sediment into a similar environment is thought to have occurred by late Wenlock times in Scandinavia. Final collision is thought to have occurred during the Ordovician in Newfoundland and in Scandinavia it could have been as late as Carboniferous (Pickering *et al.* 1988). From structural evidence observed during this study it is thought that closure of the section of the Iapetus ocean where the sediments of the North Esk Inlier was deposited, occurred at least late on in the Wenlock. Further strike-slip motion may have affected the basin post-deposition, and final emplacement in its current relative geography may not have occurred until the end of the Silurian (see Chapter 4).

Faunal endemicity is also an important marker of soft collision. Notable are the similarities of the shelly faunas in connections SE-NW of the Midland Valley inliers, the Oslo and Baltic regions (eg. graptolites), and the similarities of dendroid species with those of North America and Bohemia. Few faunal connections N-S are found, therefore some barrier to the dispersal of benthos existed, which could have been a landmass such as the proposed emergent Southern Uplands accretionary prism, or a volcanic arc, or a broad ocean. It is not known if all of the fauna preserved in the NEI have benthic or planktonic larval stages. The latter could have assisted oceanic dispersal of the fauna. Continental microplates could also have aided dispersal in the Silurian, as is suggested for the Ordovician (Cocks & Fortey 1982, Pickering *et al.* 1988:368).

The great species diversity observed in the Pentland Hills suggests that the sediments were deposited in one of the remaining marine basins of Iapetus Ocean as it changed from open "Pacific type" circulation to closed "Mediterranean type" circulation. The fauna is condensed, with such a varied fauna probably suggesting various community associations condensed in the fossil record as they migrated to adjust to the rapidly changing conditions. Some elements of the fauna, for example the ostracods, show increasing endemicity higher up section. This probably reflects the severing of contacts with oceanic circulation.

5.4.4. Provenance.

A most important factor in detecting the time of continent docking seems to be the change from marine to terrestrial deposition (Soper and Woodcock 1990). This was accompanied by a partial change in the type of sediment supplied to the area, probably related to the landward unroofing of a sediment stack.

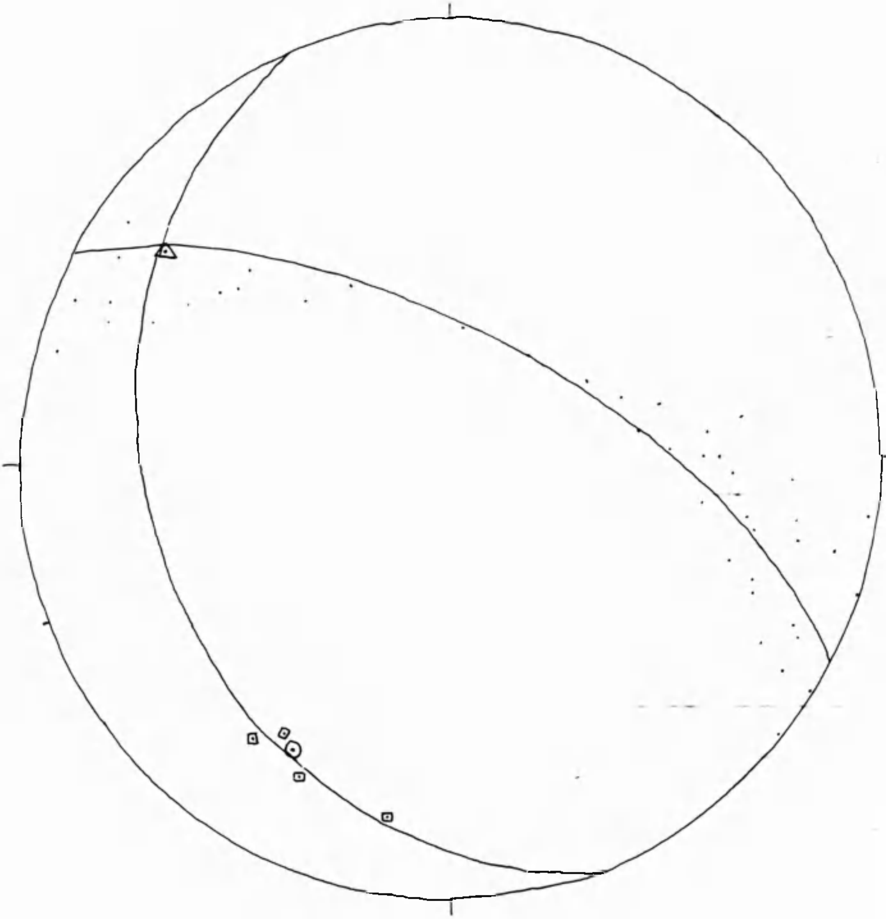


Figure 5.5 Stereographic projections of dip measurements.

C: In areas of chevron folding at Folded Gorge Locality, grid reference NT 1554 5757.
Key to sympols;
=pole to bedding
=small fold hinges
=pole to pi-pole girdle
Axial plane dips 30° towards 249°

Attempts have been made to match the provenance of Midland Valley inlier sediments, particularly of conglomerate pebbles, with so far only limited success (Elders 1987). Results have suggested that at least some strike slip motion could be involved. As noted by Ward (1989:103) a study of all of the conglomerates found in the Midland Valley Silurian inliers could be very informative about not only provenance but the presence or absence of locally derived volcanics from a proposed arc (Heinz & Loeschke 1988). The "Igneous Pebble Conglomerate" is thought to occur contemporaneously in all of the Scottish Midland Valley inliers at the base of the Wenlock (McGiven 1969; Bluck 1983) and marks the onset of ORS facies deposition. This horizon is noticeably thinner to the east. In the North Esk inlier Wenlock aged sediments, intermittent intercalated deposits are found, with fish, brachiopods and crinoid ossicles, above the Igneous Pebble conglomerate. This suggests that the ORS facies deposition at this point was not entirely terrestrial. It is thought herein that we are observing in this area, only the distal part of the first pulses of the onset of the progradation of the ORS facies into the marine environment. This follows the unroofing of a different sediment source and possible terrain docking. Other Wenlockian similarities between Midland Valley inliers have been detailed for the microfossil fauna (Wellman and Richardson 1993).

Contemporaneous deposits of the Midland Valley inliers to the west, were deposited in more proximal environments than the NEI sediments, suggesting that the plate docking was oblique. This is comparable with the situation observed in the Oslo Region (Bassett, Cherns and Karis 1982) where it is observed that as the ORS facies progrades out, so reef development moves before it. Here too a scissor like closure of the remnant Iapetus ocean is envisaged (see fig 5.6 and Pickering *et al.* 1988:371).

It is thought that the likely source-rock providing the sediment for at least the Reservoir Formation of the NEI was a mica-schist (chapter 4). This implies that the sediment source area was a metamorphosed region. In the Oslo region (Bassett *et al.* 1982) this is taken to suggest erosion of the rising nappes of the Caledonian stack, prior to the progradation of the ORS facies. Alternatively the sediment supply could have been from partially metamorphosed parts of the Midland Valley itself (Bluck 1985:446).

5.4.5 Emplacement of the North Esk Inlier.

The rapid deposition of vast quantities of sediment in a regressive sequence at the time of a regional transgression (see chapter 4), suggests that the sediments were deposited into a small basin that was gradually being filled in. The faunal diversity in the earlier sediments suggests that the basin was connected to the open ocean to allow migration. A model of a single Midland Valley basin, would suggest restricted directional marine connections. Later increases in faunal endemicity observed for corals and ostracods (Siveter and Vannier 1992), suggests that the connection to the open ocean gradually diminished as sediment choked the basin. In order to maintain faunal diversity, in the early stages of basin evolution, the depositional basin must have to remained unblocked. This suggests quite rapid subsidence, possibly associated with a pull apart basin.

The rocks now outcropping in the Midland Valley are thought to have originated at the Laurentian continental margin. The sediments now observed in the Ordovician/Silurian inliers are thought herein to have developed in marginal marine basins, probably pull-apart

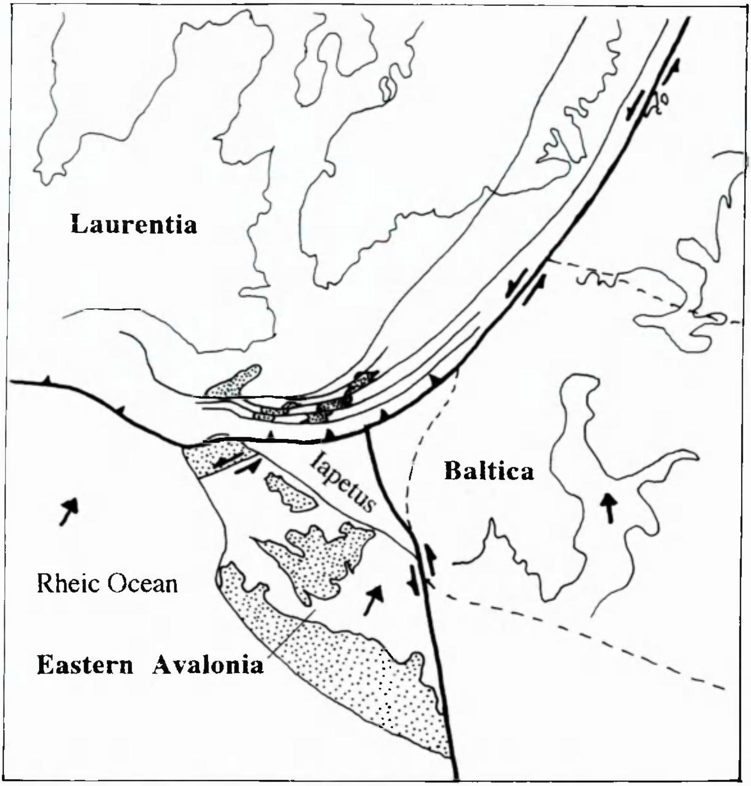


Figure 5.6
End Llandovery three plate collision between Laurentia, Baltica and Avalonia isolating a section of the remnant Iapetus ocean (after Pickering *et al.* 1992:369, fig 1)

structures along the tectonically active southern continental margin of Laurentia. The southern edge of the Midland Valley as we see it now, was probably formed later, as terranes were juxtaposed by strike-slip motion. The oceanic crust situated to the south of the NEI at time of deposition, was probably subducted beneath Laurentia someway to the east. The basin of deposition of North Esk inlier sediments, probably maintained a marginal marine position well into the Wenlock, even after the deposition of ORS facies sediments began prograding out from the north, as crinoids and fish are found in rare marine incursions, after deposition of the Igneous Pebble Conglomerate.

Fault controlled sedimentation is suggested to have occurred in the formation of Ordovician and Silurian sediments now found in Newfoundland (Arnott, 1983) and Girvan (Ince, 1984). In the latter region, the sea floor is thought to have behaved in an erratic manner, with overall subsidence associated with periods of uplift (Ince, 1984). If the basin of deposition of the NEI sediments was a pull-apart basin, then once the basin was full, trans-tension could have become trans pressure as further strike-slip motion continued. The updoming of the Lower Devonian sediments that unconformably overlie the inlier may have been formed as the sediments in the pull apart basin were squashed up beneath them. This may, however, be related to later post-Carboniferous (Hercynian) tectonism that folded areas to the North-East of the Inlier, forming the anticline syncline pairs of the Midlothian Coalfield. Alternatively, the Pentland Hills Silurian inliers may represent one limb of a regional antiform or synform, which without other Inliers or borehole records of Silurian deposits elsewhere in the Midland Valley, we have no evidence for.

A model involving fundamentally different positions of the Midland Valley inlier at the time of deposition to the time of final emplacement have allowed much more freedom of thought, particularly with the Southern Uplands considered to have been deposited on a completely separate terrane. The Midland Valley inlier sediments may now be considered to have been deposited on either one terrane, emplaced by sinistral strike-slip motion during late Silurian times, or as a number of smaller terranes (each inlier) spread out along the south of the Laurentian continental margin. The different structural style of each inlier (Ward 1989) possibly indicates that each section of the Midland Valley in late Llandovery times, may have operated as separate basins, echoing earlier pull apart basins, within one terrane with approximate lateral continuity of geology.

The thrust motion observed in the Pentland Hills Inliers (section 5.3.3) and emplacement of the strata in their current vertical position, could be related to much larger, all encompassing, tectonic models. Extrapolating from local small scale surface tectonics, possible decollement surfaces at depth could be implied. The sediment pile preserved could have been a duplex associated with an imbricate pile that has ramped up the inlier to its present position. The sense of motion and application of pressures are certainly consistent with Caledonian trends. The tectonic structures of the Pentland Hills inliers, closely mirrors the regional tectonic regime (structural grain) and the rocks have undergone sinistral strike-slip movement. This sort of extrapolation is merely conjecture as the Pentland Hills Inliers have no direct structural connections and are considered in isolation. Whilst no new tectonic models can be formulated from the evidence available, information from the Inliers can be used to confirm or deny other broader tectonic models that have evolved.

The lack of evidence so far published for the Midland Valley, particularly during early Silurian times, has been used to employ the Midland Valley terrane as a 'plastic' medium, that can be moulded to fit the juxtaposition of the surrounding terranes as required for each authors model. Evidence from the Pentland Hills suggests that tectonics had a great effect on direct faunal migration. Progressive erosion of the evolving land mass to the north, prograded out into marginal basins on the unstable southern margin of Laurentia. The final emplacement of the inlier occurred as part of a complex structural regime, not intimately tied to what was happening elsewhere but possibly acting as a separate terrane. The resulting structural style, complies with a model of complex sinistral strike-slip displacement. This acted on the Midland Valley area from the time of basin formation in the pre- or early Llandovery, throughout the period of sediment deposition, until late Silurian times, and possibly until the late Devonian.

5.4.6 Sequence of structural events for Pentland Hills Inliers.

By the Llandovery a basin had formed, possibly by pull-apart mechanisms, located somewhere on the southern margin of Laurentia. This basin was rapidly infilled with sediment during the end of the Telychian and early Wenlock times. This was associated with contemporaneous local slumping and dewatering. Volcanoes were active elsewhere and supplied material now preserved as metabentonite horizons.

Progressive lithification occurred during the late Silurian, and beneath the later (Lower) Devonian sediment pile. Folding perpendicular to strike began immediately post lithification, possibly during the late Silurian. The sediments were emplaced in their current steeply inclined position, possibly associated with complex thrust mechanics at depth, and with ongoing sinistral strike slip motion along the continental margin. This pressure continued at least into mid- Devonian times, causing the updoming of the LORS sediments after their deposition and partial lithification.

Faulting occurred after the sub-vertical position of the NEI sediments was attained, but before Devonian sedimentation occurred. All major structural activity was concluded in the area prior to the late Devonian deposition of UORS facies sediments.

Igneous intrusions utilised weaknesses in the Silurian sediments to feed through to the overlying sediments probably during the middle Devonian. The intrusions bifurcated whilst passing through the Silurian sediments.

5.5. Chapter summary

The NEI sediments were deposited in the remnant Iapetus ocean basin at the time of a three plate collision. The sediments are currently sub-vertically oriented. Emplacement at this attitude was probably associated with thrusting at depth, in turn probably related to strike-slip movement of separate terranes along the southern margin of Laurentia. Minor small scale bedding-parallel thrusts are evidence of this at the surface. The NEI sediments were part of a terrane of unknown extent.

Minor folding has affected the Silurian sediments of the NEI. Kink bands coincide with some stream beds, and areas of en echelon folding are found. Compressional kink folding took place with pressure applied at a slight angle to foliation (bedding). The axial plane to the folding, dips 10-20° towards 225°. Miror faulting perpendicualar to the Southern Uplands Fault.

The northern boundary of the inlier is not fault controlled as previously thought, but is the regional unconformity at base of UORS.

Chapter 6

Graptolite Physiology

6.1.1 Introduction

This chapter is based on the results of extended studies of graptolite material, and particularly of exceptionally preserved dendroid material from the Gutterford Burn, North Esk inlier. This study of the possible models of certain aspects of the mode of life of graptolites is based on both a synthesis of published models from the literature and on the authors direct observations made from the current study of graptolite specimens and their preservation. Tentative conclusions are drawn from the observations made from Gutterford Burn specimens. This material is used to illustrate many of the points made.

Initially, a general background section is given, to introduce the history of resarch in this field. This is followed by a survey of the currently contentious issues and problems encountered in graptolite research. Firstly, the preservation of dendroid material is considered, and how this affects the way we look at the fossilised material. This includes a discussion of how the fossilisation process can affect the information available for us to study; and the quality of the NEI material.This section concludes that the lack of sediment preserved within dendroid cones suggests that dendroids may have been able to clear at least some of the sediments out from inside the cone when inundated.

There follows a discussion of the nature of graptolite periderm and the models for its secretion. An outline of the model adhered to by the author and the reasons for supporting this model are given. The next four points are based on a discussion of the possible nature of the zooids occupying dendroid colonies. As no detailed work has previously been done on tthe nature of the zooids of benthic dendroids, outlines of the appropriate models with which they can be compared are introduced. This includes models for the zooids of now fossilised planktonic forms, and zooids of modern pterobranchs. Discussions of the conclusions that can be made about the nature of the zooids of benthic dendroids are given.

A logical consideration of the possible current paths and hence feeding opportunities available to benthic dendroid colonies follows. This is based on observations of the preserved shapes and apparent pre-burial sculpting of dendroid material, by the currents that passed through them in life. The remaining parts of this section present the authors view on issues raised in published literature. The formation and use of some of the constituent parts of dendroids is not well understood, and some models are proposed by the author. It is concluded that more accurate taxonomic work is needed, and more specimens need to be found and studied before we can fully understand this enigmatic group.

The next section is a detailed study of the nature of dendroid holdfasts, based on observations of both material from the NEI, and published material. Holdfasts are the structures found in the proximal portions of (benthic) dendroids. These were secreted by the

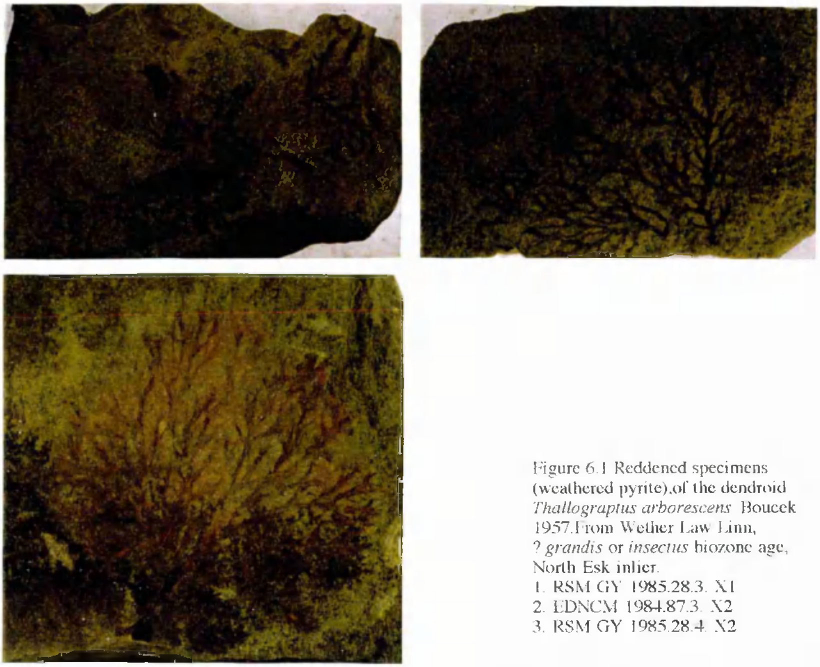


Figure 6.1 Reddened specimens (weathered pyrite),of the dendroid *Thallograptus arborescens* Boucek 1957.From Wether Law Linn, ? *grandis* or *insectus* biozone age, North Esk inlier.
1. RSM GY 1985.28.3. X1
2. EDNCM 1984.87.3. X2
3. RSM GY 1985.28.4. X2

dendroids in order to secure the colony to whatever substrate it was attached. The holdfast and stem engulf the sicula of these benthic forms.

Dendroid holdfasts have not been discussed in detail before. A number of conclusions are drawn, both concerning the nature and secretion of the attachment structures, and the conclusions that can be drawn for the whole colony, from the nature of the preserved holdfast. Dendroids and their holdfasts are suggested as possible palaeocurrent indicators. The colonisation and stablisation of the sediment surface by dendroid meadows is described and discussed. The hydrodynamic properties of benthic dendroids and their response to having been subject to a prevailing current direction are considered.

The third section is a discussion of the authors views on the possible modes of formation of new dendroid colonies. This section includes discussion of the occupation rates of the thecae; the distribution of gametes; the initial growth stages of a dendroid rhabdosome; both new zooid, and new colony formation; and the implications of the nature of zones of bifurcation are discussed and the authors ideas are presented.

6.1.2 Background

Benthic dendroid graptolites are remarkably rare. Indeed, Palmer (1991:43) suggested that "There are professional palaeontologists who have spent their working lives looking at Lower Palaeozoic strata and fossils the world over without finding or seeing a single dendroid, and yet they will have found many graptoloids."

The graptoloids are very important for correlation and biostratigraphy, and it is possible that the dendroids, with further research, will be able to contribute to this. Dendroid evolution certainly merits further study. Dendroids are very important as the ancestors of the graptoloids. In the light of new information gained from study of their living benthic descendants, the Pterobranchia (Rigby and Dilly 1994), the benthic forms may prove to be an important link in our understanding of the biology of graptolites generally.

In the Pentland Hills there are some exquisitely preserved dendroid specimens to be found. Whilst new specimens have been found in the course of this present study, there already existed a large collection of Gutterford Burn specimens, collected in 1835 and left, unregistered, in the drawers of Royal Scottish Museum, Edinburgh. This exceptionally good collection has been the source of most of the information given in Chapters 6-9.

The early history of research on dendroids is covered in Bulman (1927-1967), and the more recent and essential literature includes Kozlowski (1938, see also Bulman 1967 "Foreword"); Ruedemann (1947); Boucek (1957); Bulman 1970; Rickards (1975); Kraft (1982); Erdtmann (and others) *in* Hughes and Rickards (1986); Rickards and Palmer (1991).

Before the biological affinities of the dendroids were understood, they were assigned to various groups by comparison with living organisms, including mosses (Von Brommell 1727), plants (Hisinger 1837), corals (Eichwald 1842), algae (Goeppert 1859) and bryozoans (Salter 1866). Haswell (1865) and Salter (1861) both illustrate dendroid material from the Pentland Hills, and describe this as seaweed. Salter (1861) on Pl. II fig 1&2 figured dendroid material as *Chondrites versimilis* nov. sp. under "algae" as a "a true seaweed". The same species of dendroid (but a different specimen) was figured by Haswell (1865, pl. IV fig 20), who also on p. 42 suggested that "this sea-weed may have lived on some shoal in mid ocean". *Chondrites versimilis* Salter 1861, is actually the dendroid *Thallograptus*. Unfortunately these specimens are not available for study and have probably been lost.

Dendroid affinity is still the subject of controversy. Welsh Silurian material with a strong resemblance to *Thallograptus*, and with the cross sections of the constituent tubes clearly visible, has recently been described as a non-calcified alga (Edwards 1977, Pl III fig. 9). More specimens of this material are now available (Loydell *pers comm*) and if specimens can be isolated (extracted from the rock), it may prove interesting to compare the thecae with isolated specimens of *Thallograptus* from the Pentland Hills. Recent work by Dr. R. B. Rickards and A. Chapman (pers. comm. 1994) has involved looking at the earliest dendroids from the Cambrian, and establishing which truly is the first dendroid Family to appear.

This project has concentrated on the late Telychian benthic dendroids. Pertinent data have,

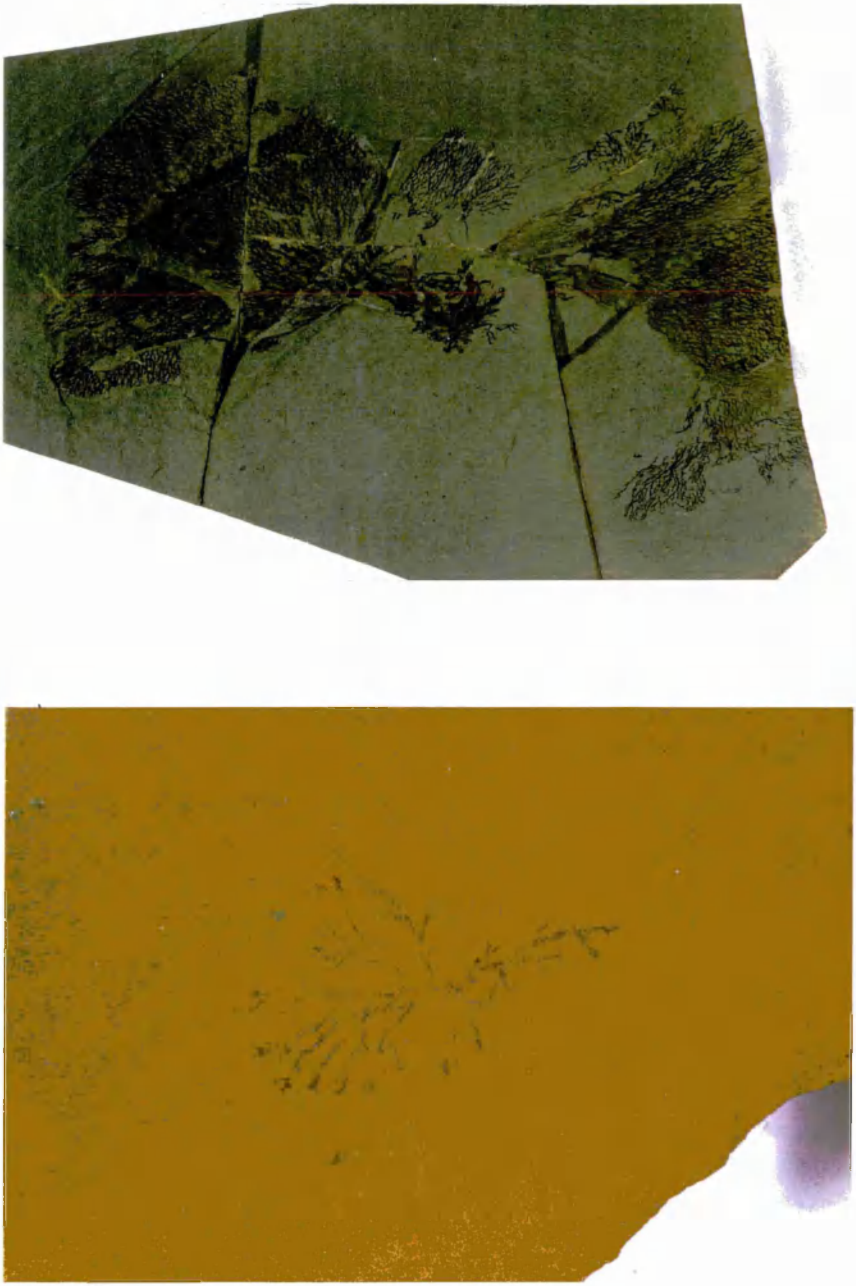


Figure 6.2.
a) Specimen of *Thallograptus* from the Gutterford Burn *O. spiralis* biozone age X 1/3
b) Specimen of *Thallograptus* from the Wether law Linn formation, attached proximally to a small green pebble EDNCM 1984 87.4 X2. *grandis* or *insectus* age.

however, been found in diverse papers on graptolites and related groups, ranging from the Tremadoc (Erdtmann 1982a) to present day organisms such as *Cephalodiscus* (Dilly 1993). There is as yet still much that is not understood about benthic dendroids. In some instances, there has been a tendency to interpret them in the light of present knowledge of the planktonic graptoloids, without full consideration of the implications. For example, Underwood (1993:195) asserted that "Among Silurian taxa regeneration occurs rarely and only within straight colonies, where it has little effect on their hydrodynamics", although he does admit that it occured rarely at the proximal ends of triangulate monograptids. This is possiby a fair interpretation of the planktonic graptolites, but benthic forms were subject to regrowth as described in Chapter 7.

Another problem encountered in the literature on dendroids is selective illustration. One particular specimen has been illustrated a number of times by different authors. This specimen shows both zones of bifurcation, and an area of regenerated growth at the margin of the rhabdosome. It is illustrated as a full photograph in Bull (1994, fig 1), Bulman (1950, fig 1), and Palmer and Rickards 1991 (fig 126). However, only part of this specimen is featured in the Treatise (Bulman 1970, fig 13). Urbanek (1982), in discussing regrowth of graptoloids, illustrated the same specimen, copied from the selective illustration in the treatise, with the area of regrowth already omitted.

Little indeed is known about the benthic dendroids. A number of controversial issues confront present day graptolithologists, some of which are discussed in Rickards (1991), and it is clear that some of these could be clarified by accurate taxonomy. Some of the issues discussed here are interdependent. For example, it is important to estimate how big the zooids were, in order to work out how much water they could have sampled. Hence it then becomes possible to establish if they would have needed to be automobile, and to have moved the rhabdosome through the water in order to harvest enough food to maintain the colony. The following sections are an attempt to summarise and extend our knowledge of this highly interesting and potentially informative fossil group.

6.2.1. Preservation

There are few localities where dendroids are found readily, and these are detailed by Palmer (1991:47), most being in the USA, China, Bohemia, or England. Almost all these dendroid assemblages (except for the Pentland Hills) were preserved in sediments deposited in quiet water, or in deep channel conditions. Palmer (1991:48) also suggests "that the dendroids were more common than the preserved record shows". They were perhaps far more common in higher energy environments such as are preserved in the Pentland Hills, but these facies faunas have a much lower preservation potential.

Dendroid bearing horizons, similar to those preserved in the NEI, have been described elsewhere as Konservat-Lagerstätten (Kluessendorf and Mikulic, 1989; Kluessendorf 1994). Dendroids, like crinoids and starfish, were fairly fragile, and would not survive long

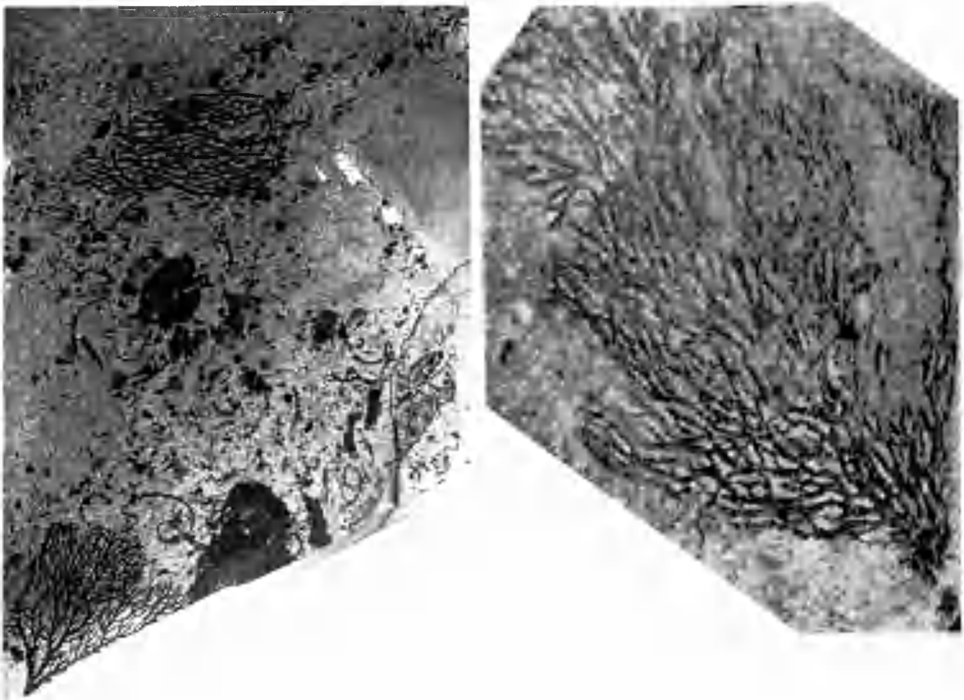


Figure 6.3 All specimens from "GBLB" locality in Gutterford Burn.

a) Specimens of *Oktavites excentricus* that has three dimensional conical shape in life are now preserved on one bedding plane, without apparent layers of sediiment separating the whorls. Other specimen on slab is dendroid *Coremagraptus kalfusi* RSM GY 1985 28.1 X1

b) *Palaeodictyota pergracillis* GSE 14165, showing a notch at the top of the stem where currents have shaped the rhabdosome. X2.

c) Specimen of *Thallograptus* with holdfast attached, used to illustrate the possilbe positions in life as a result of current distortion or moulding of the rhabdosome in response to predominant currents, X 1.5.

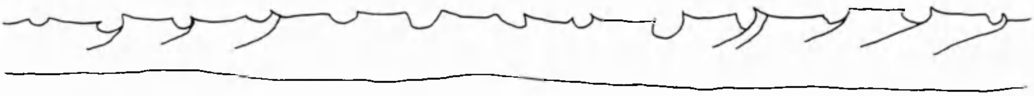
after death in an energetic environment. The holdfasts in particular, would easily be broken off. In order to preserve such a dendroid community, a sudden inundation of the area would have been required, swamping and killing off the community *in situ* by rapid deposition of sediment, as with starfish beds.

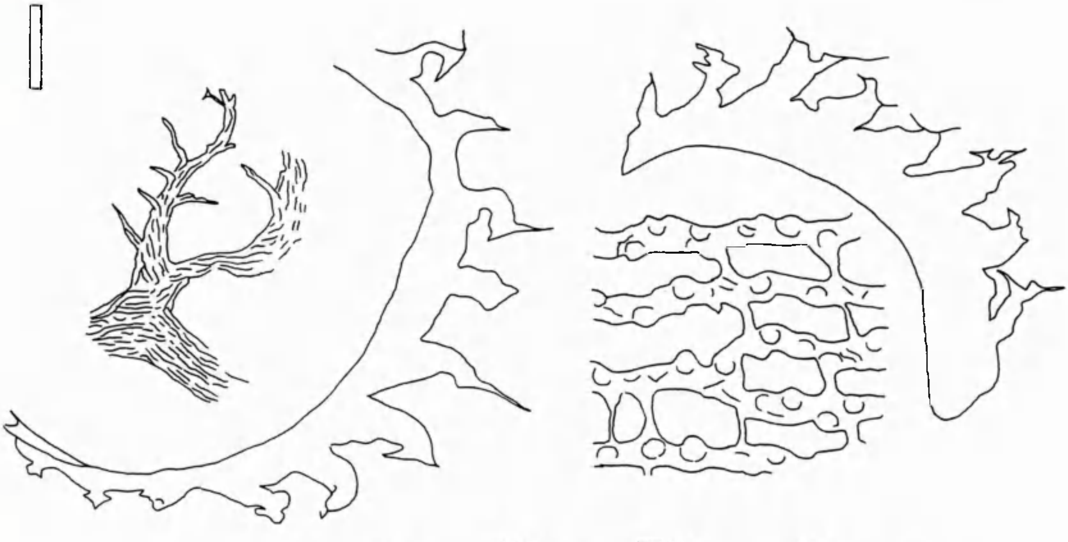
Rickards (1975:416) notes Crowther's comments that 60-80% of graptolite specimens (preserved in black graptolitic shales) were broken in some way post-mortem but pre-burial (after death, as those broken during life are known to have been able to regenerate). He suggested that this is unlikely to have happened during preservation in the quiet water environment, and "the indication is that the environment during life was to say the least turbulent." (Rickards, 1975:416). This is consistent with the repairs and structural abnormalities found in fossil specimens of benthic dendroids (as discussed in Chapter 7), and the energetic environment and rapid burial thought to have been associated with these specimens.

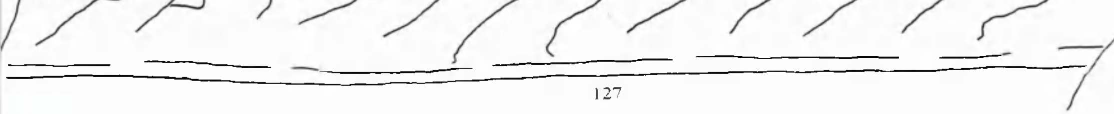
The preservation of some of the dendroids and graptoloids from the NEI is exquisite. The majority have almost perfect 3-D preservation or are just slightly flattened. The periderm is generally black, and carbonised; some specimens are pyritised, particularly some of the more robust graptoloids, *Monograptus priodon* and *Monoclimacis vomerinus.* Some pyritised specimens weather to a red colour (see fig 6.1). The stipes and thecae are filled with quite a coarse sediment, with the enclosing sediment containing a large percentage of shelly material, and calcareous matrix (see Chapter 4). Preservation is good enough for some of the original detail of the growth rings to be seen, along with the thecal structure of dendroids. The sediment weathers very rapidly and dendroids are usually found in relatively fresh material. It is unusual to find fossils of both planktonic graptoloids and benthic dendroids like this, in the same beds. Benthic dendroids are much rarer than graptoloids, which are also much more widespread geographically, consistent with their planktonic mode of life (Chapman, 1991:6).

Palmer (1991:43) stated that "Black graptolitic shales often contain shapeless and generally indeterminate carbon films scattered on bedding planes with the graptolites. It was this close association with degraded 'sea weed' like material that led Charles Lapworth, a hundred years ago now, to make a comparison with the present day organic masses of floating Sargassum weed...". The dendroids in the Pentlands are also associated with large sheets of carbonised film. In some cases the sheets are structureless, sometimes there is a distinct pattern of cracks on the surface, and sometimes these sheets can be identified as *Dictyocaris* Salter 1860 (fig 10.28). This was originally described as a crustacean carapace (Størmer 1935), although it is herein thought to be vegetable in origin (see Chapter 10).

Figure 6.5 All to same scale (X 15, scale bar 1mm.). Specimens all found from same location showing range of thecal size that the zooids inhabited and secreted .A,B, *Mcl. vomerinus* A. distal , B. proximal portion of stipe; C,D, *Mcl. geinitzi* C, proximal, D, distal portion of stipe; F,G, *O. excentricus.* G distal, F proximal portion of stipe; H. *Dictyonema pentlandica.*; E. *Thallograptus arborescens*; J,K. *M. parapriodon*, K ,*M priodon.*







At the "Limestone Bed" locality, the preserved organic material is all black, including the sheets of *Dictyocaris*, the dendroids, and the graptoloids. The specimens found on the east shore of the Reservoir, however, are red, including the specimens of *Dictyocaris*. Few graptolite specimens have been found from this locality, but those that have are preserved as black carbonaceous material, which is particularly striking against the red sheets.

Underwood (1993:199) discussed graptolite preservation, and commented that "Any graptolites containing zooid material reaching the sea floor would have been extensively scavenged. If rhabdosomes containing zooidal material were rapidly buried, scavenging would have been carried out by burrowing organisms adapted to dysaerobic conditions such as those producing *Chondrites*". The Reservoir Formation sediments are extensively bioturbated in places with *Chondrites* type burrows. The holes through the Dictyocaris specimens may have been formed by burrowing animals, and do appear to be associated with sediment bioturbation. Organic material, dendroids, and *Dictyocaris* specimens appear to have been deposited during periods when sedimentation rates were too rapid for the bioturbators to keep pace (see Chapters 4 & 10).

Specimens of *Monograptus spiralis excentricus* that had a three dimensional conical shape in life are now preserved on one bedding plane, without apparent layers of sediment separating the whorls (fig 6.3.a). It is possible that the rhabdosome was so flexible that the weight of even a small amount of sediment dropping onto the colony once it had landed on the ocean floor, was enough to flatten it out. It is unlikely that the specimens lost their elasticity very quickly, as some fossilised material that has been isolated, still retains its elasticity, indicating the preservation of collagen.

Post depositional sediment compaction flattens graptolite specimens. The sediment filing up the cone of a dendroid rhabdosome would be expected to be compressed to a thinner layer than it was when deposited. At the time of burial, dendroid rhabdosomes had a relatively high degree of elasticity, and initially, sediment would have accumulated within the cone. Burial compaction will have competed with the elasticity of the rhabdosome, but eventually overcome its strength and compressed the sediment within into a thin layer. Fig 6.2.a shows a specimen preserved with sediment encased between the two surfaces of the cone. In this case, if the rhabdosome was originally conical and filled up with sediment on deposition, then this represents about 95% compaction.

The amount of sediment encased between the layers of a cone is often remarkably thin, and as discussed by Chapman (1991:8) it is common for the amount of sediment encased within a conical form to represent more than 60% compaction. In many cases no sediment whatsoever is trapped between the layers and all of the specimen may be compressed on one bedding plane. This is a difficult phenomenon to explain, and the final resolution of the problem and explanation may need to be based on experimental studies, which in turn depend on estimates of the original strength of the periderm (Williams *et al.* 1982).

One possible reason why so little sediment was caught within the sides of the rhabdosome cone, is that the zooids may have had at least some sediment clearing capacity. Certainly extant encrusting bryozoans are known to be able to clear themselves of a thin layer of mud in 10 to 15 minutes (McKinney and Jackson 1991:121). If we consider that zooids of planktonic forms were automobile, even to a small degree (Rigby and Dilly 1994:472), then we must at least envisage their benthic relatives to have been able to generate enough current strength to remove waste products and unwanted sediment-build-up, from inside the mesh.

6.2.2. Zooid vs. extrathecal tissue model

In recent years, the general ultrastructure of graptolites has been studied (Urbanek and Towe, 1975; Crowther 1981; Rickards *et al.* 1982; Rickards and Dumican 1984). This work has increased our understanding of what graptolite periderm was made of, and the fabric and construction of the colony. There is as yet, however, no certainty about how this material was formed.

Graptolite periderm is made of two layers of collagen. Firstly there is the fusellar tissue, forming growth rings or half rings, made of fibrous collagen. These rings were built up one on top of the other as the "building blocks" of the rhabdosome. Secondly there is the cortical tissue, constructed of crisscrossed bandage-like structures, also of collagen. These features are illustrated in Palmer and Rickards (1991). It is quite likely that the same secretory cells produced all of the collagen of which the skeleton is constructed, both fusellar fibrils and cortical fibrils. The mechanism however is as yet undecided (Bates *et al.* 1991:15).

If we accept that graptolites are related to *Rhabdopleura* and *Cephalodiscus* by virtue of comprising of a colony of interconnected zooids, then they are hemichordates. If we consider that they had an external layer of soft tissue (extrathecal tissue), that connected the zooids, and was involved in the secretion of new periderm (Rickards and Palmer 1991:1), then we should consider them to be coelenterates, or cnidarians (related to corals).

The main supporters of the extrathecal tissue model are Dr. N. Kirk and Dr. D. Bates, and they have argued their case very eloquently and at length (Kirk 1972; Kirk 1975; Kirk 1978; Kirk 1980; Kirk 1991; Bates and Kirk 1987). Some authors have suggested that extrathecal tissue may have been involved in some elements of secretion, such as of the holdfast structures (Rickards 1975:411).

The alternative model suggests that the graptolite zooids were responsible for the secretion of their periderm. This could have been achieved in the same way as in their closest living relatives the pterobranchs (Dilly 1993; Rigby 1994; Rigby and Dilly 1994), using their cephalic shield to secrete the tissue of the rhabdosome. The secretion of Cephalodiscus spines is particularly well described by Dilly (1993:74). There is still a great deal of debate with respect to this model, particularly as to how far it is envisaged that each zooid could have travelled to secrete periderm. It is thought possible herein, that certain zooids could have been specially adapted for certain roles such as travelling to the edges of the holdfast and secreting further anchoring fibres, whilst the majority of the dendroid rhabdosomal zooids were based fairly close to the thecae. Most authors agree that graptolite periderm was secreted by the zooids, and this seems more and more convincing as more details of pterobranch biology emerge.

Further evidence to support the zooid secretion rather than the extrathecal tissue model, comes from two other sources; the studies of Mitchell and Carle (1986:387) on graptolite nematularia, and the work of Zalasiewicz (1993:205) on "functional analogues" of dendroid dissepiments being formed by the "opportunistic behaviour" of the zooids of Monograptus turriculatus, producing dissepiments to buttress or strengthen the rhabdosome to cope with the greater hydrodynamic stresses on the larger rhabdosome (see also section 6.2.8).

It has been suggested that dendroids used a non-secretory extrathecal membrane to shut off the fenestellae in turbid conditions, and hence protecting the zooids inside (Rickards 1975:413). This tissue could have been like "skin" covering the collagen "skeleton" of the graptolite. No direct fossil evidence of this tissue exists, however, not even a "halo" of organic material. Some dendroid-bearing sediments are considered to be Konservat Lagerstätten (Kluessendorf 1994), with some soft bodied animals preserved as the result of very special conditions, yet even in these beds there is still no sign of any extrathecal tissue. Underwood (1993), suggested that the defensive adaptations of graptoloids were quite good.

The presence of thecal spines, and the elaboration of the thecal aperture, particularly in some of the later monograptids, would have afforded excellent protection to the zooids. This would have provided protection particularly from a predator trying to prise an individual zooid from its theca (considered by Underwood to be one of the main types of predation on planktonic forms). Clearly the dendroids' tactic of housing the zooids within the cone, ensures at least a partial security from attack. For graptolites to have surrounded themselves with a large, unprotected amount of extrathecal tissue, would no doubt have made them very interesting prey to predators. There is little evidence of rhabdosomes being ingested whole, as would be suggested if such extrathecal tissue were present. Dilly (1993:77) suggested that there is no need for any graptolite extrathecal tissue to be envisioned. This conclusion was drawn both from observations of *Cephalodiscus graptolithoides* (Dilly 1993), and the ability of the zooids of this species to secrete all of its periderm including thecae, nema and spines, and also from extensive comparison with graptolites.

The model adhered to throughout this work is the pterobranch, hemichordate model in which zooids secreted all of the rhabdosome, and without any extrathecal tissue. The only soft parts being the zooids themselves and their interconnecting stolon system.

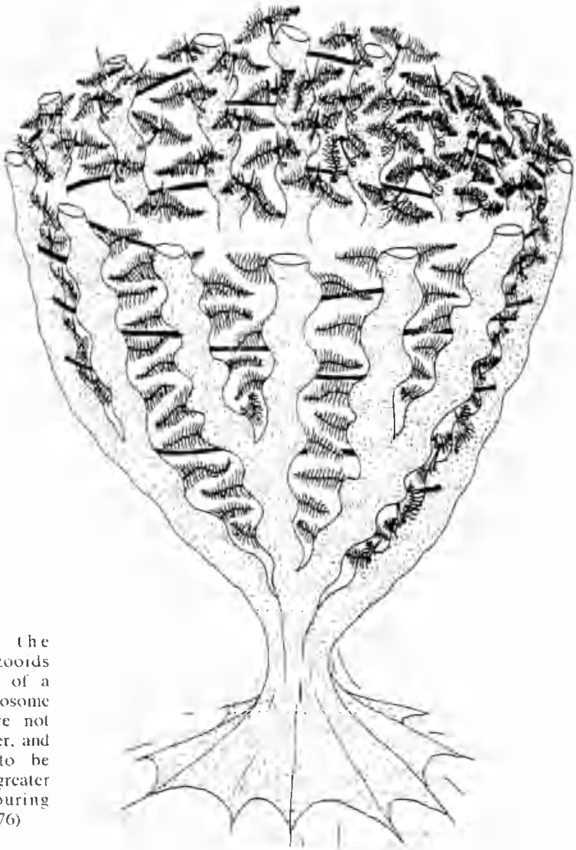


Figure 6.6 illustrates the possible distribution of zooids around the rhabdosome of a feeding *Dictyonema* rhabdosome Note that the zooids are not interfering with each other, and some are suggested to be utilising spines to gain greater separation from neighbouring zooids. (After Rickards 1976)

6.2.3 Automobility

Whether or not the planktonic graptolites were able to move actively through the water column to maintain or change their position, respond to currents, find nutrients or gather in defensive or reproductive swarms, has captured the imagination of many graptolite workers. Issues such as whether the graptoloids orientated themselves vertically with the sicula up (Kirk 1990), with the sicula down, perhaps spiralling to sample more water (Rigby 1992), or horizontally (Underwood 1993; Erdtmann 1982), have been discussed at length.

Initially, the supporters of "passive plankton" versus "automobility" were mutually exclusive groups. The work of Rigby (1991a; 1992; Rigby and Rickards 1989) and most particularly the work on the life span of graptolites (Rigby and Dilly 1994) which has suggested that the longevity of graptolites was so great, that they must have been partially automobile, otherwise they would have passively sunk to the ocean floor, long before they died. This has gone a long way towards bridging the gap between the two camps. Essentially, for a planktonic form to maintain a position in the water column (horizontal or vertical), it must have some mechanism for sustaining that position. Otherwise any current would buffet, rotate and tumble the colony and no constant orientation would be maintained.

This present study is primarily concerned with the benthic forms, for which automobility is not an issue. However, if as the conclusions of the workers on planktonic forms suggest, zooids could coordinate their effort to affect the flow of water (or their position relative to it), then the same was probably true of the zooids of benthic dendroids. This would mean that they could create currents to remove waste products form the cone, or any material that might threaten to block up the fenestrules. Other colonial animals such as bryozoans, have methods of preventing ingestion of unwanted particles, and mechanisms for expelling filtered water so that it is separated from in-current water. However, most encrusting bryozoans are not directly comparable with dendroids. To ensure the separation of inhalant and exhalant currents of bryozoans (McKinney and Jackson 1991:119), their current-paths are directed along morphological pathways, and out through "chimneys" into water in the surrounding area that is flowing at a greater rate. Constraints on erect colony growth are however comparable for dendroids and certain fenestrate bryozoans, and this is discussed further in Chapter 7.

6.2.4. Zooid size.

Working out the size of graptolite zooids has only recently become an issue, but clearly it is important to establish how much feeding an individual zooid could manage, and hence the amount of water each zooid would have to sample to maintain the colony as a whole.

Sudbury (1991) suggested that graptoloid zooids were relatively small compared with the thecae that they secreted. This was based on the size of cortical bandages that they secreted. Similarly, some thecae are relatively large but their apertures are highly ornate and have only fairly small openings, further suggesting that the occupying zooids were quite small. Zooid size is considered further by Rigby and Dilly (1994:469), who discuss the ability of zooids to move freely inside the colony, the likelihood of leaving several thecae empty for some time, and the possibility of more than one zooid occupying a theca at any one time. It is not known what the relationship was between the number of thecae and the number of zooids present at any one time. In *Cephalodiscus* (Rigby and Dilly 1994), the more zooids there are, the faster the colony is secreted, particularly as more than one tube can be secreted at any one time. One graptolite theca does not need to have been finished before the next one was started. As yet we do not know whether each graptolite theca was secreted by one zooid alone, or whether theca construction was a corporate effort.

It is possible that graptolite thecae were secreted by immature zooids, which were still small enough to be able to emerge through restricted thecal apertures. When these zooids had completed their thecae secreting phase and reached adult proportions, they may have became feeding zooids alone, each confined to its own theca. The apparent ability to produce secondary thickening of the base of a dendroid colony, or to continue secreting anchoring fibres, would suggest that zooids retained the ability to leave the thecae to secrete this tissue, and possibly to feed using the apertural spines as a support. The observations by Rigby and Dilly (1994), of pterobranch zooids co-operating to secrete new thecae, does not presently support the juvenile secretion model, but the issue will no doubt be made clearer by further observations of living pterobranchs.

Considering adult zooid size, either:

-the zooids of all graptolites were basically all the same size (relatively small), but the zooids secreted different sizes of thecae. Some may have had lots of space around them, right down to the snug fit of the zooids in the smallest thecae; or

-the zooids were different sizes, depending on the species (species-specific zooid size); or

-zooid size was variable within each specimen, and in the monograptids they tended to increase in size with maturity, as echoed in the general gradual broadening of the width of the stipe (increase in theca size) distally. Since dendroids had very constant thecal sizes, this could suggest constant zooid size for dendroids.

Fig 6.5 shows illustrations of the range of thecal size that various zooids had to inhabit and secrete, all taken from specimens found at one locality, and illustrated at the same scale.

6.2.5 Feeding volume

Fig. 6.4.2 illustrates the possible distribution of zooids around the rhabdosome of a feeding *Dictyonema*, where all of the thecal apertures lay inside the cone, thereby protecting the zooids from predation, although they may have been able to go outside the cone as well. See Chapter 8 for a discussion of the hydrodynamics of flow through a meshwork, and the implications for the positioning of the zooids.

The stipes of dendroids appear to be secreted so as to provide the maximum separation of the zooids, whilst maintaining the conical shape of the rhabdosome. If the parent theca were not occupied, then the most efficient bifurcation angle for the thecae would be 180° (see fig 6.7). The actual bifurcation angle however is approximately 120° which maintains maximum separation from the parent theca as well as the two daughter thecae. At bifurcation, the stipes diverge sharply initially then turn to run parallel again, sweeping out the maximum separation from neighbouring zooids until normal stipe separation is attained.

The autothecae of *D. pentlandica* are regularly distributed with alternate thecae pointing to either side of the stipe (see fig 7.3). As the autothecae of this species are equipped with large apertural spines, the slight displacement to either side of the stipe ensures that the spines are angled away from one another, and slightly across the fenestrule. This would have assisted the zooids, which may have used the spines as a feeding support (see Dilly 1993), positioning themselves at optimal separation from their neighbours.

6.2.6. Feeding strategy.

Currents can be considered to have flowed either in through the open end of a dendroid cone, and out through the mesh, or *vice verca*. The possible current paths for benthic dendroids have not been discussed in any detail previously. Various models exist for the

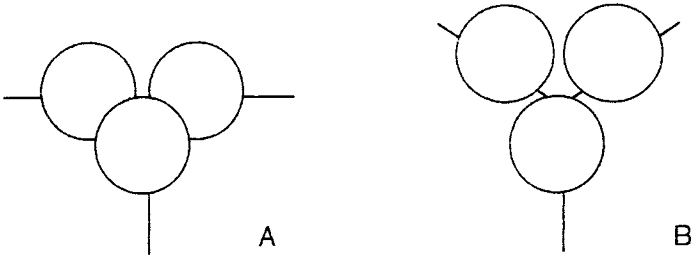


Figure 6.7 Diagram suggesting the sphere of influence of zooids and the affect on the separation of the zooids of different angles of divergence at a point of bifurcation
A : divergence at 180°, B: divergence at 120°

feeding efficiency, rotation and astogeny (Rigby 1992) of the planktonic graptoloids, their life habits (Rigby and Rickards 1989) and their feeding strategies (Rigby 1991). Comparisons can be made with the models of current paths and hence feeding strategy of planktonic forms, and some conclusions can be drawn about the possible mode of life of benthic dendroids. Calculations of dendroid feeding density and feeding area could be compared with those of the graptoloids, and correlated with the graphs published by Rigby (1991). This will eventually be the subject of further work, although much of the work on graptoloid feeding strategies is based on mathematical modelling, and the calculations are inapplicable to net-like dendroid structures (Sue Rigby pers. comm. 1994)

It is assumed that the benthic dendroids were ancestral to the graptoloids, and that at some point in their evolution, the planktonic forms had to break free from the ocean floor. One intuitive difficulty graptolite workers face, is imagining the evolutionary path followed by the colonies from being oriented and attached sicula-down, to inverting to a sicula-up, suspended habit. It has been suggested that the current entered via the sides of benthic forms and left through the mouth of the cone (Rickards 1975), whereas by the time they had adopted a planktonic lifestyle, the feeding currents and zooid sampling direction were reversed. This seems however a very large step to take in a single evolutionary event, the dendroid had to "learn" not only how to live, but to also feed the other way up. Some authors have sought to explain this by suggesting that the planktonic forms remained with the sicula at the lowest point and water passed through the cone to the zooids and out through the mouth of the cone (an "upward widening plankton net" Kirk 1978). The consensus of opinion today, however, is that the planktonic cones were oriented cap like, with the apex upwards. They then probably functioned as a spiralling "trawl" or "drift" net, with the current entering the mouth of the cone and being funnelled up through it, past the feeding zooids (morphotype 1 of Underwood 1993). Such an orientation would allow the easiest automobile passage back up through the water to start another traverse down through the water column.

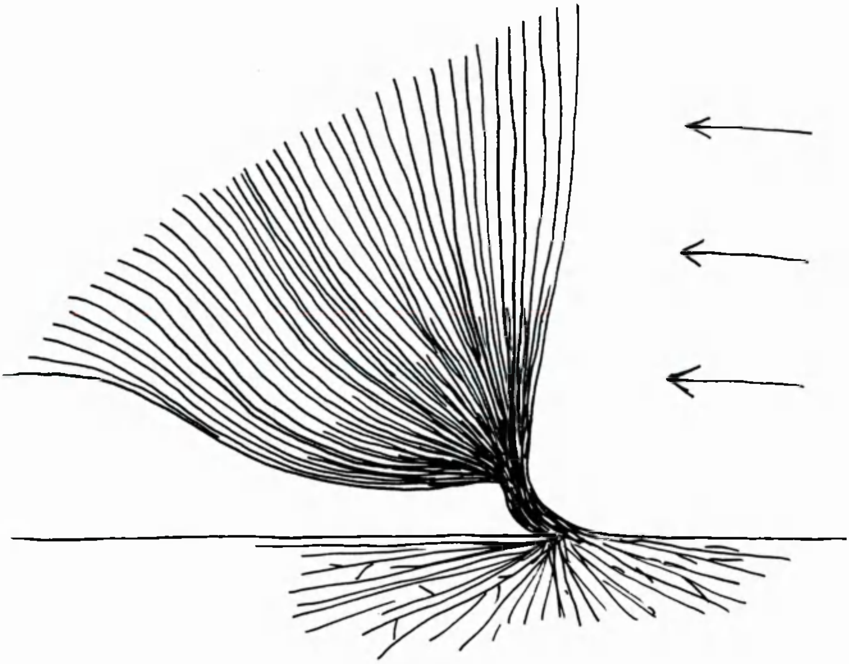


Figure 6.8. Reconstruction of the possible mode of life of a benthic dendroid. The cone was probably orientated relative to the direction of flow, hence the stem of the dendroid is curved, and a notch is formed on possibly the downcurrent side. Shorter,older attachment threds buried deeper in the sediment.

Rigby (1991) considered the possibility of neutrally buoyant graptoloids, feeding on particles of food that went past them (Finney 1979), and included this suggestion within her calculations. This neutrally buoyant "stationary" habit could be considered analogous to that of static dendroids feeding from passing currents.

Erdtmann (1982:10) (in a section entitled "Functional and biological factors relevant to the dispersal of planktic dictyonemids") discusses the direction of flow of nutrient rich currents through a passive sessile dendroid colony. He differs from Rickards' (1975 text-fig 4) model of lateral currents entering the cone and passing out through the open end. Erdtmann (1982) interprets the current direction, as having entered through the mouth of the cone. He suggests their feeding was controlled by diurnal, temperature induced gravity currents that simultaneously bought nutrient rich water and flushed any waste products out of the cone. The benthic dendroids therefore were considered by Erdtmann (1982) to be especially adapted to tranquil habitats.

The applicability of a model whereby the incident currents entered through the open end of the cone of benthic dendroids, is that the benthic/planktonic transition would have involved only reorientation, and the current flow direction through the colony would have remained the same. Predators would have followed the current direction, and the autothecal spines would then have been of value in protecting the zooids. Waste material would have been cleared from the cone, but not carried away on major currents and would have sunk by gravity in the region surrounding the holdfast, further covering up any anchoring fibres.

The factors which inhibit such a model representing the actual situation in life are that:
-Most currents become horizontal when near to the sea floor. Since the majority of dendroid specimens are less than 10 cm axial length, it is unlikely then that gravity driven currents would fall directly into the mouth of benthic dendroids (this has no bearing on whether this direction of current flow operated on planktonic forms);
-If the incoming currents were sediment laden, the dendroid might rapidly become buried in sediment or the fenestrules blocked with larger particles (sediment infilled cones are rare). In such a case much of the zooids effort would be involved in emptying out the sediment;
-Small (dead) animals and vegetable matter would become trapped in the cone. Dendroids have not yet been found with other taxa caught in the cone;
-Dispersal of gametes for sexual reproduction would be difficult, as the water mass incident on the colony would have descended from the surface without passing over or through any other benthic dendroid colonies. Similarly, the potential for larval distribution would be limited.

On balance it is considered here that the "passive basket waiting for nutrients to fall into the open mouth" model of dendroids (Erdtmann 1982) is not appropriate, particularly as predators may be carried in by the prevailing current direction and it would seem unlikely that an animal would grow pointing its unprotected opening at predators.

An apex up, automobile model for planktonic dendroids would suggest that nutrient laden water could have entered the mouth of the cone and passed out through the mesh after filtration as the colony sunk, possibly during passive gravity-induced decent through the water column. The currents would also have flowed through the cone in the reverse direction whilst the cone was moved up through the water column. Whilst such an automobile dendroid was moving against gravity, fewer of its zooids would have been available for feeding. It is probable therefore, as suggested by Rickards (1975:413), that both planktonic and benthic dendroid zooids could tap currents irrespective of their direction, either into the mesh or out of it, and that zooids could have actively created currents to draw water in through the side of the mesh. The presence of autothecal spines, angled up towards the mouth of the cone, would serve to divert any current created in this way and deflect it out through the aperture (see section 6.3.3).

In some benthic dendroids, there is evidence the cone having been orientated in life relative to the direction of flow (figs 6.8). Hence the stem of the dendroid is curved, and a notch is formed at one point. The two possible current directions through a cone in this position are shown in figure 6.9. which illustrates that current flow could enter the cone through one side and out through the other side, although in the case of *D. pentlandica* the spines would tend

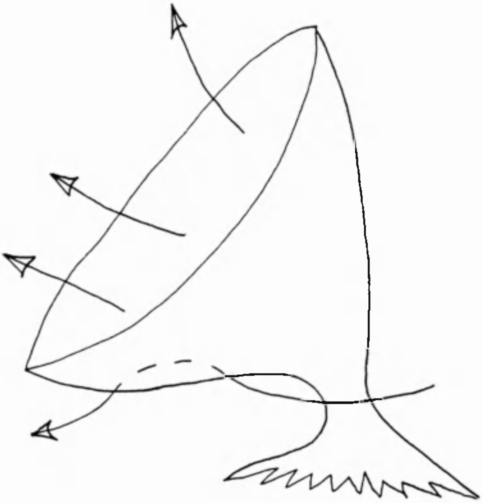


Figure 6.9. The possible current direction through a proposed asymmetrical shape dendroid cone that was orientated by the prevailing current direction. Note the sugestion that the flow could pass either way through the mesh.

to direct the current up and out of the mouth. The sculpting of the colony by the prevailing current direction is thought to be responsible for the asymmetrical shape observed in figure 6.8 (see also 6.10). This is the most stable position if the current were flowing from right to left in the diagram given, ie through the mesh first then out through the mouth of the cone. Therefore fig 6.9 is considered to be the most likely flow direction. The specimens considered here from the Pentland Hills are thought to have lived in a fairly energetic environment prior to deposition (see Chapter 4). As discussed above (section 6.2.1), it is unusual to find dendroids preserved in this environment, specimens found in the future may well have potential as palaeo-current indicators.

As yet no specimens have been found that show evidence of the cone being pushed too far over and buried in the sediment. If this did happen, the zooids lining the inside of the cone might have lived for some time lying on the sediment surface, possibly extending their apertural spines, and changing the growth direction of the edge of the cone, up away from the sediment at the periphery.

The fan shaped dendroids (e.g. *Thallograptus)* were perhaps orientated perpendicular to current flow, and so did not have to create feeding currents. Some erect conical forms show no signs of moulding by any preferential current direction and possibly inhabited quiet crevices or sheltered hollows. The zooids in these cases could have created their own feeding currents, drawing water in through the mesh and out through the cone.

To have survived so long, dendroids must have been extremely well adapted to the niches they occupied and there must have been regularly available niches for them to inhabit. Like the graptoloids, the variety of feeding densities and feeding areas covered by the different species, probably indicate a wide range of niches with different availabilities of food. This is a worthwhile area of possible further study.

It seems most likely that the shapes of benthic dendroid colonies were adapted to sample the available nutrient supply with optimum efficiency. They were sculpted by the current at times, and their zooids were capable of both extracting food from currents flowing in any direction, and of creating eddies themselves, to enhance water sampling and flow through the mesh.

6.2.6. Benthic to planktonic transition

Perhaps one of the biggest puzzles that graptolithologists have faced, is identifying the evolutionary pathway between the benthic and planktonic forms. The crucial transition of dendroids from benthic to planktonic mode of life, that eventually gave rise to the graptoloids, probably occurred around the Cambrian/Ordovician boundary (Fortey *et al.* 1982).

Throughout their history, the planktonic graptolites underwent substantial morphological evolutionary changes and environmental adaptations, but the benthic dendroids changed very little from the Cambrian onwards, even until the Carboniferous (Chapman et al 1994). Erdtmann (1982:134) proposed that the name *Rhabdinopora* be adopted for the planktonic "*Dictyonema*" forms as they derived not from the sessile benthic dictyonemids to which they are so similar in gross morphology, but from the anisograptids, and so are phylogenetically distinct. The generic separation of *Rhabdinopora* and *Dictyonema* has now been accepted, despite the assertion by Bulman (1927:10) (quoted by many recent papers) that "a subdivision of the genus (*Dictyonema*) according to whether the proximal portion is represented by a sicula or a stem seems unlikely to prove of value.......there is much to suggest that one is but a variant of the other"

Fortey (In Fortey et al. 1982:104), established that the first planktonic dendroids originated as a result of the failure to settle by the planktonic prosicular/sicular zooid, rather than the breaking away of an adult benthic form. Lapworth's (1897) original model of the benthic/planktonic transition via a epi-planktonic form attached "like the bell at the end of a rope" to floating seaweed, had earlier been shown to be wrong (Bulman 1964). Fortey and Skevington (1980) suggested that the first planktonic graptolite was *Radiograptus*, of which *Rhabdinopora* was recognised as a descendant, although the stratigraphically precursive position of *Radiograptus* to *Rhabdinopora* has subsequently been questioned (Erdtmann 1986:21). There is much hope here for future research, particularly if material containing early growth stages of all of these key dendroids, becomes available.

At present the main standard way to differentiate between fossil benthic and planktonic "*Dictyonema*" type graptolites is the presence of either a stem and holdfast, or a visable sicula respectively. Recently however, Rickards *et al.* (1993) have described a planktonic species of *Dictyonema*, with an evident sicula and flotation sacs. It is indeed surprising that so far, apparent modification for a planktonic mode of life (such as fat, or gas body secretions) are rarely seen in floating dendroids, although some species have nemal vanes and nematularia to help maintain buoyancy or induce drag (Mitchell and Carle 1986). In contrast with benthic dendroid holdfasts, however, the nema of most planktonic forms are not seemingly modified for attachment (Rigby and Fortey 1991:24), hence an epi-planktonic mode of life is not considered likely.

6.2.8. Ecophenotypic variation

Extant benthic animals commonly show a great deal of ecophenotypic variation. Some recent species of coral form fragile and branch-like shapes when growing in sheltered conditions, and rounded compact forms where they are exposed to waves. This is not the case for planktonic forms, where environmental stresses are more evenly distributed, and intraspecific variation is minimal.

An ecophenotypic response of *Rhabdinopora flabelliforme* to environmental pressures was discussed by Erdtmann (1982:135). He invoked gerontic astogeny (in response to environmental pressure), from a thin meshed "morph" (*Rhabdinopora flabelliformis graptolithinum)* to a thick meshed "morph" (*Rhabdinopora flabelliformis norvegicum*) as the cause, when putting into synonomy (as *Rhabdinopora flabelliformis*) two originally separate species. He suggested that thick meshed variants were structurally strengthened morphs of thin meshed forms. In other words, the zooids were capable of producing second and third order dissepiments, and of thickening each stipe considerably, at late stages in the history of an individual colony. He suggested that a formerly slender form could have become greatly thickened if it came to inhabit a high energy environment, and that for *Rhabdinopora*, dissepiment density and stipe width are not phylogenetically controlled. It has been suggested (Erdtmann 1982:136; Bulman 1970:V32) that this may have been the exceptional response of one endemic species.

Dendroid cones increased in size by addition of more thecae to the ends of the stipes at the mouth of the cone. The zooids of the original thin meshed "morph" would continue secreting thin stipes according to their genetic pattern, therefore, if thickening were to be added later, a size gradient from newly secreted stipe to that that had been secondarily thickened, would exist. This has not been observed.

It is still possible that the two "morphs" (Erdtmann 1982) were ecophenotypic variants of the same species. It is not envisaged herein that the individual grew initially as a thin meshed form, and then thickened up all of the mesh when turbulent conditions were encountered. It is thought herein more reasonable to suggest that if a larval sicula started to grow in a turbulent environment, like the corals, it would grow much thicker, whereas if it started to grow in quiet conditions, then a thin meshed form would ensue. However, it is thought herein, that the relationship between the rate of addition of new material by the zooids and the environment was unconstrained. To some extent, this may have been regulated by hormonal signals released on impact with turbulent conditions.

The ability of *M. turriculatus* to add additional strengthening to its structure was discussed by Zalasiewicz (1993). He identified structures that he called "functional analogues" of dendroid dissepiments. He suggested that such "buttressing" may have been associated with the maturity of the colony, and was not the result of the fortuitous overlap of adjacent spines. Species of graptoloid in which cross-rhabdosome connections were feasible are rare, and the hydrodynamic stresses on larger rhabdosomes were greater. Zalasiewicz's conclusion was that dissepimental growth represented opportunistic behaviour of the zooids. Whilst the addition of dissepiments was considered to be a merontic feature, it was on a very small scale, with only a nominal amount of extra material added to the rhabdosome. The gerontic astogeny model proposed by Erdtmann (1982) cannot be compared with the example of Zalasiewicz (1993) as the order of magnitude of the changes in rhabdosome structure suggested, is quite different.

Differences in colony shape have been observed during laboratory studies of bryozoans. In particular, McKinney and Jackson (1991:120) warned palaeontologists to note that:-
a) colony shape could have been affected as much by interaction with the biological environment as by physical causes, and
b) colonies of the same species which grew in different environments, or at different times of the year (when different types of food were available) within the same environment, may look radically different.

Ecophenotypic variation of fossil forms has been identified for a population of echinoids (Smith and Paul 1985). In that study, specimens were microstratigraphically collected over a quarry section, where associated slight changes in sedimentary environment, particularly the amounts of mud present, could also be logged and interpreted accurately. The variations in echinoid test shape observed for a single species of *Discoides*, were suggested to be the result of ecophenotypic variation for two reasons. Firstly, variations in echinoid test shape are known from extant specimens, and the fossils were following patterns that had been observed previously. Secondly, the variations observed in the fossil record appeared to reverse, as sedimentary conditions changed.

To finally establish whether the two species (*Rhabdinopora flabelliformis graptolithinum* and *Rhabdinopora flabelliformis norvegicum*) are thin and thick meshed morphs of *Rhabdinopora flabelliforme*, caused by ecophenotypic variation, would require similar tightly controlled microstratigraphic sampling to that of Smith and Paul (1985). However, these dendroids are planktonic forms and are not preserved *in situ*. The thin meshed forms are reported stratigraphically earlier, but the bedding planes represent spasmodically killed, bathymetrically-controlled communities (Erdtmann 1982) and are unlikely to yield the necessary evidence to prove ecophenotypic variation. It is herein thought quite likely that the "*graptolithinum*" (thin mesh) and "*norvegicum*" (thick mesh) type of morphological variants of *Rhabdinopora flabelliformis* were probably not juvenile and adult forms (Erdtmann 1982), but both may have been fully grown phenotypical variants of the the same species. Ecophenotypic variation is, however, presented here as a further factor to be considered in the study of graptolites.

6.2.9 Other phylogenetic factors.

Many dendroids are ascribed to "form genera"; merely useful packages, without phylogenetic meaning (Fortey *et al.* 1991:71). Much more accurate taxonomic work is needed before the evolutionary relationships between the dendroid genera can be fully understood. As yet, there is not enough chemically isolated material available, and the existing data on the nature of the proximal ends of dendroids is limited. We do not, as yet, understand the significance and evolutionary pathways between dendroid genera with different characteristic rhabdosome shapes and growth patterns, or why some had distinctive fan, cone, disc, or shrub like habits. We do not know the phylogenetic significance of anastomosis, or of dissepiment growth, in dictating the shape of fenestellae, or even how phylogenetically important secondary thickening was. There are still many gaps in the knowledge of dendroids and much more material and detailed studies of the remains of these animals are required.

6.3 Holdfasts.

Dendroid holdfasts are often referred to as taking the form of "roots". In this volume the term "roots" has been replaced with "anchoring threads" to avoid any confusion with plants. The dendroids were animals and are unlikely to have secreted their holdfast in a manner similar to plants. The holdfasts, unlike plant roots, probably served no nutrition gathering purposes. A 'root' is also often referred to as the origin or cause of a structure; likewise dendroid holdfasts were not the first secreted part of the rhabdosome, and the anchoring threads were perhaps secreted long after the sicula had settled and rhabdosome secretion had begun. Therefore, it is suggested herein that the term "root" should not be associated with the dendroid holdfasts.

In 1897 Lapworth proposed the now famous model of benthic dendroids having become attached to floating seaweed, like the bell at the end of a rope, and drifting off into the ocean. It was suggested that the adoption of an epi-planktonic mode of life enabled them to escape from benthic predators, and was a crucial step in evolving towards the single stiped graptoloids and their fully planktonic mode of life. The difficulties with the adoption of Lapworths model are twofold. Firstly the implication that the thecal zooids were able to cope with being turned upside down suddenly is not readily acceptable, and secondly, phylogenetic differences have been identified between the planktonic and benthic dictyonemids. These issues have been the subject of a great deal of debate, mostly focusing on the planktonic forms (Erdtmann 1982). Undoubtedly this issue is not yet fully resolved. Here however, the subject of concern is the benthic forms.

Of fundamental importance to the understanding of holdfasts will be the elucidation of the larval stages of benthic dendroids, and in particular their settlement, attachment and the initial stages of holdfast growth on a variety of substrates. At present, material with even a few growth stages is not available. It is possible however that material may eventually be found, in sufficient quantities to allow chemical isolation and the hunt for very early growth stages to begin. Herein, the Rickards (1975) model (text figs 30-32) for the settling and attachment of the larvae is adhered to.

The presence of a stem and disc for attachment of benthic dendroids has always been readily accepted. This was reviewed as early as 1947 by Ruedemann (1947: 20) who gave a description of a channel covered with a miniature forest of tough seaweeds and dendroid graptolites. In 1957 Boucek (1957:21) described the various types of stem, trunks and secondary thickening of the lower part of the rhabdosome. He also described the basal discs, "root-like excrescences", and bases or thecae by which the rhabdosomes were attached.. Later in the same work, Boucek (1957:161) expressed his preference for the model of an epi-planktonic mode of life for the dendroids, suggesting that the "roots" and holdfasts may have attached to floating bodies such as large algae. He says, "We cannot explain a quantity of such a fine and elastic material as chitin is only for use on the bottom. In this environment other mineral substances are suitable e.g. SiO2, CaCO3."

Dendroid basal structures were discussed by Størmer (1933; 1935), who described them as "floating organs". These were referred to by Bulman (1964: 466) as probable abnormalities,

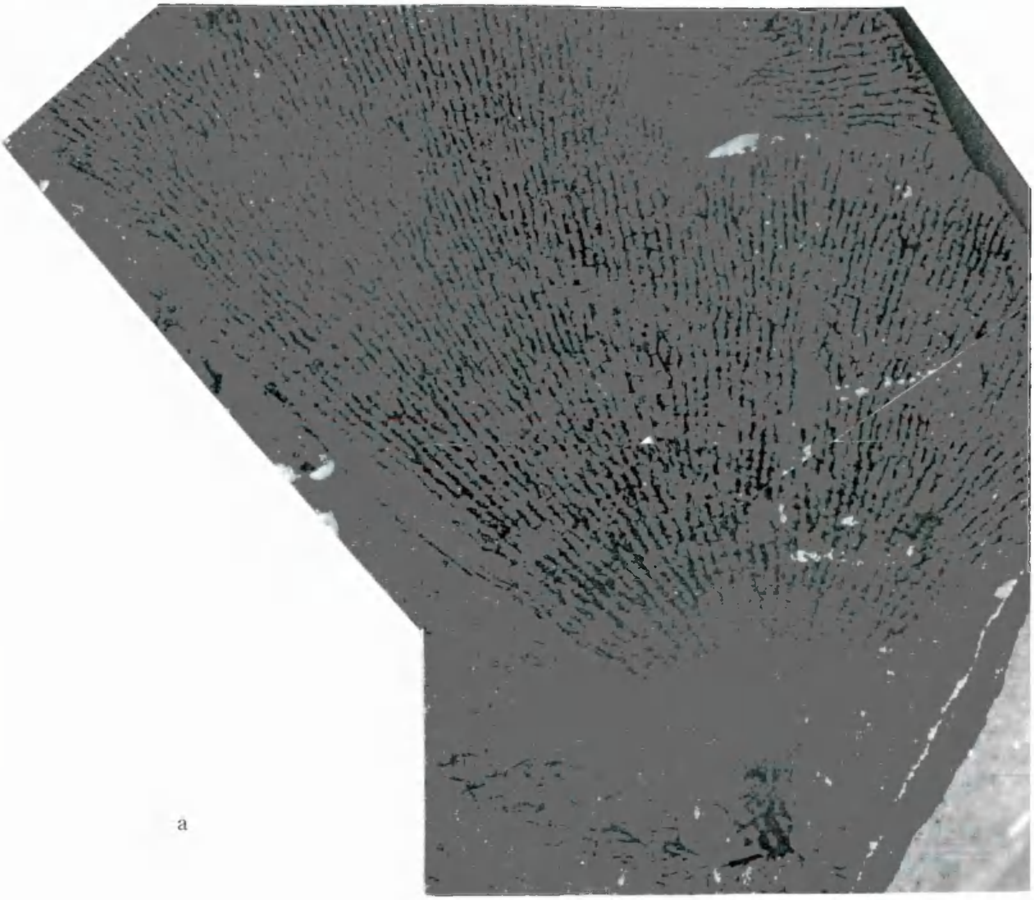
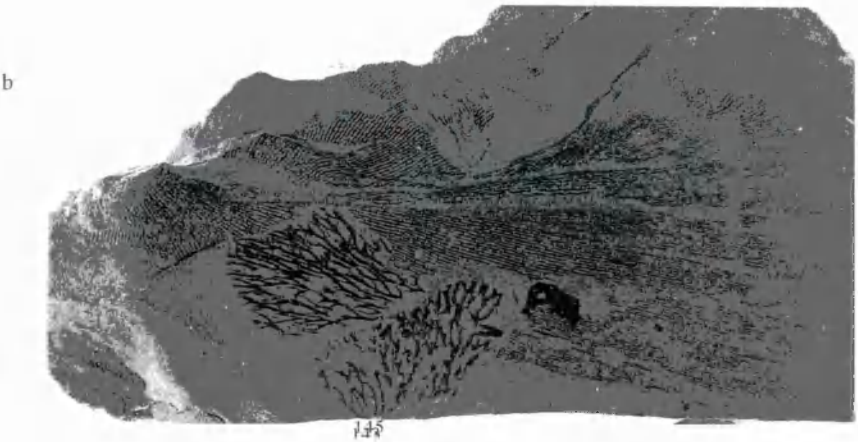


Figure 6.10. *Dictonema pentlandica* Bull 1987.
a) RSM GY 1985. 29.4 X 3. Note asymmetric shape relative to curved stem and Holdfast surface. Notch suggested to have been causd by the gentle folding of the base of the cone in response to prevailing current direction. Note also secondary thickeneing in proximal regions.
b) EDNCM 20237 X1. showing rhabdosome curved into gentle folds on deposition. Overlain with two specimens of *Coremagraptus*.



but by 1971 (Bulman and Størmer 1971), the "existence of between 20 and 30 rhabdosomes possessing such structures" could not be ignored, and they were referred to as buoyancy structures for planktonic forms.

A great step forward was taken when the separate phylogenies of both benthic and planktonic forms was recognised (See section above), and the evolutionary step of the transition from benthos to plankton of mature, colonies was no longer envisaged. Erdtmann's (1982:124) main criteria for distinguishing the benthic *Dictyonema* from the planktonic *Rhabdinopora* included (a) whether there was a holdfast present, (b) if fossilised specimens are commonly found on the same bedding planes as other attached dendroids, or (c) whether they are found in the same synecological situation generally as other benthic taxa. He also suggested that delayed branching could still have occurred in forms with a stem. Later (Erdtmann 1986:23) the primary criterion for distinguishing between the two genera was considered to be the presence of either a sicula or a stem, yet the different evolutionary pathways of the two genera (Fortey *et al.* 1982) are clear. It is possible that other factors will be recognised as taxonomically important for separating these two important genera. This may, in the future, be based on proximal branching patterns.

6.3.1 Nature of holdfasts

Palmer (1991:43), echoing Boucek 1957, suggested that the nature of some of dendroid holdfasts does not necessarily prove attachment. Indeed some of the holdfasts preserved are so small that it is difficult to imagine that they could have anchored colonies at all.

It has been accepted for some time (Rigby and Fortey, 1991) that dendroids generally lived in relatively shallow inshore facies, and that they secreted basal discs which vary in form depending on the substrate to which they were attached. The adapted the type of holdfast secreted either as basal discs for hard bottoms and anchoring threads which gave a better grip on soft substrates. It is also accepted (Chapman, 1991:6) that benthic forms, if fossilised still attached to their holdfasts and still fairly complete, this indicates that they were buried in the same area as they lived, with little transportation. In high energy environments, where dendroids were transported prior to deposition, the rhabdosome would first have to be be ripped away from its secure holdfast (Chapman 1991:6). This fact is borne out by the general rarity of specimens with rhabdosome and holdfast still united. A number of the specimens (of various species) collected from the NEI, still have their holdfasts articulated.

Figure 6.11
1. RSM GY 1985.28. X 1/2. *Dictyonema pentlandica* . "Dendroid meadow" with at least three specimens all with holdfasts preserved. Little secondary thickening. Stems up to 1 cm long and curved. Specimens bowing to current.
2. RSM GY 1985.30 . 1 X1.*Dictyonema pentlandica* Bull 1986. Holotype. Attached to brachiopod *Leptaena* sp. which securely attached itself to sediment. Anchoring threads wrapped along brachiopod ridges. Cone very broad. Slight secondary thickening proximally with 4? primary stipes. Immature specimen.
3. Unregistered specimen. X2 (part and counterpart). *Thallograptus* sp aff. *arborescens* Boucek 1957. (From 980 in log section). Apical disc preserved. Two primary branches. 3 zones of bifurcation, and branches angled at 38°. Shrub or fan shaped. Small form (juvenile?) and apical disc diameter only 1/4. of axial length.
4. RSM GY 1985.28.7 X1. *Thallograptus inaequalis* Boucek 1957. Short (<1 cm) stem with up to 6 stocks or cones attached to it. Main stem secondarily thickened with anchoring threads wrapped around a brachipod shell. Individual stems thecate and up to 2 cm long with no lateral branches until the main stock forms, or any thallograptid type theca termination. Fragment of *Dictyonema pentlandica* in bottom right hand corner.
5. RSM GY 1985.28.10 X1.5. *Thallograptus* sp aff. *inaequalis* Boucek 1957. Anchoring threads wrapped around bundle of pale sediment. Secondary thickening proximally. Possibly 4 zones of bifurcation present. Shrub like form flattened so stipes superimposed, zone of regrowth distally (counterpart known).

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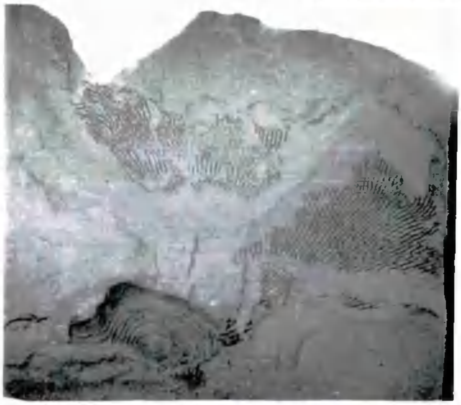

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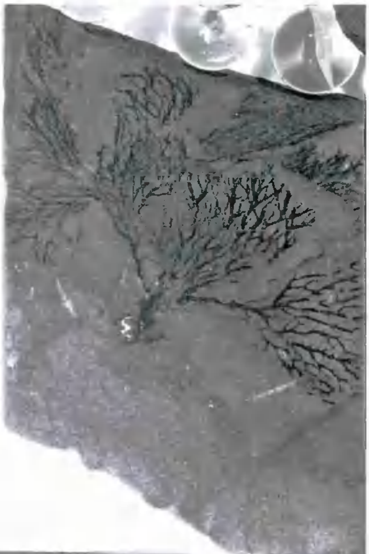


3

3a

Erdtmann (1982a:124) stated that direct benthic attachment resulted either from a cortical disc encrusting a firm substrate, or through the active penetration of a fibrous holdfast into a soft substrate. There are three main types of holdfast structure observed in the fossil dendroid specimens of the NEI.

1) anchoring threads, which are considered to have fixed the dendroid in soft substrate, mud etc. (see figs 6.2.a, 6.10.a1, and 6.11b)

2) attachment to a solid object, 2a) pebble or rock (see fig 6.2.b)

2b) shelly material, including possibly living brachiopod shells (see figs 6.11.b and 6.11.c).

3) attachment disc (apical or basal disc) (see fig 6.11.e).

Generally it is observed that the larger the specimen was, the larger the holdfast associated with it. For smaller specimens of axial length less than 4 cm, the holdfast seems not to be greater in diameter than one quarter of the axial length, and less if a solid object is secured within the base. For larger specimens, the radius of the area of attachment is larger, and for specimens larger than 6 cm axial length, the radius of the anchoring threads spreads up to one third of the axial length. Of course, they may have also been larger in life than the remains suggest.

Larger specimens have a great deal of secondary thickening in the most proximal portions, which can be up to ten times the normal stipe width (see fig 9.2.7.1), tapering off to normal stipe width by one third of the height of the colony. Most of the stems of NEI fossil dendroids, particularly of *Dictyonema pentlandica* are about 1 cm long and are often slightly curved. The top of the stem is often associated with a slight notch, and with an asymmetry of the cone (see fig 6.10.a, 6.2.b and section 6.2.3.2 for explanation).

There appear to be roughly the same number of anchoring threads as stipes preserved, and these become thinner further away from the stem. The apical discs observed are unfortunately structureless. Fig 6.11.B shows an apical disc lying within an area of paler sediment, this disc also has some fine anchoring fibres present too. The area of paler sediments may suggest that the apical disc originally had a glutinous surface texture. Alternatively the paler area may have been where the zooids incorporated fine particles of sediment into the disc to give it added weight, in the manner of present day pterobranchs (pers comm. Prof. N. Dilly, see also section 6.2.3.2) The specimen illustrated in fig 6.11.A has the same feature.

It is possible that some shrub like forms such as *Thallograptus,* and likewise some of the small, poorly preserved specimens, could be the anchoring structure for another dendroid species. Thus it is important to record the known holdfasts of as many species as possible to avoid such confusion. For example, the small specimen in fig 6.1.a might have been a candidate for consideration as merely the anchoring threads of either of the other larger dendroid specimens, except for its close similarity to the dendroid in fig 6.2.b, with known holdfast. It is possible, however, that some of the less well organised and poorly preserved specimens, featured as dendroids by other authors, may simply be the anchoring fibres (which have an inherantly higher preservation potential) from which the main body of the

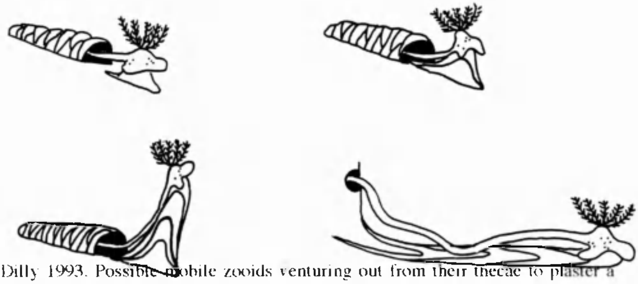


Figure 6.12 Reconstruction after Dilly 1993. Possible mobile zooids venturing out from their thecae to plaster a blob of new material to ectend the length of a spine.

dendroid has been torn away. An unusual type of "holdfast" is illustrated by Rickards *et al.* 1994. *Dictyonema ghodsiae* has twelve vesicular bodies of diameter 0.50 mm surrounding the nema which may be floats. This specimen has little to separate it from the other benthic *Dictyonema* as a separate genus, but the presence of these floats has prompted the authors to suggest that it must have been a <u>planktonic</u> *Dictyonema* .

<u>6.3.2 Holdfast secretion</u>

Precisely how holdfasts were formed is one of the remaining subjects of debate among graptolite workers. It is thought that cortical bandages were important both in forming the holdfast, and strengthening any stem. It is easy to illustrate holdfasts, but not yet possible to adequately explain their secretion. It will be necessary to dissolve and/or analyse in detail many holdfasts to try and confirm the mode of secretion. Unfortunately they are so rare that material has not yet been treated by chemical solution, since most of the specimens are the property of museums. A number of suggestions are put forward here, based on observations of the dendroids of the NEI. First of all we should exclude the idea of the anchoring threads growing into the surface of the mud like plant roots, or unfurling like the fronds of a fern, across the surface of the sediment. Although it is tempting to think of the anchoring threads in terms of plants, the dendroids were animals, not plants, and all of their skeleton was secreted, not grown. In 1975 Rickards (p. 411) suggested that the basal discs of dendroids were secreted by a constant supply of extrathecal tissue from the sicula, and that anchorings were nema-like tubes.

Although modern day pterobranchs are encrusters, and hence cannot give us direct evidence about the way holdfasts were formed they may assist in our understanding, and certain aspects of their behaviour may prove to be a useful analogy. It is now known that pterobranch zooids are mobile zooids (Dilly, 1993, see also fig 6.12), able to come out of their tube, for example, to exend the length of a spine. Observations of pterobranch material (kindly supplied to members of BIGG by Prof. N Dilly) suggests that a great deal of sedimentary material adheres to the surface of the colony, and its incorporation could well be a specific strategy. More information about this will become available as studies of pterobranchs progress (Dilly pers comm. 1994).

It is thought here that dendroid holdfasts were secreted by zooids which emerged fully from their thecae to do so. There may have even been some specially adapted thecae on the stem to house holdfast zooids. It is thought here that secretion was achieved in much the same manner as pterobranch spines are secreted, by adding increments to the end. It is not thought that the zooids burrowed down through the sediment, but rather that they laid out the anchoring threads across the surface. They may have incorporated sediment particles into the the surface of the anchoring threads or disc like holdfast to give it some weight, quite possibly the anchoring threads may have been sticky. Fine sediment falling out of suspension would therefore have built up on the surface, so that if the new anchoring threads were maintained in a level position, perhaps natural silting would eventually cover them up.

Each of the three types of holdfast could have been secreted by the same kind of zooids. The apical disc type was presumably secreted when the larval zooid alighted on a relatively firm substrate, perhaps also being favoured by some species on other substrates. This more compact type of structure would have involved minimum travel for the secretory zooid. The outer edge was probably enlarged by adding more cortical bandages, and by incorporating sediment into the surface of the disc. This would make the disc the heaviest part of the colony if, as is likely, the remainder of the rhabdosome was neutrally buoyant. Where the settling place of the larva was a solid object, such as a brachiopod shell or pebble, then anchoring threads, along with other cortical bandages, seem to have been twisted and wrapped around the host, extending out onto the sediment surface. Specimens are also known both with apical discs and attached anchoring threads (see fig 6.11.b and Rickards 1975:409 fig 25), possibly due to an influx of soft sediment around the base of the dendroid during its lifetime, requiring a holdfast more suitable for soft substrates, to be secreted.

An interesting feature can be seen on the specimen with the best developed anchoring threads (fig 6.10.a). Those threads that are shortest, lie deepest under the rhabdosome, the thicker, longer threads are higher up. It is suggested therefore, that the secretory zooids did not return to old threads that had become buried in the sediment, but as the colony became larger, and longer threads were required, new ones were secreted along the surface. The holdfast zooids may not necessarily have needed to travel out to the end of the thread tip to secrete it; they may have relied on the elasticity of the collagen and unrolled the anchoring thread when it reached the required length. Alternatively, new holdfast zooids may have been produced at any time, and they may have continued secreting at the end of the thread until their connection with the colony became severed, they died, and were washed away (disposable zooids!) (see fig 6.13).

The holdfast threads that may have been secreted on the surface, could have been equipped with barbs, which might have improved the anchorage of the rhabdosome by being pulled into the surface as the colony moved in the current. Alternatively, the threads may have been like elastic bands which lassoed the sediment, or they might have used the inherent elasticity of the collagen in some other way. The 'barb' model certainly seems to be supported by the angular and branched nature of the preserved threads (fig 6.10.a). Those dendroids with anchoring threads are thought to have been completely sessile, and the growth of their holdfasts might have assisted in stabilising the sediment surface.

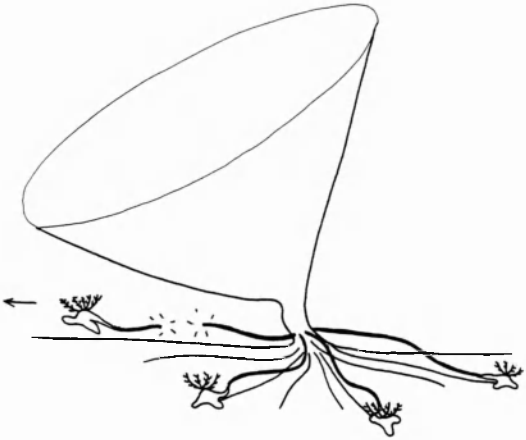


Figure 6.13. Reconstruction of the possible method of zooidal secretion of dendroid attachment fibres. Zooids are suggested to extend the fibre until reaching the limit of their possible range and eventually becoming washed away, to be replaced by another generation of holdfast zooid. Fibres being secreted from the stem outwards, and the previous fibre was progressively covered by sediment.

Benthic dendroid holdfasts are usually relatively quite small; those from the Pentland Hills are unusually large. Most dendroid holdfasts appear too small to have supported a colony in a current of any strength, although tree roots support trees in full leaf in gales over 70 m.p.h., sometimes with roots that only extend a small distance into the ground, relative to the height of the tree (see fig 6.14). Comparison with trees is thought reasonable here, as we are only considering analogies with the physical attributes of a similar shaped structure under stress, and not the mode of formation and growth of tree roots (Rigby and Rickards 1989). It is thought possible that the dendroid apical disc was suckered in some way, and stabilised the sediment in the same way as the anchoring threads. It is possible (but unlikely) that some specimens did move in currents or became dislodged frequently. Perhaps pebbles that were included in the holdfast area acted as a keel in some way.

The work on graptolite nematularia of Mitchell and Carle (1986:387), led them to advocate acceptance of the pterobranch model and reject the extrathecal model of graptolite periderm secretion. The 'secretion by zooids' model is accepted here, and as suggested by Rickards and Palmer (1991:3-4) it is "....unreasonable that such zooids could extend the 'root' system of a benthic form by burying into the mud and adding increments to the 'root' tips!" Some idea of the ultrastructure of anchoring threads and apical discs would help in understanding their secretion.

6.3.3 Colonisation of soft substrate by dendroid meadows.

Erdtmann (1976) described "dendroid meadows", the association of many dendroid specimens on one bedding plane (first described by Ruedemann in 1925), as pioneering communities occupying low oxygen environments and muds after storms. Erdtmann (1976) saw the cyclical deposition of these sediments, as repeated colonisation by the " dendroid meadows" after storms. He suggested that the dendroids were able to use their anchoring threads to colonise and, most importantly, to stabilise the surface of newly deposited muds. This made the surface more hospitable, for other species .

The presence of a large number of dendroid specimens together on one slab in the Pentland Hills, suggests that dendroid meadows may have been formed (fig 6.11.a). It is interesting to note that the specimens believed to have been part of the closely packed meadow, have slightly reduced radius of anchoring fibres. Stabilisation of the environment by many individuals living in proximity may have rendered a large holdfast unnecessary.

Recent work on starfish (Gale 1987) suggested that Palaeozoic asteroids lived on the substrate and fed by direct ingestion of mud, and therefore may also have been part of a pioneering population. Blake and Guensburg (1988) disagree, however, and suggest the starfish were predators.

In the NEI, possible dendroid meadows are preserved on a number of horizons. They are found in sediment lenses (pools of soft sediment), separated by muddy sediment layers (shale and fine silt) that are thought to have been deposited very rapidly. They are associated with starfish, suggesting that both the dendroids and starfish may have been pioneering communities, similar to that described by Erdtmann (1976).

It is thought that in the Pentlands the dendroids are preserved more or less where they lived. They formed pioneering dendroid meadows and repeatedly colonised the sediment surface after storm influenced sedimentation. The starfish also repeatedly pioneered this basin and the associated eurypterids were able to wander freely among the communities in this relatively shallow environment. Once the sediment surface had been stabilised by the dendroids, other kinds of marine invertebrates were able to move in. The "debris - beds", with shelly material were probably derived from storm reworking of shell beds, but the intervening muds with dendroids, crinoids starfish and eurypterids, show no evidence of transportation.

6.3.4 Hydrodynamics

While the hydrodynamic controls on planktonic graptolites have been considered at length elsewhere (Rigby 1992), references to benthic forms are often hidden away in papers on planktonic subjects. For example, Erdtmann (1982:10) (in a section entitled "Functional and biological factors relevant to the dispersal of planktic dictyonemids" in a paper entitled "Palaeobiogeography and environments of planktic dictyonemid graptolites during the earliest Ordovician") discusses the direction of flow of nutrient rich currents through a *passive sessile* dendroid colony (see section 6.2.2.5). It is only the effects of currents on benthic dendroids that we are considering here.

Figure 6.14
A,B, Examples of trees shaped by the prevailing wind,
C-E Examples of the relatively small root mass of trees uprooted by wind or water.

It is a commonly held view (Palmer 1991:48) that the benthic forms occupied quiet water, and they are usually considered to have grown fairly symmetrically. In Chapter 7, various responses of dendroids to trauma and hostile environmental conditions are discussed. Rickards (1975:416) noted that in some instances, 60% of the colonies found are broken, and suggests that this is likely to have happened during preservation in a quiet water environment but "the indication is that the environment during life was to say the least turbulent." Which prompts us to consider the dendroids' response to growing in turbulent conditions, and to establish the strength that the holdfast would need to prevent the colony from being washed away or "blown" over by the current.

Biomechanical studies of water flow through a fenestrate meshwork, and comparison with the hydrodynamics of flow through screens, has only been considered for the bryozoans (Stratton and Horowitz 1974), but their conclusions can be broadly applied to benthic dendroids. In particular they detailed experiments of flow through fenestrate models, and found the main effects were baffling caused by the frond, slowing flow as it impinges on the front of the model and increasing in velocity around the sides. This caused the water to jet through the fenestrules, and formed a low energy zone just behind the model. Low pressure and eddying caused a curtain of quieter water to form adjacent to the fenestrule jets immediately downcurrent of the model. From this (Stratton and Horowitz 1974:434) suggested that "position on the downcurrent side of the frond would be most advantageous for individuals of the colony. In this position they suggested, bryozoan polypides could feed more effectively and perhaps more continuously because of reduced current flow." It follows that the best position for dendroid zooids was on the inside of the cone, with the incident currents impinging on the outside of the rhabdosome, and exhalant currents passing through the mouth of the cone.

The flow of water through the dendroid fenestrules would be laminar, and once inside the cone, any spines or processes would tend to deflect the current up towards the mouth of the cone, taking with it any waste products, or even releasing larvae. Currents of a strength greater than 5 cm/sec. would be too strong to enter the fenestellae and would be deflected around the cone, shrub, or fan, and it is at this stage that the strength of the holdfast would determine the ability of the colony to survive this particular storm without being washed away.

Pterobranch zooids are nervous creatures (Rigby pers comm. 1994), and retreat into their coenecia at the slightest disturbance, taking quite a while to re-emerge. Dendroid zooids would presumably have reacted in a similar way during storms, and this would undoubtedly have affected the hydrodynamic properties of the colony.

What would have been the difference in hydrodynamic properties of a colony if all of the zooids were out with their tentacles extended, as opposed to the same colony with the zooids retracted within the thecae? The presence of the extended zooids would have increased the surface friction and slowed down any current movement. It is difficult to calculate the rate of flow through meshes. This is an area covered by advanced mechanical and chemical engineering, and reliable calculations have not yet been produced. Similarly, the equations for movement through the water column break down when applied to mesh like or larger forms (Sue Rigby pers. comm. 1995) .

If the current did not have a prevailing direction, then the dendroid would probably have grown very symmetrically, each side of the colony being buffeted equally. Many examples of symmetrical dendroids can be found in the literature.
If a prevailing current direction did exist, then asymmetrical specimens would be expected. Some specimens that superficially appear symmetrical, are not. Fig 6.10.a appears at first sight to be very symmetrical. However on closer inspection, the stem can be seen to be appreciably curved, and whilst one side grows up directly from the top of the stem, the other is curved over, seemingly forming a notch where the cone bent over by the current has caused buckling. Since the stipes have remained at their normal spacing, it is probable that this has happened as the cone has grown, rather than by a sudden crumpling. This specimen has been reconstructed in fig 6.3.8. Now that this phenomenon has been identified, a perusal of the literature reveals it to be not uncommon, for example see figs 6.2b, 6.10.b and 6.11.b, also Boucek 1957 plates 25, fig 3, 26 fig 3, 33 fig 1 and 35 fig 3, and Ruedemann, 1947, plate 15 fig 8.

A dendroid zooid living at position (a) (of fig 6.9), had the advantage of being first in line for any incoming food, but also took the greatest force of current, and more energy would possibly be required just to build a theca in these conditions. Position (b) shows a more sheltered and less energetic position for a zooid to be located on the rhabdosome wall, with the zooid being afforded slight protection in the lee of the other cone face, but possibly reduced food supply in incident current. This is considered further in section 6.2.2.6.

Fig 6.3.c is an illustration of current distortion or moulding of the rhabdosome in response to predominant currents. All three postures were possible, (b) being the least stable and a response to a sudden event having blown over the earliest formed part of the colony. The zooids may have built the mesh as orientated relative to the predominant current direction, or the colony may have been passively washed over; either gradually turned further while continuing to build, or blown over in one traumatic event, which the animal survived. This specimen is believed to have grown in position (c), as that is the posture indicated by the relative position to its holdfast..

6.3.5 Colony size

Logically one might expect delicate forms to inhabit quieter conditions, and more robust forms to be representative of more energetic conditions. This is certainly the model envisaged by Erdtmann 1982b (see section 6.2.8).

Dictyonema pentlandica is one of the most slender dendroids known. It also has one of the greatest axial lengths known, thought to reach up to 50cm axial length. Bulman described *Dictyonema delicatulum* as having very slender stipes (22-23 per cm), comparing well with *Dictyonema pentlandica* (17-22 per cm), and he noted (1928, p.52) that "The rhabdosome [of *Dictyonema delicatulum*] was extremely large for such a delicate-meshed species, having an axial length of not less than 5 cm". suggesting that *Dictyonema pentlandica* was indeed particularly long.

We know from studies of abnormal structures of *Dictyonema pentlandica* (Chapter 7) that despite its size, it was relatively robust (section 6.2.7), and also had a larger than average holdfast structure. Gerontic specimens of other species have been described (Erdtmann 1982), and their maximum axial lengths do not approach that of *Dictyonema pentlandica.* Possible explanations of the exceptional axial length are that *Dictyonema pentlandica* kept on growing for longer, or grew particularly fast. It is possible to estimate from comparison with known growth rates of pterobranchs (Rigby and Dilly 1994), the time taken to secrete the rhabdosome, which suggests that the specimens must have been several years old at the time of death. There is the possibility that this species grew particularly fast, but not excessively so.

A model proposing that dendroids with the most slender mesh, occupied the quietest water conditions, does not seem to apply in this case, as *Dictyonema pentlandica.* is thought to have colonisd an energetic environment. It is possible that together with the elasticity of the rhabdosome; the zooids' ability to mend the rhabdosome; and the size of the holdfast; another factor that enabled dendroids to withstanding energetic environments, was hydrodynamic adaptation. Perhaps the very fine mesh is well adapted to stronger currents, giving the zooids good water sampling capacity for nutrients, whilst lessening the risk of the whole colony being washed away. This cannot be proved until we have more information about zooid activity, and the hydrodynamics of flow through meshes. It is possible that dendroids with different mesh structures, occupied areas with current strength to suit the mesh type.

6.4. Reproduction

Whether graptolite reproductive processes were sexual or asexual is unknown. Even the reproductive cycle of pterobranch zooids is not yet understood (Sue Rigby pers. comm. 1994). When this is known, graptolithologists will at least be furnished with a possible analogue. Meanwhile, some relevant observations can be made and some questions posed.

6.4.1 Larval stage.

It is believed that the graptolite sicula, the first formed part of the colony, was the planktonic larval stage. We do not know how long these larvae could survive in the water before finding a suitable substrate to colonise, or developing into the full colony for the planktonic forms. Dendroids from the NEI show associations with both American and Bohemian forms, and their larvae could have been quite widely distributed by ocean currents. Therefore, it is though herein that the larval stage of dendroids may have been quite long lived. The crucial transition from benthic to planktonic, that gave rise to the graptoloids, probably occurred around the Cambrian/Ordovician Boundary (Fortey *et al.* 1982), when the larvae of benthic forms simply failed to settle. We are concerned here with only the benthic forms, the siculae of planktonic forms having been discussed at length elsewhere (Palmer and Rickards 1991).

The siculae of dendroids are approximately cylindrical. Rickards (1975, text figs 30-32) illustrates both the sicula and the existing model of the settlement of the larval stage. Rickards' model includes "extrathecal tissue" for secreting the anchoring threads or apical disc, thought herein to also be secreted by the zooids, with the initial anchoring threads possibly secreted by the sicula zooid (see section 7.3). If specimens of dendroid siculae and early growth stages could be found in abundance and isolated from the rock, then this would assist with our understanding of the timing of the initiation ofthe various stages of colony formation and holdfast secretion. Dendroids are very rare in any case, and such material is not abundant, but some specimens, suitable for isolation, may become available in the near future (Fortey pers. comm. 1993).

6.4.2.1 Colony secretion

Dendroid rhabdosomes were probably secreted by thecal zooids (see section 7.2.2). The rhabdosome is certainly formed in a precise manner, probably according to a predetermined genetic blueprint (see section 7.7). The rhabdosome is composed of collagen, secreted as either fuselli forming the thecal half rings or the cortical bandages of the cortex, and secondary thickening. The physical structure of graptolite rhabdosomes has been described in great detail elsewhere (Crowther and Rickards 1977; Rickards and Dumican 1984), and illustrated using remarkable pictures of isolated material taken on the SEM.

6.4.2.2 Occupation of the colony by zooids

Dendroid zooids were interconnected via a central stolon system (dendroid thecal connection and budding of daughter thecae has been discussed by Bulman (1970:V26), and will not be considered further here). The stolon system possibly carried a nervous system and also transferred nutrients, therefore it would not have been necessary for all of the zooids to have been feeding at once. The pterobranch *Rhabdopleura* has sexual zooids, with degenerate tentacles and digestive systems; presumably these must receive their nutrition from the rest of the colony (Rigby *pers. comm.* 1994).

The work by Rigby and Dilly (1994) on the tube building mechanisms of pterobranchs, and in particular *Cephalodiscus* suggests some assumptions that can be made about *graptoloid* zooids, including the possible extent of their mobility. These authors discuss the tacit assumption of most graptolite workers that only one zooid contributed to the formation of any one theca at a particular time. Some morphological features of a graptoloid colony, especially nemal veins and proximal webs suggest they must have been the result of corporate efforts, and these involved members of the colony other than those actively growing thecae. In *Cephalodiscus* the entire colony is built by cooperating zooids, and at certain times all of the effort concentrated on colony secretion and none on feeding (Rigby and Dilly 1994:468). The zooids of *Rhabdopleura* on the other hand are confined to a single tube, and only in exceptional circumstances will they leave their tube (Rigby pers. comm. 1994).

In some respects it is more appropriate to compare the pterobranchs with the dendroids than the graptoloids, for as with the pterobranchs, dendroids must have had a large number of thecae being secreted at any one time, producing the complex 3-dimensional colony. Similarly the pterobranchs are benthic like the dendroids were, whereas the the graptoloids were planktonic. Like the graptoloids however, little is known about the degree of mobility available to dendroid zooids. It is highly likely that zooid corporate activity contributed to the maintenance of the colony, the production of secondary thickening and structural repairs to the rhabdosome.

Rigby and Dilly (1994) make clear that more work is needed on the relationship between the number of thecae and the number of zooids in a graptolite colony. Whereas they referred particularly to the graptoloids, their comments have even further implications for the study of the dendroids. Any conclusions drawn from comparison of graptoloids with pterobranchs can be based upon a large data set of observations of the many graptoloid species and specimens, and their relatively simple uniform construction. To extrapolate from this to the more morphologically complex and poorly known dendroids, requires a more tenuous extension of theory.

The next issue to be considered is whether or not all of the thecae of dendroids were occupied at any one time, or if only the "growing edge", or outermost margin of the cone was constantly inhabited by theca-building zooids. It is also uncertain whether or not each theca was the result of the labours of only one zooid, or whether thecal secretion was a corporate effort, nor if the secreting zooid were damaged or removed by internal or external means, if that theca would have continued to have been built by another generation of zooid.

The apparently limited ability of dendroid colony zooids to effect repairs to holes in the rhabdosome (see Chapter 7), tends to suggest that the thecae were occupied throughout the lifespan of the rhabdosome. It is conceivable that the individual zooids at the site of a hole or tear in "old" rhabdosome could only mend the rhabdosome by plastering on more cortical bandages. The zooids were possibly no longer able to reproduce, to form more zooids, or to secrete more thecae. The "old" zooids may well have become simply feeding structures, and could in later life only secrete cortical bandages to strengthen, maintain, or mend the rhabdosome by thickening the cortex. The formation of new zooids possibly only occurred at the outer margin of the colony, and was strictly linked to the triad division of the stolon system for the formation of new thecae. The stolon system appears not to have allowed the production of new side branches in old rhabdosome.

Some stipes have been observed that are thought to have been broken when at the growing margin of the cone (because neighbouring stipes have bifurcated to fill the gap). If the thecae of that stipe remained occupied, then the stolon system must have remained connected to the main system, suggesting a two way flow through the stolon system, so that the thecal zooids could remain attached to the flow of nutrients and other systems such as nerves or hormones carried by the stolon system.

If only the outermost margin of the rhabdosome was occupied by zooids, then once they had built the colony to sufficient height above the sediment surface to gain clear water for feeding, there would have been little advantage to the zooids to produce more thecae. If the individual zooids were physically growing, and had outgrown their previous theca, then there would have been a need to secrete a new and larger theca, but for dendroids, all of the thecae are remarkably similar in size. Indeed there must have been an optimum size of dendroid colony since the higher above the sediment surface the cone was built, the more hydrodynamically unstable the colony became and the more energy would have been required to secure the rhabdosome in place, and hence more feeding zooids would have been needed to supply nutrients to the whole colony (see also Chapter 7).

Another factor to consider is the longevity of zooids. What happens when "old" zooids die; did each specimens' full complement of zooids continue to live until the whole colony died off, or were they replaced by successive generations of zooid? As has been suggested elsewhere (Chapter 8), zooids were probably unable to build new thecae in a damaged area, so were new zooids generated? Estimates of the lifespan of each individual colony, suggest that individual zooids may not have lived very long. Consecutive use of the same tube by several generations of zooids has been observed (Rigby 1994), and it is thought herein that dendroid zooids may have been regenerated annually or seasonally in the same way as the pterobranchs do today.

The proximal portions of a dendroid colony are usually secondarily thickened, and the thecae may no longer be inhabited by the time the extra surface strengthening tissue was completed. There must however have been some zooids present to plaster on the cortical bandages, as secondary thickening seems necessary to the stability of the colony, and if each theca was repeatedly occupied by a new generation of zooid, the addition of secondary thickening could seriously affect the feeding capacity of these proximal zooids. Roving zooids attached by long tethers, able to thicken up the cortex at will, are a possibility. It is important to note that the fenestrules are not completely occluded, and there are no signs of old thecae atrophying, such as might be expected if the zooids had died (see also Chapter 7, wherein a comparison with similar mechanisms observed for bryozoans is made).

As has been described in section 6.2.5, dendroid stipes appear to have been secreted so as to maintain the optimal separation of zooids, whilst maintaining the conical shape of the rhabdosome. Therefore, after consideration of the above, it seems most appropriate to assume that all of the thecae of dendroids were occupied, possibly by successive generations of zooid, throughout the lifespan of the entire colony (see fig 6.7).

6.4.3 Primary Branches.

The number of primary branches that originate from the sicula of a dendroid, and from which the whole colony is built, is as phylogenetically important as is the proximal end of graptoloids. It enables the distinction of morphologically similar species which were unrelated, and for the recognition of evolutionary lineages. The primary branching patterns of some dendroid genera were illustrated by Bulman (1970:V34).

The tendency of some benthic dendroids to form robust proximal stems, suggests that we may never know how many primary stipes they originally had, since they are covered by masses of secondary thickening. The lack of good material available for chemical isolation exacerbates the problem. The production of separate stocks from one common stem as described for *Thallograptus inaequalis* Boucek 1957 is a further complication to our identification of the primary branching patterns of dendroids. In this work, *Dictyonema pentlandica* Bull 1987 has been observed to form four primary branches, and specimens of *Thallograptus* that do not have a pronounced stem, have two primary branches.

6.4.4 Sexual or Asexual Reproduction

Most studies of graptolite reproductive strategies have focussed on planktonic forms. The planktonic graptoloids, which have no subdivision into autotheca and bitheca, are thought to have been hermaphroditic as they had only one thecal type (Hutt 1991). At present the breeding biology of hermaphroditic living animals is not well known, therefore we have little hope of being certain of the breeding mechanisms of fossil animals. Similarly, comparisons with plants (Urbanek 1990:334) are unlikely to be helpful, especially if sessile plants are compared with planktonic graptoloids. However, some morphological features of dendroids are possibly indicative of reproductive processes and will be described below. Also some comparisons of dendroids can be made with conclusions drawn for the graptoloids.

Hutt (1991) suggested that graptoloid zooids may have changed their role with time. She suggested that those zooids that were maturing at the proximal end were initially males, whilst those occupying larger distal thecae became the female phase, so progressing along the colony. This implies that each zooid had the potential to be male, female, or neuter at different stages of colony formation. Also she suggested that in the biform monograptids, a permanent sex change could have occurred and zooids of different sexes may have occupied the different types of theca.

The benthic dendroids, being sessile, would not normally have been able to reproduce sexually with another colony. It is recognised that prolonged self fertilisation weakens the stock, but is useful to many living organisms, for rapid multiplication (Roberts 1983:401).

Analysis of the reproductive processes of the sessile pterobranchs may shed some light on dendroid reproduction. Pterobranchs are thought to reproduce sexually as well as asexually (Hutt 1991:50), and this may also have been the case for dendroids (see below). Dendroids had two thecal types, conceivably related to sexual reproduction. The thecae of each rhabdosome are so similar as to be almost certainly clones, and must have been part of the dendroids genetically predetermined growth "blueprint". Whereas graptoloids are thought to be predominantly hermaphroditic as there was only one type of theca, yet each colony produced a range of thecae shape, which for many species changed dramatically along the stipe.

6.4.4.1. Production of new zooids

It is almost certain that new dendroid zooids were formed by simple asexual or clonal reproduction of the zooids. This would mean that all zooids in same colony would have the same genotype (Hutt 1991:51). The presence of autothecae and bithecae in dendroids does however suggest some sort of male /female differentiation and hence sexual reproduction. The proximity of the aperture of the next generation of autotheca to the previous generation of bitheca may have avoided in-breeding in the production of the next generation of zooids. Whilst it is preferable to have completely different parents, to have pairing partners of different generations is at least preferable to having partners of the same generation (Roberts 1983:380). Similarly, "self fertilisation .. need not necessarily be a bad thing provided it is not the only method of reproduction. In the absence of a pairing partner, self fertilisation is better than nothing and does at least ensure increase in numbers" (Roberts 1983:400). Certainly sexual reproduction by successive generations seems to be a better mechanism for survival than simple cloning of one hermaphroditic autothecal (or bithecal) zooid to produce the next.

The apparent juxtaposition of bithecal and autothecal apertures may be coincidental, and the staggered generation-proximity of dendroids may result from different sexes reaching sexual maturity at different stages, thereby lessening the possibility of self fertilisation. If all autothecal zooids became sexually mature at the same time, while the bithecal zooid were still secreting their thecae, then the autothecal zooids would be receptive to the gametes released by other colonies, thereby encouraging cross-fertilisation. When graptoloids originated from dendroids the zooids may have become hermaphroditic, and may have had a genetic incompatibility system which inhibited self fertilisation.

6.4.4.2 Production of new colonies.

The basic assumption is well established that the cycle of production of a new dendroid colony, or rhabdosome, originated with a planktonic larval stage, the prosicula, to which was added asexually the metasicula (Rickards 1975:403).

The opportunities for benthic dendroids to cross breed with other colonies would have been limited, unless they were very abundant in certain areas. Erdtmann (1976a:249) described the formation of "dendroid meadows" at the Huntington locality in the Mississiewa Shale, of the Niagaran Lockport Group, North America, suggesting that because of their roots, the dendroids were repeatedly able to colonise and stabilise muds after storms. Certainly in these horizons the dendroids are relatively common. The 'parent' dendroid communities seem to have been regularly inundated. The larvae of these dendroids must have been present in the water column and able to settle and recolonise the surface after the such events. Where an abundance of dendroid specimens is recorded in close proximity to one another, the possibility of benthic dendroid cross fertilisation by current-borne gametes seems possible. Hutt (1991:52) suggested that "it is conceivable that graptoloids used the two reproductive options to advantage : cross-breeding with other colonies during 'normal' conditions, and resorting to in-breeding during times of stress." Perhaps the repeated colonisation of substrates by dendroid meadows was also a result of both mechanisms. For the moment it is not possible to say more.

The release of gametes into the water column allowing cross-fertilisation, would depend on water currents passing from one cone to the next. The possible current pathways through dendroid cones is considered in section 7.2.6. It is herein considered essential to a healthy population that this cross fertilisation occurred at some point in the formation of new dendroid colonies, and the remarkable survival of the dendroids (Cambrian to Carboniferous) indicates that they were a highly successful group, very well adapted to their ecological niches.

Dendroid eggs and embryos have been described (Bulman and Rickards 1966). In order then to produce cross-fertilised larvae, the gametes from one colony had to have been released, possibly from the bithecae, into the water. From there, they must have been carried by currents into possibly the autothecae of another colony, and fertilised the eggs. These would possibly have developed into embryos and then full larvae within the rhabdosome of the parent colony. The larvae would then have been released again into the water column to settle on suitable substrates and probably at this stage, begin to secrete the skeleton of the sicula (Rickards 1975:410). Siculae have so far always been observed whole, not partially formed, so may have developed their hard parts before being released from the parent colony. Also, however, no siculae have been observed within dendroid autothecal tubes either. Herein, two water-current borne stages are envisaged in the reproductive cycle of dendroids. Hence it is thought herein that dendroids must have been very dependent upon water currents, and their adaptations to currents is considered in sections 6.3.4 and 6.2.6.

The suggestion that graptolites could regenerate from broken portions of the colony has received much attention. Urbanek (1990:335) considers this was an important mechanism for asexual reproduction and dispersal of graptoloids, but notes that the survival rate of the regrown portions would have been diminished because of poor hydrodynamic stability, and depressed feeding capacity as a direct result of the trauma. Whereas numerous broken fragments of graptoloids are commonly found (e.g. Crowther (See Rickards 1975)), Underwood (1993) dismisses this mechanism as rare. This process may have been important for the planktonic forms. It is not herein considered likely for benthic forms that a broken off section of the rhabdosome could have survived and reproduced itself, because of the difficulties of forming a holdfast and maintaining the fragment above the sediment surface.

6.4.5 Zones of Bifurcation.

The formation of new stipes is the only way a cone consisting of parallel, equally spaced stipes can expand whilst still maintaining equal stipe spacing. Simple bifurcation, producing two daughter stipes identical to the original, is a fairly energy-efficient way of producing new stipes. Zones of bifurcation observed in the NEI graptolites are illustrated in fig 6.15.

Graptolite branching patterns have been computer modelled (Fortey and Bell 1987), and close correlation between predicted and observed patterns was generally found. They found that a few simple rules govern the generation of almost all branched graptolite colony patterns (Fortey and Bell 1987:2) and concluded that "rhabdosome morphogenesis is under primary genetic programming." Additionally they noted that certain growth structures result from modifications made by the interaction of zooids, as there seems to have been some degree of sensitivity to the approach of neighbouring stipes. The nature of this interaction is not yet understood. A further structural rhabdosome modification (discussed further in Chapter 7) has been observed during this study, namely the ability of dendroid stipes to bifurcate to fill any gap or hole in the mesh. Therefore it is possible that the zooidal interaction may have been comprehensive, recognising not only the close approach of neighbouring stipes, but also too great a separation between stipes. Furthermore this interaction must have been linked in to the potential ability to trigger stipe bifurcation to fill any gap forming in the distal growth of the mesh. This mechanism was apparently only available at the distal margin of the rhabdosome (Chapter 7).

The most efficient distribution of zooids seems to have been the aim at all stages in the growth of a colony (see section 6.2.5). The only time that the efficiency of feeding range of a zooid was challenged was at the time of the production of a zone of bifurcation, where a trigger, which was probably genetic, must have caused the stipe secreting zooids to form two new thecae and zooids instead of one. At this level, many more stipes are found per unit width (see fig 6.15). It might have been a more efficient mechanism to allow or to trigger bifurcations to take place at irregular points, whenever the neighbouring stipes were becoming too distant from one another. This would have avoided zooid crowding and "frilling" at the margin of the cone (fig 7.3.2.2) as a result of many of the stipes bifurcating at once, no doubt with resultant detrimental effects on the hydrodynamic stability of the colony. Evolution towards a purely spatially triggered mechanism would have resulted in a random arrangement of bifurcations. It is possible that the genetic pattern for formation of zones of bifurcation may have been not just associated with spatial arrangement of stipes, but may have been linked with other biological processes.

Very rough calculations of the age of dendroid colonies, can be made by comparison with the work of Rigby and Dilly (1994 :472), if it is assumed that the zooids worked on each stipe constantly and not one at a time; and that a bitheca and autotheca were secreted at the same time by separate zooids. If the average *Dictyonema pentlandica* colony was about 10 cm long, and consisted of about 300 autothecae, then its average age would have been about five and a half years old. Larger colonies of 40 cm axial length therefore would possibly have lived for over 20 years.

Of the *Dictyonema pentlandica* specimens, an average 10 cm long specimen will have about four zones of bifurcation. This seem to accord with an estimated lifespan of over five years, suggesting that zones of bifurcation could have been annual (if most of the first year was taken up with secreting proximal parts, and the colony died in its fifth year). The "return to juvenile" pattern of growth rate described by Bulman (1950) would be consistent with a slower growth rate following a trauma. The bulbous nature of the autothecae of *Dictyonema pentlandica* and the closed-off aperture, may have had some association with reproduction, and with the possibly fast growth rate of this species.

Possible influences that may be linked with bifurcation patterns are:-
-Genetic "blueprint" of colony secretion.
-Coincidence of bifurcation with sexual reproduction (the initiation of new colony formation, larvae etc), with the cyclical sexual maturity of the zooids being timed to coincide with periods of higher current strength ensuring a wider spread of gametes.
-Certain seasons bringing higher food supply giving the colony the greater energy required to invest more vigorously in colony building.
-Bifurcation may have been the site of egg fertilisation, maybe the site of a brood pouch, where embryos were formed. Stipe formation may have been inhibited during the formation of embryonic siculae, and bifurcation took place as the initial stage of regrowth.
-Internal hormonal system. Zooids might have detected hormones released by their neighbours, and when the concentration of the hormones detected fell below a certain level then a further hormone triggering bifurcation to occur may have been released. Or simply the hormones to trigger bifurcation may have been released after a set time, or amount of periderm secreted.

6.4.6 Synrhabdosomes.

Graptolite synrhabdosomes are not commonly preserved, but have fascinated graptolithologists for years, most authors suggesting that they were in some way related to the reproductive process, especially in the planktonic forms. Zalasiewicz (1984) suggested that graptoloid synrhabdosomes had a disordered structure as they just came together temporarily to facilitate breeding (sexually) in highly favourable conditions, not needing symmetry for optimum feeding. Underwood (1993:195) suggests that graptoloid synrhabdosomes imply a congregation of graptoloids for asexual reproduction, a view not supported here.

Benthic (dendroid) synrhabdosomes have not yet been described. Clearly their benthic habit would not allow dendroids to "congregate" for breeding purposes, so in that sense a dendroid synrhabdosome is not appropriate. However there are a number of Pentland Hills specimens that suggest close association. Firstly there is the specimen of *Thallograptus inaequalis* that consists of a number of "stocks" attached to a common stem and root structure (figure 6.11.d). It is possible that each of these stocks were genetically independent. Secondly is the specimen of *Coremagraptus* illustrated in figure 6.2.a, that appears to have two or more distinct cones growing from the same stem. This is a museum specimen and no further excavation is allowed that might further confirm this. It is quite reasonable to expect a number of dendroid larvae to settle on the same substrate. If indeed this latter specimen does represent two rhabdosomes joined together it suggests cooperation of zooids. The zooids must have combined their efforts to strengthen each of their stems to form one substantial trunk. The great size reached by this specimen is certainly testimony to the success of having a robust stem.

6.5. Chapter summary.

It is suggested that graptolite rhabdosomes (both of graptoloids and dendroids) were secreted by the zooids that inhabited the thecae and some evidence is presented for this. A number of other zooidal functions, and the nature and formation of dendroid holdfasts are discussed.

It is suggested that the zooids of dendroids, which were situated within the cone, were able to clear out the mesh of fine layers of settled sediment. In some cases the zooids (which were probably of constant size throughout a dendroid colony) were protected within dendroid cones by thecal apertural spines, and these may also have served as mechanisms for directing current flow, and as zooidal feeding platforms. It is suggested that the thecae were secreted so as position the zooids housed within at optimal positions for feeding. It is suggested that the zooids were capable of extracting food from either direction of flow through the rhabdosome, but that the predominant direction was in through the mesh and out of mouth of cone, and this is backed by the observations of dendroid rhabdosomes that appear to have been shaped by the prevailing current. Slender mesh dendroid forms are shown not to have inhabited the quietest water.

The thecae of dendroids are suggested to have been occupied throughout the life of the whole colony, but with reduced colony secretion ability and increased feeding abilities in older rhabdosome. It is suggested that zooids may have been regenerated cyclically, either annually or seasonally. Hermaphroditic reproduction is suggested to have been used to produce new zooids, and sexual reproduction used to produce new colonies. The male and female zooids of each colony may have reached sexual maturity at different times in order to maximise cross fertilisation. This cyclical sexual maturity may have been associated with the formation of zones of bifurcation of dendroid rhabdosome.

Dendroid holdfasts are discussed. The various types are described, including; anchoring threads; attachment to a solid object; attachment disc and combinations of all three. The ratios of holdfast radius to colony axial-length are discussed and how this is affected by increase in colony size, presence of other colonies nearby , and the stabilisation of the sediment surface by the formation of dendroid meadows. The surface if dendroid holdfast structures are in some cases suggested to have been "sticky", allowing sediment particles to adhere to the surface. Models for secretion of holdfasts are discussed and specially adapted zooids are proposed. It is suggested that these holdfast-secreting zooids continued extending the anchoring threads across the surface of the sediment until contact was severed with the main colony, and that they may have been, in effect "disposable zooids".

Chapter 7

Implications of normal and abnormal growth of a Scottish Silurian dendroid graptolite.

7.1 ABSTRACT. Normal growth patterns and structure of one species of dendroid, *Dictyonema pentlandica* Bull, 1987, are described in detail and considered to be the result of the secretory zooids adhering to a strict characteristic growth pattern. Types of variation from the norm, aberrant structures, and abnormal growth patterns are described. The possible causes of these abnormalities are discussed as the response of dendroid zooids to external and internal influences. Some details of dendroid palaeobiology and palaeoecology are revealed by this work, and it is thus shown that dendroids can be used as indicators of palaeoenvironment. It is suggested that more palaeoenvironmental and palaeoecological data could be obtained by similar recognition of aberrant features of other animal groups.

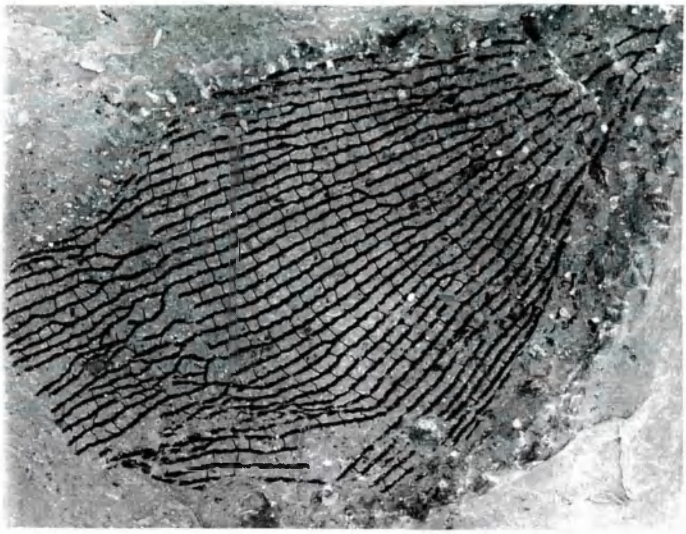
7.2 Introduction

Dendroids were a group of marine invertebrate fossil organisms, in existence from the Cambrian to the Carboniferous. They are thought to be ancestors of the widely studied, biostratigraphically important, graptoloids (Elles and Wood, 1901-1918; Bulman 1922-1967; Ruedemann 1947; Rickards 1975; Fortey and Cooper 1986), and the pterobranchs are considered their closest living relative (Rigby and Dilly 1994).

They were colonial animals, with a complex skeleton (or rhabdosome) consisting of overlapping tubes (thecae), made of collagen. This was occupied by many zooids, that secreted the precisely determined shapes of thecae in which to dwell. These thecae formed in a remarkably constant and regular pattern, with thecal size, shape, ornament, and orientation, very accurately repeated and constant for each species. The thecae, it is thought, were all linked in some way by living tissue. Each dendroid had a stolon system of interconnecting canals which branched at very regular nodal points, where a triad bud produced two thecae (the bithecae and autothecae) which opened into the ocean, and a third stolotheca which continued the string. Each thecae overlapped with its neighbour by predetermined amounts, combining together to form long chain or rope-like stipes, which in turn split, bifurcated or terminated according to seemingly predetermined patterns. This then built throughout the dendroid's life, to form three dimensional structures that included fan, shrub, disc or cone -shaped forms, specific to the pattern, or blueprints, of growth characteristic of each species. Each colony is highly integrated, the size and shape of each theca is independent of its position in the colony. Unlike the graptoloids, there is no proximal to distal thecal size gradient (Urbanek 1973:475).

Dendroid species are identified by studying details of standard rhabdosome structure. Taxonomically important features include; thecal morphology and distribution; stipe width, separation and branching patterns, including the number of primary branches or stipes; presence, dimensions and arrangement of dissepiments; gross rhabdosomal morphology and dimensions; proximal growth (siculate or with a stem, root or holdfast structure).

Figure 7.1 Rhabdinopora flabelliformis anglica (Bulman 1950) S. M. A.23397; Shineton Shales, Shropshire. Originally figured by Bulman (1950) as plate XVII, and (1970) fig. 26. Eight zones of branching are apparent, five before the specimen reaches the normal adult proportions for this variety, and three in the zone of rejuvenation; X2. Note : in the Treatise (Bulman, 1970, p. V3 fig. 26) magnification is 1.5, not the stated 1, and only part of the specimen is featured, the area of regrowth is not included, this illustration was then copied by Urbanek (1973, fig 24, p. 477, to the same (wrong) scale), see also Palmer and Rickards (1991, fig. 126).



Measurement and description of these features can enable production of statistically reproducible data. For this study, a detailed examination of normal thecal and rhabdosome structure has been made. The blueprint of thecal structure and rhabdosome shape of one species, *Dictyonema pentlandica* Bull 1987, are described and illustrated. Additionally, abnormal structures are described.

Studies of living colonial animals such as bryozoans have concentrated on two-dimensional encrusting colonies (Taylor 1988), where not only standard patterns of bryozoan colony growth have been identified, but also more complex histories of zooid mortality, colony fission, regrowth, repair and fusion. A comparison with regenerative and reparative patterns described for bryozoans and other taxa is considered later.

Recent work on the pterobranch *Rhabdopleura* (Rigby 1994), has shown that zooids are aware of their spatial position in the tube that they are secreting. Even when successive generations of zooid are involved in the secretion of one tube, tube growth is a highly ordered process. The overall shape of the final tube is less ordered than that of dendroids, due to the encrusting nature of *Rhabdopleura.* The comparison of dendroids with these their closest living relative, has not yet been attempted. Relationships between patterns of colony construction and ultrastructure of graptolites and pterobranchs were discussed by Rigby (1994); Rigby and Dilly (1994).

Astogeny (growth history of a colonial animal) is not an easy process to study for three dimensional, complex, erect colonies such as dendroids. Controls on colony growth are dependent on both internal forces such as the genetic design of colony that each species is programmed with (the normal structure), and external forces such as space (competition with neighbouring dendroids or other taxa) and environment (temperature, food supply, predation, mechanical damage).

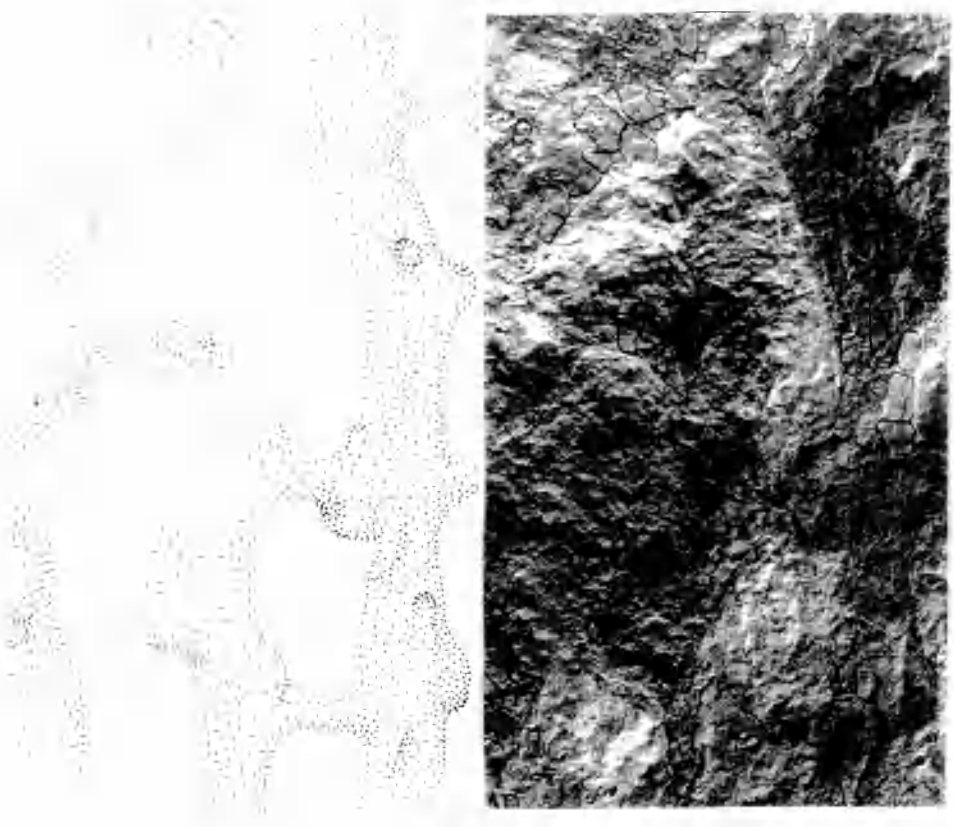
Extended study of this species has revealed that a number of aberrant structures are also present in the growth patterns of dendroids, similar to those described in the bryozoans. It is difficult in all fossil material to distinguish pre-mortem from post-mortem damage; however, certain damage and changes occurring during the life of the colony can be identified by their effect on surrounding stipes. The likely causes of these aberrant structures including trauma, predation, mutation, and change in external conditions, are also discussed. While this study concentrates on the regrowth of the mesh, it also focuses attention on our understanding of the growth patterns of the whole rhabdosome.

In 1950 Bulman described a single well preserved specimen of *Dictyonema flabelliforme* cf. var. *anglica* from the Shineton Shales of Shropshire, displaying an unusual discontinuity at the periphery of the rhabdosome. This showed the species to be capable of either regeneration after damage, or rejuvenated growth after a pause. He also suggested that the cause was more likely to be rejuvenation, unassociated with regeneration (fig. 7.1). This specimen is doubly important as it is not only featured as the first indication of such renewed growth, but it is also used as the illustration of the zones of bifurcation characteristic of the species `*Dictyonema' flabelliforme* in the Treatise (Bulman, 1970, p. V3), although only part of the specimen is featured.

Whilst Bulman (1950) recognised the implications of the specimen he was describing, rejuvenation and regeneration are both present to varying degrees in many other dendroids. A number of workers have unwittingly figured species with aberrant structures, such as *Reticulograptus snajdri,* (Kraft 1982, Pl. IX); *Dictyonema delicatulum* (Kraft 1984:407); *Dictyonema desmoides* Gurley, (Bassler:35) and various species figured by Ruedemann (1947). However, only one other author (Boucek 1957:22) mentions this phenomenon directly. His entire statement on regeneration is as follows,

> 'It happens sometimes that one or several of the lateral branches finishes its growth prematurely. So a certain gap in the uniform network of the rhabdosome should arise. But such gaps did not form completely. The adjacent branchlets reacted namely very quickly to the space in the neighbourhood and began at once to furcate laterally into the gap soon healing it'.

Figure 7.2 Dictyonema pentlandica Bull, 1987, RSM.GY 1995.XX.X; O. spiralis Biozone, Reservoir Formation, North Esk Inlier; A) Photomontage of S.E.M. images; X70. B) Drawing of the important features at the same scale. The autothecae form large bulges on alternate sides of the stipe. The upper surface curves inwards and in some cases back on itself forming a distinct notch (n) in the wall of the main stipe above the flat upper surface of the autotheca. This notch is observed in some cases to be occupied by the bitheca curving over the top of the autotheca. The bithecae occupy the ridge seen crossing the autotheca at (r), and structures seen at (a) are thought to be bithecal apertures; X70



Bulman (1928:47) discussed the variations of dendroid thecal structure with time. He noted that thecal isolation is the only trend that has been proved, but the increase in the production of thecal spines also seems to indicate another line of development. The information obtained from the specimens described in this paper, is therefore a quite important addition to the scant knowledge of any evolutionary patterns for Lower Palaeozoic dendroids. The separation of benthonic and planktonic dendroids such that *Dictyonema* includes only sessile forms and *Rhabdinopora* replaces *Dictyonema* as the generic name for the planktonic forms (Erdtmann 1986), is now mostly accepted, although the phylogenetic differences between the two have not yet been clearly established. The response of *Rhabdinopora flabelliforme* to environmental pressures was discussed by Erdtmann (1982:135), and he suggested that some species were capable of 'gerontic astogeny' by thickening of stipes and addition of extra dissepiments, in response to exposure to high energy environments; this may in fact be a record of dendroid species' ecophenotypic variation.

Both planktonic and benthonic dendroids are only sporadically found in the fossil record. It is thought however, that they were once widely distributed in shallow marine environments or perhaps throughout the oceans. The relatively low abundance of dendroids in the fossil record, particularly as completely articulated fossils, is due to the low preservation potential of such fragile three dimensional colonies. As discussed below, it is possible that the benthonic forms were able to withstand quite rough conditions in life, but fairly exceptional conditions are required in order to preserve the biota from such environments.

The dendroid specimens described in this study were deposited in an active tectonic regime (Stone 1987, p. 761) (see below), in an environment possibly subject to frequent changes in conditions. The dendroids seem to have been able to cope with these changes, whereas those in other areas may not have been able to. This suggests that the amount of disruption that a species can withstand may have an important implications for our understanding of the environment of deposition. Similarly we may eventually be able to identify dendroid species that have evolved to inhabit different niches or colonise distinct environments.

Aberrant structures are not a universal occurrence and this survey is by no means thought to be exhaustive. In the material from the Pentland Hills studied, there is usually at least one 'imperfection' per colony, which seems to be a recognisable increase in the percentage of specimens with distinctive variations as compared with the norm in other areas, which could reflect more energetic conditions at the time of deposition.

7.3 Material, location and stratigraphy.

Most of the dendroids studied for this paper are excellently preserved, some in partial 3-D, although no isolated material is yet available. *Dictyonema pentlandica* Bull, 1987, is known from more than fifty specimens, and is the most common species of a varied dendroid fauna of late Llandovery (Telychian), *Oktavites spiralis* Biozone (Bull and Loydell 1995) age, found in the North Esk Inlier, Pentland Hills, near Edinburgh, Scotland, (locality details are outlined in Bull (1987:118) and stratigraphy in Bull and Loydell (1995). All of the known specimens of *Dictyonema pentlandica* Bull 1987, are from the Reservoir Formation, and most specimens are preserved within a 15 metre thick series of calcareous siltstones, found at one locality, the site of the famous 'Gutterford Burn Limestone Beds' (Robertson 1990) and 'Gutterford Burn Eurypterid Bed' (Waterston 1979).The presence of dendroids in rocks of this age, fills in a gap in our previous knowledge, particularly of *Dictyonema* in Britain. This species has not yet been identified from any other localities.

The North Esk Group (Robertson 1989) represent a continuous sequence of marine sediments recording a regressive sequence from outer shelf environment (BA 3-4), through lagoonal conditions, to terrestrial sediments. The tectonic history is complex. The depositional basin was in a restricted position, separated from the remnant Iapetus Ocean by

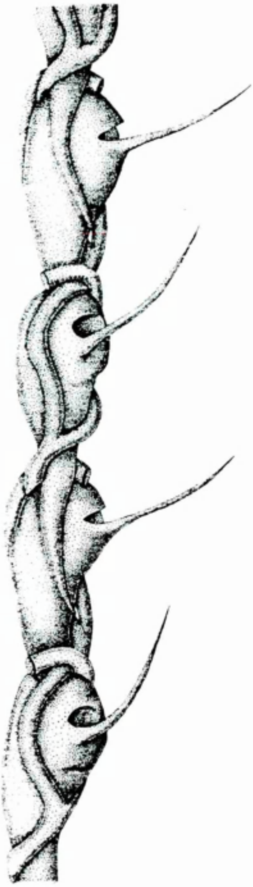


Figure 7.3 Dictyonema pentlandica Bull, 1987. Sketch of the idealised thecal structure, showing the relative positions of the autothecae and bithecae and the autothecae in profile view, showing the apertural spine and the bulbous nature of the genicular margin (approximately X 60).

the emergent mass of the Southern Uplands. The sediments are now considered to have been deposited at the margins of the eastern end of a rapidly subsiding, elongate (Midland Valley), interarc basin, deepening to the west (See fig. S7 in Cope *et al.* 1992). The dendroid specimens are mostly found in the Reservoir Formation, the deepest water sediments preserved, which were previously thought to have been deep marine turbidites (Robertson 1989). Subsequent analysis (by the author) and interpretation in the light of current models for the tectonic history of the South of Scotland has suggested that although distal turbidites cannot be ruled out, there is some evidence for storm generated deposits. Furthermore, faunal evidence (articulated dendroids, starfish and crinoids deposited *in situ* along with articulated shallow water eurypterid specimens) is not consistent with a deep marine environment of deposition, and an outer shelf depositional environment is considered more appropriate.Faunal diversity in the Pentland Hills also extends to other fossil groups (see Robertson (1989, p. 130) for further faunal lists), some of which have been well documented, such as crinoids (Brower 1975), trilobites (Clarkson and Howells 1981), eurypterids (Waterston, 1979), echinoids (Kier 1973), and starfish (Spencer 1914-1940), and taxa which require further revision such as the brachiopods (Davidson 1868) and bivalves (Lamont 1954). All specimens described (except for fig.7.1) are housed in the collections of Royal Museum of Scotland (RMS), Chambers Street, Edinburgh, Scotland, or Grant Institute of Geology (EDCM), Edinburgh University, Scotland.

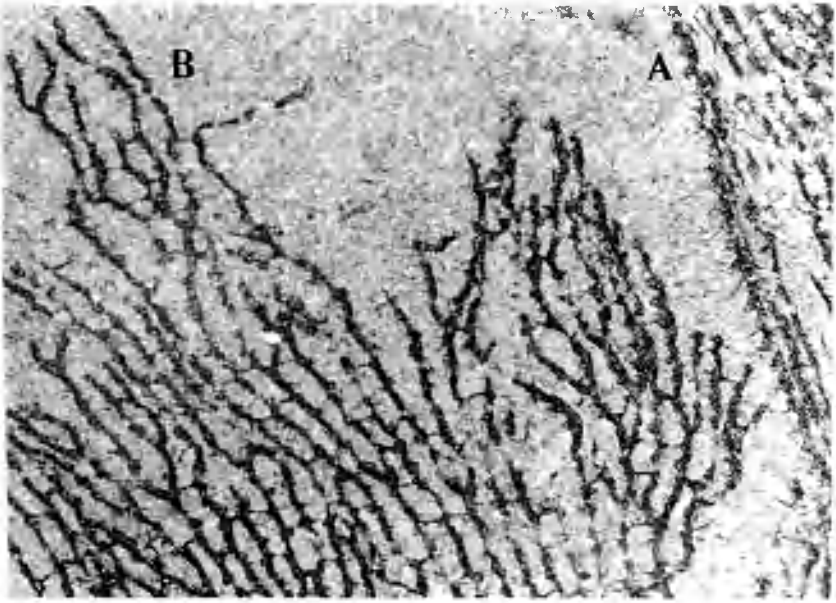
7.4 Normal thecal structure of *Dictyonema pentlandica*

In the course of this detailed study of *Dictyonema pentlandica* , further details of the gross morphology have been elucidated by using a Scanning Electron Microscope; in particular, the autothecae have now been observed in detail, and the bithecae are also described. This section is a description of the normal growth pattern, or the 'Blueprint' for growth adhered to as closely as possible by the zooids when constructing the thecae and hence the rhabdosome. This normal growth pattern is remarkably regular, and is probably the result of genetically controlled processes, characteristic to each species. It is vital to the understanding of dendroids to ascertain a clear picture of normal growth patterns. Any alterations to this normal pattern (abnormalities) can then be considered independently in terms of variations in external, internal and environmental factors, as discussed later.

7.4.1 Whole Rhabdosome. The rhabdosome forms a broad cone with opposing sides diverging at an angle of 30°-50°. Most specimens are partially three-dimensional, although there may be some element of increased angle due to sediment compression. The walls of the cone fall into gentle folds (Bull 1987, fig. 6). At the base of the cone is a short stem up to 10 mm long which is generally attached to a solid object such as a pebble or shell (fig. 7.9.3) or has root fibres attached to secure the specimen to the substrate. The base of the cone is sometimes secondarily thickened (fig. 7A; Bull, 1987), and usually consists of four primary branches.

The species grows quite large, with sections of the rhabdosome up to 0.5 m long preserved, that are portions of even larger specimens in life. Most species of *Dictyonema* previously described are 30-50 mm. long, exceptionally reaching 100 mm. The size of this species is remarkable since its constituent stipes are some of the most slender known (0.22 mm wide and spaced 0.29 mm apart or 17-22 in 10 mm). This is consistent with other graptolite material from the Pentland Hills (Bull and Loydell 1995). The more robust species normally characteristic of sediments deposited during the *Oktavites spiralis* Biozone are missing, and generally the more slender forms are present (eg *Oktavites excentricus*, *Monoclimacis geinitzi*).

The vast majority of the stipes of *Dictyonema pentlandica* attain remarkably even distribution, with constant positioning of thecae and dissepiments at standard spacing (fig 7.8.1) with zones of bifurcation evenly arranged, occurring every 20 mm (fig 7.9.3). Bulman (1950:351), noted '..well-marked zones of branching..', suggesting that these might become features of systematic importance. These zones are apparently present in other



7.4) Dictyonema pentlandica Bull, 1987, RSM.GY.1985.29.5; O. spiralis Biozone, Reservoir Formation, North Esk Inlier. The slab has two specimens on it, preserved with the openings of the cones facing one another. (A) An area of the rhabdosome (right-hand side of fig. inverted view of these particular stipes) with the thecae rotated to show the profile view and in particular the apertural spines of the autothecae. (B) The specimen occupying most of the image (left and centre of figure) shows an uneven regeneration zone at the growing margin of the rhabdosome, the dendroid has started to grow again in one region, and has not been able to reinstate the normal pattern of growth, being unable to produce dissepiments; X7.

genera, and although clear enough in the plates, they rarely feature in the text descriptions. This was discussed by Urbanek (1973:475) who noted how the branching pattern can determine the shape of the whole colony. He also suggested that changes in branching frequency could indicate that dendroids had 'a latent gradient of morphogenetic ability', or that the branching pattern was part of the essential predetermined normal structure of blueprint of dendroid construction. The main obstacle to the systematic use of such zones (Bulman 1950:352) is the need for complete and well preserved rhabdosomes, without the stipes having been stretched apart or broken on deposition, or weathered away. Such specimens are uncommon. As noted below, when some species grow beyond a certain size the growth pattern can appear to revert irregularly to the juvenile pattern, the whole structure of the rhabdosome can then become contorted. Some *Dictyonema* species have stipes that bifurcate irregularly and sporadically at all times (Boucek, 1957:51), or do not have zones of stipe bifurcation recognisable as regularly spaced branching zones.

7.4.2 Autothecae. The autothecae of this species were previously thought to be the bithecae (Bull 1987:124). Further study has revealed more detail, and an idealised reconstruction is given in fig.7.3. From its base, the theca rapidly expands to form a tube with a diameter occupying most of the stipe (0.2 mm). Towards the end of the theca the tube again rapidly swells to form the large (up to 0.3 mm diameter) bulbous spherical termination, which thins again forming a narrow aperture. This aperture is a simple opening in the middle of the ventral wall of the autotheca, approximately 0.06 mm diameter, considerably narrower than the main body of the theca. The thecal aperture is adjacent to the thecal wall of the succeeding theca. The autothecae are not isolated, but their terminal swellings are observed displaced alternately to either side of the main stipe so that the apertures are angled at 60-70 degrees to either side of the ventral line of the stipe. The upper surface of the autotheca curves inwards and in some cases back on itself forming a distinct notch in the wall of the main stipe above the flat upper surface of the autotheca. This notch is occupied by the bitheca curving over the top of the autotheca (fig 7.3). It is the distal swellings of the autothecae, regularly spaced along the stipe at intervals of 0.67 mm (28-30 in 10 mm), that give the rhabdosome the very distinctive knobbly appearance (figs 7.2, 7.9). There is as yet no clear explanation for the terminal swelling of the autothecae, although it is probably related in some way to zooecial behaviour.

Lateral views of the autothecae show that each theca has a slight geniculum and the supra-genicular wall is strongly convex, and each autothecae has large ventral sub-apertural process. This spine is angled towards the open end of the dendroid rhabdosome cone at about 70 degrees to the stipe. The spines are consistently about 0.07 mm wide for most of their length, tapering very slightly distally. Spines can reach up to 0.4 mm. long but the average length observed is 0.3 mm. These dimensions are almost identical to those of the dissepiments, so in normal preservation the thecal spines and dissepiments are indistinguishable and can only clearly be differentiated in profile view (figs.7.3, 7.4, 7.7, 7.8.3).

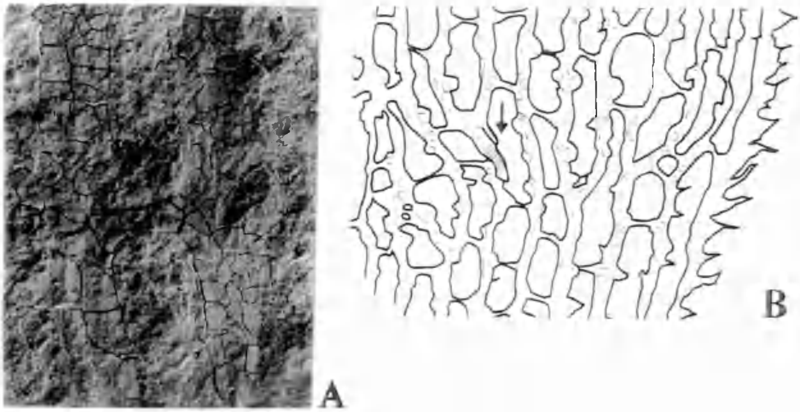


Figure 7.5 *Dictyonema pentlandica* Bull, 1987; *O. spiralis* Biozone, Reservoir Formation, North Esk Inlier. Dissepiment structure.

A) RSM.GY.1995.XX.X. S.E.M. photograph of a clear dissepiment. Not preferentially attached to either stipe and strengthening appears to follow the margin of the fenestrule rather than supporting a dissepiment growing from one stipe to another; X50 .

B) RSM.GY.1985.29.2. Diagram showing extra growth (arrowed) of a single stipe in the opposite direction to that expected, turning back to grow towards the sicula rather than away from it. Also right hand margin shows thecae turned partially to show profile view; X20.

Ruedemann (1947:27) discussed spinosity in dendroids and suggested that species armoured in this way are the weaker taxa. Since then, very few spinose specimens have been described. The bulbous, spinose nature of the autothecae of *Dictyonema pentlandica* may have evolved to protect the zooids, particularly from predation. This species had relatively slender stipes, possibly as an aid to directing the currents through the mesh with maximum efficiency and least drag, the spines may also have directed water currents within the cone.

Spines may have been developed by this species to form platforms enhancing zooidal feeding strategies. By providing support for the zooids to extend themselves considerable distances from the aperture of the theca, this may have resulted in greatly improved water sampling capacity for the colony. Living *Cephalodiscus* zooids (Rigby 1994) have been observed using spines for feeding in this way. The distinctive swellings of the ends of the autothecae may suggest that the autothecal zooids could have been larger than average. This is unlikely however, as it has been shown recently that graptoloid (Sudbury 1991) and pterobranch (Rigby and Dilly 1994) zooids are generally small relative to their thecae.

The dorsal faces of the autothecae of this species are often subject to slightly more weathering than neighbouring parts of the stipe. It is relatively common in even fairly well preserved specimens for a number thecae to be abraded, leaving the matrix infilling the thecal cavity exposed (fig. 7.8, fig. 7.9.2 and 7.10), these openings superficially appear to be the autothecal apertures, although none have the distinct edges expected for aperture margins. This pattern has been studied on the Scanning Electron Microscope, and they are clearly artifacts caused by weathering. The true position of the thecal apertures is described above. The autothecae may have had thinner walls at the point of curvature originally; they certainly protrude a little from the plane of the rock because of partial 3-D preservation, being therefore more prone to abrasion and weathering, alternatively this could be due to compression and stretching at the time of deposition.

7.4.3 Dissepiments. A dissepiment is associated with every alternate autotheca. In areas of normal rhabdosome growth they are very thin (0.06 mm diameter) (fig. 7.5), and arranged in a regular pattern with 11-13 in 10 mm, 0.8 mm apart and perpendicular to the main stipe. The fenestellae so formed are of fairly constant size, one fifth longer than wide. Continuous lines of dissepiments often form at the site of bifurcation (see Bull, 1987, fig. 8).

Dissepiments probably originate from the bithecae as described by Bulman (1927, 21-22). They probably consist of bithecal tissue, formed by continued growth of alternate bithecae. They arise from the stipe close to, opposite, or passing over, the distinctive bulge of the autothecae (fig. 7.2 & 7.5a). Strengthening, seen under S.E.M. as concentric rings, appears to symmetrically follow the margin of the fenestrule rather than supporting a dissepiment in its direction of growth. A stipe of origin is therefore not apparent, rather the dissepiments and stipes define the margin of the fenestrule, maintaining the rectangular shape to a regular size (0.4 x 0.6 mm). This may have been due to the importance of controlling the water currents passing through the mesh to the zooids within, as the size of any aperture and the

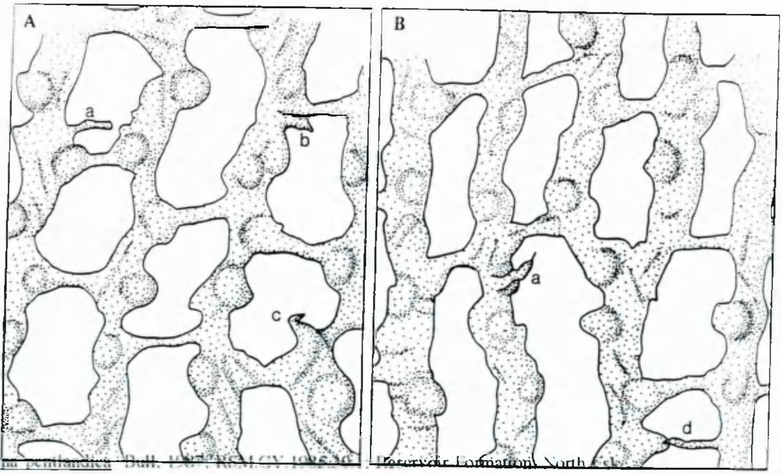


Figure 7.6 Dictyonema pentlandica Bull, 1987; RSM GY 1986.30.[illegible] Reservoir Formation, North Esk Inlier, O. spiralis Biozone; camera-lucida drawings A and B (oriented with proximal portions at base of drawing), showing types of aberrant growth of bithecae. X25

a. Tubular outgrowth.

b. Growth along a dissepiment

c. Outward growth from the stipe recurving back later.

d. Outgrowth crossing to adjacent stipe.

thickness of the walls, will dictate the flow rate and turbulence of currents passing through that aperture (Stratton and Horowitz 1974).

7.4.4 Bithecae. The bithecae of this species are thin with a constant width of 0.03 mm, and inconspicuous. They do not protrude from the stipe in normal circumstances, but are thought to form a slight ridge crossing above upper margin of the terminal swelling of the autothecae. Each autotheca is associated with a bitheca, which loops across the side and curves around the bulbous part above the aperture of the adjacent autotheca, before the swelling of the next autotheca commences. This can give the illusion of an apparent geniculum when viewed in profile. The bithecae have simple, unornamented apertures, opening in the side of the stipe (figs. 7.2 and 7.3).

7.4.5 Discussion. The taxonomically significant features of this species have been described and discussed both as above and in the original systematic description (Bull 1987:125; Bull 1995) wherein comparisons with other species are made. The presence of a holdfast structure confirms the attribution to the genus *Dictyonema*. Combinations of the following features allow its distinction from other described species; the presence of simple (unforked) autothecal apertural spines; the identification that the swelling of the stipe giving its distinct knobbly appearance is caused by swelling of the autothecae and not by bithecae passing round the outside of the stipe; the very slender dimensions of the stipes and high stipe density; and the regular close arrangement of the dissepiments. *Dictyonema pentlandica* is subject to aberrant structure growth on both microscopic and macroscopic scale, including tubular outgrowths of the bithecae and large scale regrowth or mending of the rhabdosome following changes in growth patterns or predatorial attacks, or other environmental factors. The details of these aberrant structures are discussed below.

7.5 Description of types of aberrant and abnormal structures.

Abnormal structures are not normally discussed in taxonomic work as they distract attention from the features considered typical of (or normal for) the species. Yet almost every specimen of *Dictyonema pentlandica* studied by the author, has some feature which does not conform to standard taxonomic description. Despite the abnormalities however, the majority of the rhabdosome of each specimen is the normal size and shape, with a normal stipe and dissepiment distribution pattern. Examples of the different types of aberrant structure observed, are illustrated and explained in figures 7.4-7.7 and Figs 7.8 &7.9. These fall into five main categories.

1) Stipe truncation and compensatory growth by neighbouring stipes.

a) One or more stipes are truncated within a section of otherwise unaffected rhabdosome. The surrounding stipes cover the gap so formed either by bifurcating, or by curving across the gap (fig. 7.8.(1,2), fig.7.9.4). The normal pattern of rhabdosome growth is continued afterwards.

b) A hole formed in the centre of an otherwise strong section of rhabdosome, the surrounding stipes may crumple with the extra load they are forced to bear and become secondarily thickened to support the remaining stipes (fig 7.8.3). The ends of the truncated stipes left trailing backwards, may appear to wither slightly.

2) Change in rhabdosome growth pattern. A change in the rate of growth (either increase or decrease) can affect large areas of the rhabdosome at the same time. Not every stipe is necessarily involved in the change. Some stipes may be terminated (figs. 7.1, 7.7 and fig. 7.9.4) some continue through the area of disruption unaffected, while neighbouring stipes seem unable to regenerate, forcing those stipes that are able to grow, to bifurcate immediately and regularly thereafter, in order to reunite the mesh. In some areas of the rhabdosome, all of the stipes bifurcate at the same time, causing the rhabdosome to grow in another plane giving the appearance of a frill forming at the margin (fig. 7.9.3). In other areas the stipes start to regrow but do not attain the normal pattern (fig. 7.4, 7.11). This is the type of rejuvenation described by Bulman (1950) (fig. 7.1). The growth pattern that emerges following renewed activity can represent either a return to the juvenile pattern (Bulman 1950), a continuation of the adult pattern or growth in an apparently random fashion.

One section of the main body of the rhabdosome may become enlarged, forming a bulge in the normally planar surface of the cone. An increase in the density of stipes commences with a number of stipes bifurcating together, the resultant bulge may be resorbed into the main body of the rhabdosome by one or more stipes terminating. More usually however, the normal bifurcation pattern of the main rhabdosome continues for the surrounding stipes and

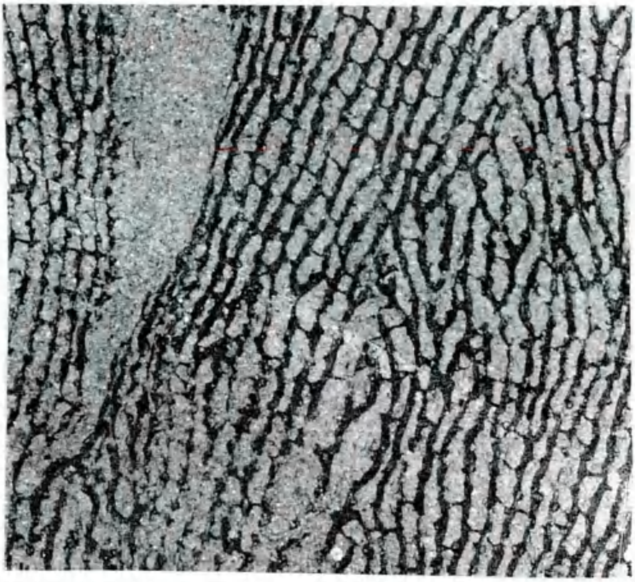


Figure 7.7. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.29.5; Reservoir Formation, North Esk Inlier, *O. spiralis* Biozone; Major split forming in the rhabdosome (a). The stipes on either side of the split no longer attempt to form dissepiments to join up with the stipe on the other side of the split. The base of the split secondarily thickened (b). Some of the autothecae are seen in profile as the stipes to the left-hand side of the split have been rotated on deposition, and autothecal spines are visable (c). An area (d) to the right of the split shows some stipes terminating, while those that continue to grow, curve in both directions until aligned with an adjacent stipe at the appropriate spacing. Certain areas of the rhabdosome involved in stipe termination, other areas (e) continue more or less unaffected; X8.

Figure 7.8

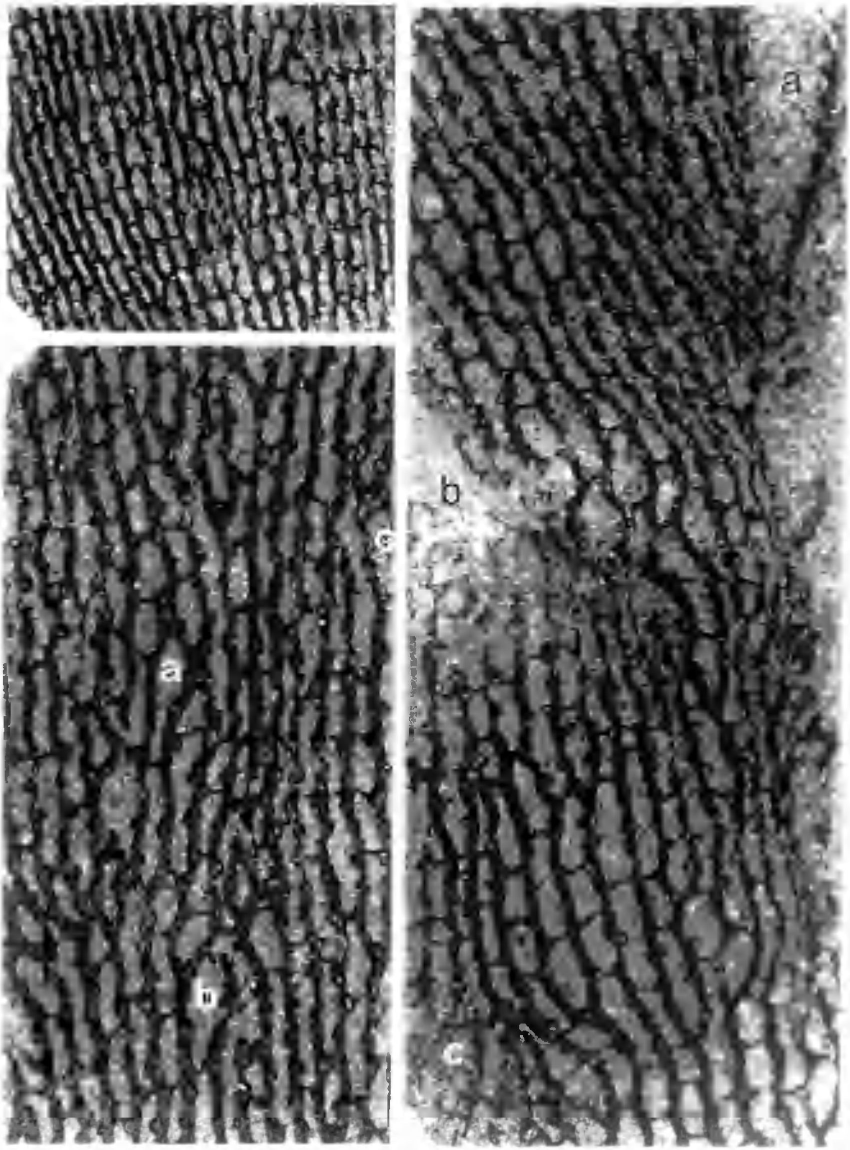
Dictyonema pentlandica Bull, 1987. Gutterford Burn, Reservoir Formation, *spiralis* graptolite Biozone, Upper Llandovery.

Examples of holes in the rhabdosome.

Fig. 1. RSM.GY.1985.29.5. An area of normal growth with regular spacing of stipes and dissepiments, suddenly interrupted as two stipes terminate, presumably when they constituted the outer growth margin, due to either growth pattern defect or predation. Neighbouring blocks of stipes move relative to one another due to weakening in one area and surrounding stipes bifurcate after the termination of the two stipes, to regain normal stipe spacing. Some of the autothecae have been slightly weathered where they protrude from the specimen, giving the false impression of being matrix filled thecal apertures; X7.

Fig. 2. RSM.GY.1985.29.2. Extra growth of one stipe causing it to bulge (middle arrow). Stipes withering (lower arrow). Stipe termination followed by bifurcation of other stipes to fill the gap (top arrow); X10.

Fig. 3. RSM.GY.1985.29.2 Photograph of the edge of flattened cone of the rhabdosome. The upper portion of the photo (top arrow) shows the stipes rotated into profile view showing the apertural spines. The centre of the image (middle arrow) shows the result of a hole forming in a strong section of the rhabdosome, the surrounding stipes crumple with the extra load they are forced to bear and become secondarily thickened to strengthen the remaining stipes. The ends of the stipes left trailing backwards appear to wither slightly. The lower portion of the photo (level of bottom arrow) shows a sudden surge of growth within the rhabdosome, which probably formed a bulge in the side of the cone and is seen here compressed and flattened; X10.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a
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Figure 7.9.

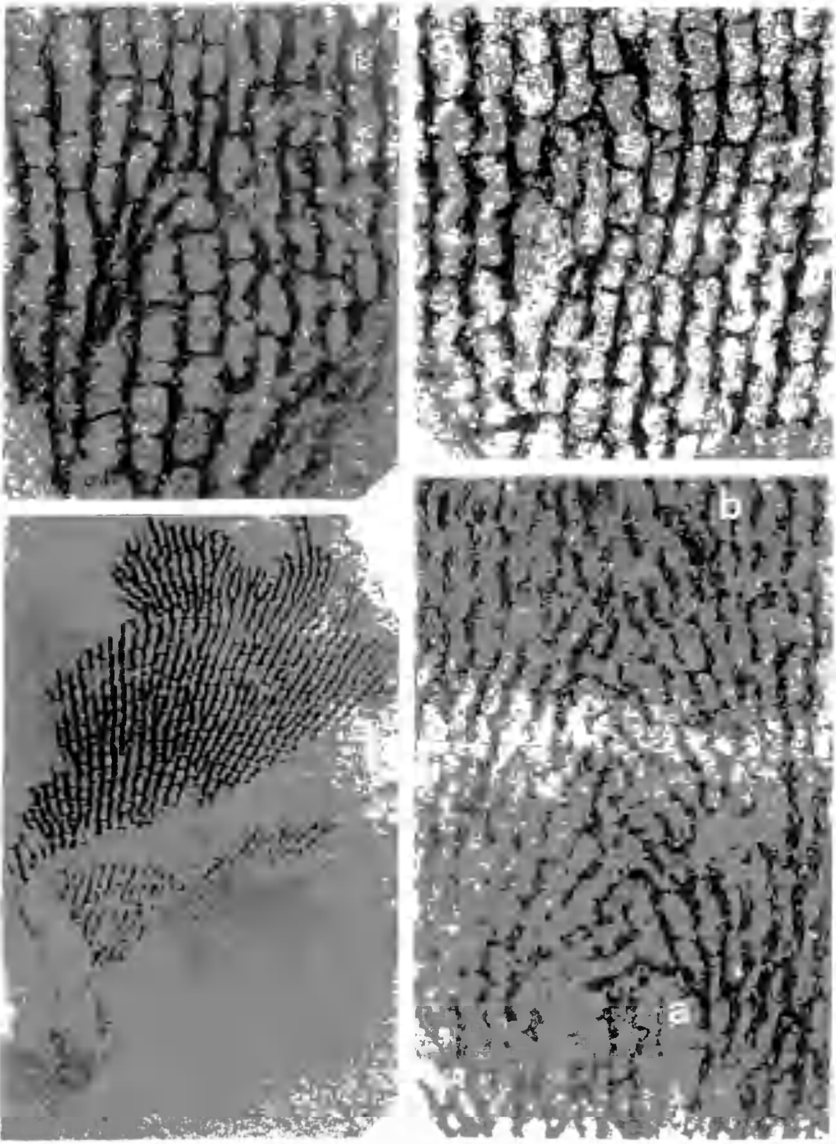
Dictyonema pentlandica Bull, 1987. Gutterford Burn, Reservoir Formation, *spiralis* graptolite Biozone, Upper Llandovery.
Examples of bursts of growth of the rhabdosome.

Fig. 1. RSM.GY.1985.29.1. Sudden surge in growth in the centre of the rhabdosome. Increase in stipe density in one area only, forming a bulge in the side of the cone as a response to increased activity and growth of a few stipes, which are superimposed on one another on deposition; X10.

Fig. 2. RSM.GY.1985.29.1 One stipe growing longer than expected, relative to the stipes around it. The stipe that has experienced extra growth has to curve to accommodate the extra length on deposition. Normal growth is resumed after the formation of the next dissepiment; X10.

Fig. 3. RSM.GY.1985.30.1 All of the stipes are involved in this case, some terminate, the rhabdosome expands and the new growth area forms a frill at its outermost margin (specimen attached to brachiopod *Leptaena*); X3.

Fig. 4. RSM.GY.1985.29.5 Some stipes terminate (arrowed), neighbouring stipes bifurcate and curve to fill the gap, resulting in stipes obliquely approchng one another. Some stipes then terminate on reaching normal stipe separation distance from adjacent part of cone. Pattern contiues until normal stipe separation achieved distally; X3.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eventually regular stipe spacing is achieved. The extra sections of the stipes are compressed on top of one another on burial (figs. 7.7, 7.9.1 and 4).

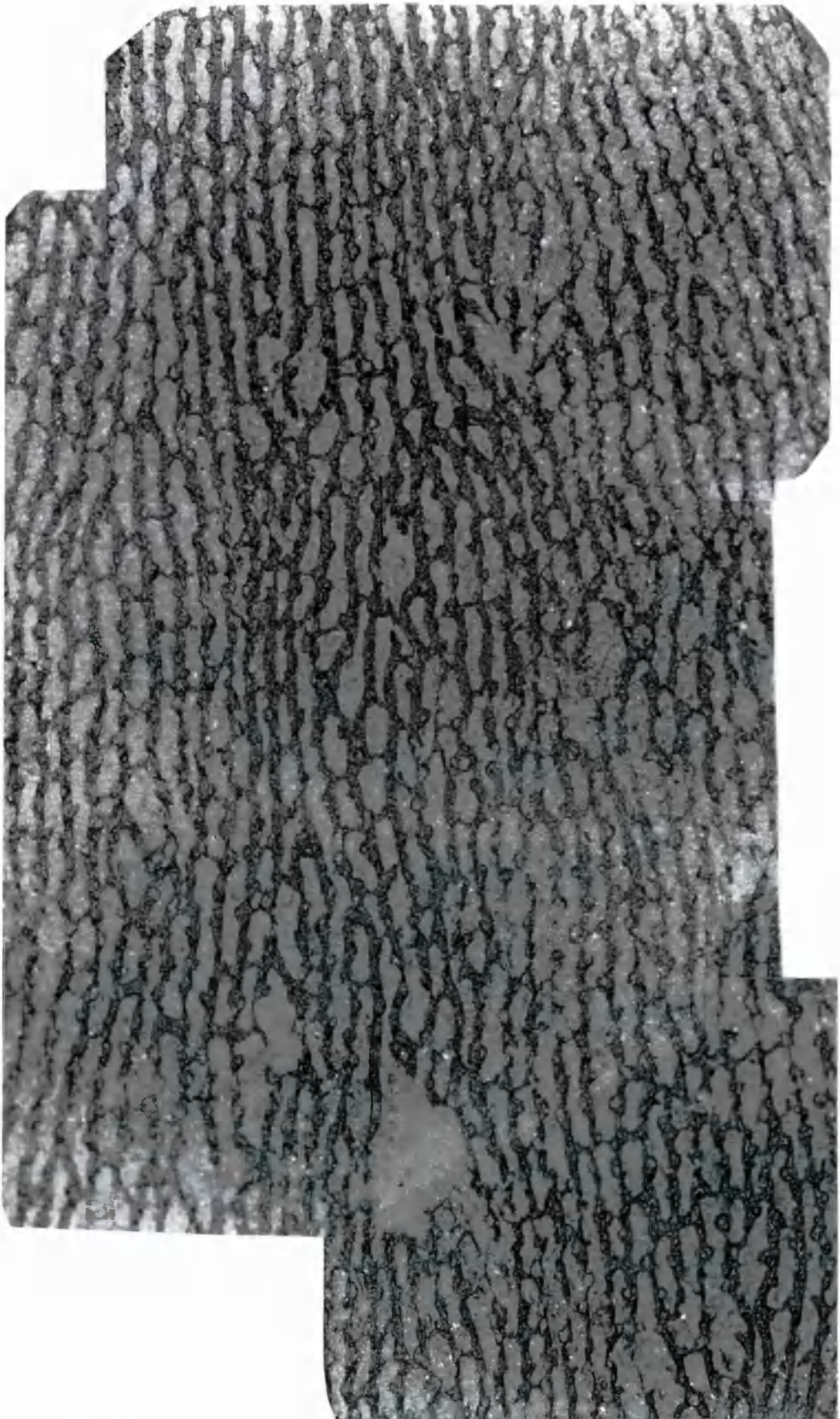
3) Abnormal bursts of growth by one or more stipes. Individual stipes may accelerate in growth, the result is a distortion of the regularity of the meshwork. Normal patterns are usually resumed after the formation of the next dissepiment, although one or two dissepiments may be omitted. The section of stipe in question becomes either slightly longer than expected (fig. 7.9.2) or begins to grow in a completely different fashion, such as recurving in the opposite direction, growing towards the sicula instead of away from it (fig. 7.5b). In the former case the stipe is deflected, because it has to curve relative to the stipes around it to accommodate the extra length. In the latter case the new growth is superimposed on the pre-existing stipe.

4) Tearing or splitting of the rhabdosome. A split may form in the rhabdosome and the whole mesh can be pulled apart. The proximal end of the split may become secondarily thickened and the remainder of the stipes on either side of the split continue unaffected (fig. 7.7), with normal stipe spacing. The stipe on one side of the split is not observed to attempt to form dissepiments to join up with the stipe on the other side of the split, nor to grow new stipes in the gap formed.

5) Abnormal thecal growth. The bithecae of *Dictyonema pentlandica* are usually thin (0.03 mm) and inconspicuous. On rare occasions they become enlarged and distorted and can develop tubular outgrowths, in no regular pattern. Such growth structures are usually difficult to distinguish from broken or incomplete dissepiments and only in exceptionally well preserved material can they be clearly identified. Bithecal outgrowths are normally either thinner than dissepiments (0.03 mm compared with 0.06 mm dissepiment diameter), or where they are growing around the dissepiment this appears thickened for at least part of its length. Initially apparent as disruption of regular dissepiment arrangement (fig 7.6), and they are easily confused with autothecal apertural processes (spines). These are usually of constant diameter, are quite straight and arise from the centre of the bulbous part of the autotheca on the ventral surface of the rhabdosome. So, if spines are seen from the normal dorsal view of the rhabdosome, they will be displaced to one side of the centre of the autotheca and not any other position, whereas abnormal outgrowths occur at irregular intervals and positions, and are usually not straight.

Bithecal outgrowths (fig. 7.6) are short, thin (0.02 mm diameter) tubular structures, most commonly extending the bithecae across the fenestrule instead of following the normal path and wrapping around the top of the autotheca, almost as if the bitheca has become lost. This is usually followed by the formation of the next autotheca at a reduced spacing, and the stipe may be thinned at that point. Alternatively the outgrowth may eventually curve back towards the original stipe, or approach another stipe, or may grow around or along a dissepiment,

Figure 7.10. *Dictyonema pentlandica* RSM GY 195 29.2 X10. An area of rhabdosome showing how common "abnormal" structures are with a number of examples of stipe termination, holes in the mesh and also zones of bifurcation.



giving the impression of being further strengthening at the site of a dissepiment. At other times the outgrowths are indistinguishable from broken parts of the stipe wall.

As yet, apart from broken spines, no distinctive abnormal structures of the autothecae have been observed. Abnormal growth of the dissepiments and bithecae have previously been noted by Bulman (1927, pt.I p. 21; 1933). Two types of abnormal growth (1927 pl.1 fig.4, p. 28) are illustrated. Similarly Chapman and Rickards 1993 illustrate abnormal dendroid growth, in the form of sac like outgrowths that may be of autothecal tissue.

7.6 Possible causes of abnormalities.

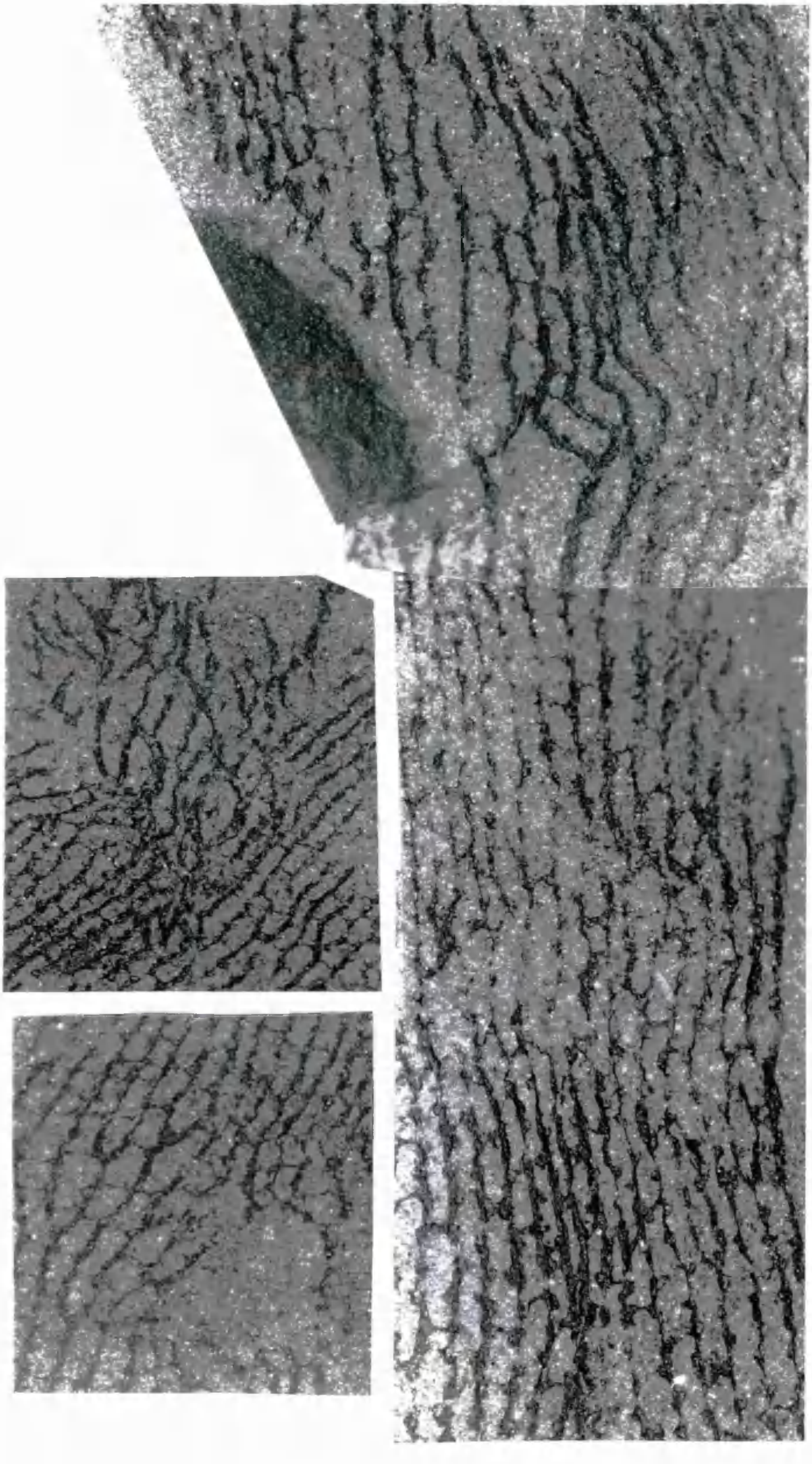
The standard patterns of normal dendroid growth are probably controlled by a simple epi-genetic phenomena. This dictates the species "blueprint", or normal structure common to each species, that the zooids secreting each colony strive to build. The normal pattern for this species is discussed above. The "blueprint" appears so rigidly adhered to that the abnormalities discussed in this section must have been caused by something. Inevitably however, it is impossible to determine unequivocally the causes of abnormalities.

Five processes likely to have caused interruptions and disturbances in normal growth patterns may be identified, 1) mutation, 2) injury or trauma, 3) disease and parasites, 4) change in conditions (external influences), and 5) preservation. Similarly, the timing of such changes cannot be quantified, as a cessation of growth for a period, will appear identical to a sudden change in growth, unless obvious wear and tear of the margin during a halt in rhabdosome secretion can be identified.

It is quite possible that each rhabdosome was subject to more trauma than we now have clear evidence for. It is unlikely however, that the animal was able to effect comprehensive repairs to its framework that leave no fossilised trace (effectively 'invisible repairs'), but we may now only see the results of repairs incomplete at the time of burial. The fact that the results of trauma on dendroids has not been described in detail before could be due to such features not being observed by previous authors. Alternatively it suggests that either the species currently being described was particularly bad at 'invisible repairs' leaving the clear scars to be fossilised, or that this species had an increased susceptibility to damage such as if it existed in a particularly energetic environment. Each specimen of this species examined, has at least one departure from the norm, which is possibly more trauma per specimen than in other areas. The effects of trauma are probably more common in other areas than has been previously recorded.

This particular species attained larger than average sizes, with some specimens reaching at least 50 cm long. It is not certain if this was due to an extended growth period, or more rapid growth. Estimates of graptolite growth rates are being attempted by comparison with living pterobranchs (Rigby & Dilly 1994). Similarly, study of the response of pterobranchs to trauma, predation and change in conditions, will hopefully lead to more information about

Figure 7.11 Dictyonema pentlandica. a.RSM GY 1985. 29.1 area of rhabdosome unable to resume growth of stipes correctly after trauma, b. RSM GY 1985. 29.2 example of hole in the mesh and stipe bifurcating to close the gap. c. RSM GY 1985. 29.1. Weakening at the site of trauma and stipes curving to fill the gap



dendroid growth patterns as this information emerges. Estimates of the degree of mending that the animal was actually able to effect for itself, may then become possible.

7.6.1 Dendroid abnormalities, causes and responses.

1) Mutation in the genetically controlled growth pattern. If mutations were generally the cause of abnormalities, then the pattern would be irrevocably changed. In most cases the original growth pattern is resumed after a change.

Bulman (1970, fig. 13) noted that for some species the distance between the regions of bifurcation increases gradually distally. If a regrowth had been spurred by mutation, a return to the juvenile pattern as described by Bulman (1950), would be unlikely (fig. 7.1). For *Dictyonema pentlandica* the zones of bifurcation are approximately evenly spaced (fig. 7.9.3) and this remains unchanged after any regrowth, as does fenestellae size and shape and general rhabdosome morphology. Occasionally the growth pattern of a section of rhabdosome appears completely changed, this could be the result of a individual zooid mutation, but is more likely to be local manifestation of disease. Growth in distorted fashion does not seem to continue for long before the complete cessation of growth (fig 7.4).

Teratology is the study of genetically or externally controlled malfunctions at embryological stage. This is considered quite an important, relatively common factor in the abnormalities of some arthropods, including trilobites (Owen 1985, p.269) and trilobite teratological abnormalities usually involve substantial deviation from normal morphology. Alternatively, examples of teratological conulariids are considered exceedingly rare, Babcock *et al.* (1987:95), only recorded one indisputable teratological conulariid specimen in a sample of 5000. When considering teratology of dendroids, there is the added difficulty of studying a colonial organism, with poorly known embryology and juvenile stages. It is unlikely that dendroids with teratological abnormalities would have survived into adult form in a recognisable shape and may account for some of the species described from a single specimen with affinities to another species. It is thought that teratological dendroid specimens, like conulariids, are rare.

2) Injury or trauma. Large splits occurring in the mesh (fig. 7.7) are almost certainly the result of damage. After tearing, the broken dissepiment remnants might have dangled loosely at the edge of the mesh. Such irregular margins have not been observed however, suggesting that they have probably been resorbed, possibly to avoid impairing the action of the remaining zooids. The normal pattern of growth for this species is to fill all of the available space, and the obvious growth direction to the side of the torn stipe is not exploited. No further growth seems to occur in the gaps formed by splits, and it does not seem possible to trigger regrowth in an already mature area. Such growth would rapidly result in the two sides of the mesh becoming superimposed or interfering with one another. In the original description of this species (Bull, 1987:124) it was noted that 'Bifurcation is concentrated on certain stipes, while others are continuous straight and unbroken.' This phenomenon also seems to be a control on the ability of the rhabdosome to spread out and fill any gaps caused by injury to its structure. The areas at the bases of splits are secondarily thickened, acting as strengthening for a weakened area.

Different responses to injury might be expected depending on whether it was the outermost growing edge of the cone or the already formed central part of the mesh that was attacked. As small holes in the structure are fairly common, in most cases the reaction of the dendroid results in a mesh stretched around the hole (fig. 7.8.1). The dendroid seems to have been capable, almost always, of repairing its mesh at whatever point it had been attacked, although details of early stages of ontogeny of this species are unknown. The zooids are thought to have been able to plaster cortical bandages on the surface of the mesh (Crowther and Rickards 1977), and this method could have been used to mend damage to the rhabdosome, particularly in cases where the stipes are now seen to be slightly thickened at the site of damage (see fig. 7.7 and fig. 7.8.3).

The sites of individual predatorial attacks may be determined by looking at patterns of regrowth. Thus, where the associated, succeeding and surrounding stipes have been activated to either bifurcate, or curve and stretch across to heal the gap (fig. 7.2, figs. 7.8.1 and 2) it is probable that the attack took place at the outermost growing edge. It is only here that new growth in an outward direction is expected to occur and new phases of bifurcation and thecae production stimulated. In order to rejoin with pre-existing stipes on the other side of an area of damage, it is thought unlikely that the stipes would be able to grow backwards (towards the sicula instead of away) for any distance (fig. 7.5b), as this would involve either producing thecal apertures that faced the wrong way into the current passing through the cone, or else secreting the distal end of the theca first.

A traumatised area, particularly in the main body of the rhabdosome, where a hole has been punched through the side of the pre-existing mesh, could be mended by the application of cortical bandages to the damaged area by the zooids from neighbouring thecae (fig 7.8.3, fig 7.7). Any obvious holes remaining in the fossilised rhabdosome are usually fairly large (fig 7.8.1), involving two or more stipes, where the injury incurred has been too much for the dendroid to mend without disrupting the normal growth pattern. The impetus is only for onward growth, and dendroids appear to have little capacity for reinstatement of growth in an area already abandoned (fig. 7.8.3, fig .7.7). This does seem to occur rarely, although it is not always completely successful (fig. 7.8.2).

3) Parasites and Disease. Conway-Morris (1981:497), suggested that tubular outgrowths of graptolites consist of thickened cortical tissue plastered on by the zooids in an attempt to contain intruding parasites. It is thought possible that the tubular outgrowths of the bithecae described above, could be the result of parasitic invasion (fig. 7.8.) The sac like outgrowths, possibly of autothecal tissue, described by Chapman and Rickards 1993 are suggested to be possibly also caused by parasites.

It is difficult to attribute observed features to disease, but it is possible that it may have caused the apparent abrupt loss of the ability to grow in a normal pattern (fig. 7.4). That this can occur to just a few stipes of one colony, suggests that only zooids in that area of the colony were effected. Where only part of a single stipe seems to have withered away (fig. 7.8.2) it is possible only that part became infected.

4) Change in conditions, external influences. The rejuvenation of the rhabdosome of *Dictyonema* was described by Bulman (1950). It is not clear if growth of the whole rhabdosome actually stops and then recommences, or if only certain stipes stop growing while others continue. Nor is it certain what the likely cause of interrupted growth may have been.

If prevailing conditions change, then it is highly likely that growth patterns would be affected. There is no certainty as to which conditions dendroids were sensitive, but various factors can be suggested. Berry and Boucot (1972) discussed this at length, and although graptolites are generally widely dispersed throughout the oceans, some planktonic forms are affected by depth of water, as could the benthonic *Dictyonema* species. Changes in both salinity and water temperature are not known to have affected graptolites, but it is possible that we are observing their effects here. It is possible that a change in temperature, or shortage in food, would cause a dendroid to temporarily cease growth, and to regrow again on reinstatement of original conditions. In a rough environment, inevitable damage would follow a temporary halt in growth, not seen in calm conditions. Short term changes such as damage caused by storms could contribute to irregular growth patterns, as could the presence of some impediment to growth such as another dendroid growing close by, or temporarily turgid water conditions such as caused by the fall of a volcanic ash (many graptolite bearing beds are associated with bentonite horizons (Batchelor and Weir 1988)) leaving the water column unsuitable for the filter feeding of the zooids for some time. If changes in conditions are considered as causes of cessation of growth, such changes would have to be fairly major and universal, in order to affect so much of the dendroid colony.

Regular bifurcation is one of the few ways that an expanding cone consisting of longitudinal rods of constant diameter and constant spacing, can grow. Zones of bifurcation may be triggered by seasonal fluctuations in external conditions, such as a new spurt of growth in the spring after a relatively dormant winter period. Rough calculations of the life span of fossilised colonies can be based on estimates of growth rates of pterobranchs (Rigby and Dilly 1994), and result in estimates of ages in years approximately consistent with the number of zones of bifurcation present. The application of such growth rate calculations to dendroids relies on making a great deal of assumptions, and further work on the associations between pterobranchs and dendroids would be necessary before these calculations can be confirmed.

5) Preservation. Growth abnormalities can usually be distinguished from preservational breakage. Post-mortem damage and displacement of the rhabdosome on deposition were mentioned by Bulman (1950:352) as a possible cause of the distorted structures observed at the margins of dendroid rhabdosomes. This is commonly observed, and where damage has occurred during the deposition process, it usually forms a recognisable pattern. Whole sections of stipe are displaced, en-masse, so that all of the affected stipes take up the same angle of curvature or the mesh is visibly stretched, and the stipes are either superimposed on other stipes, or the distance between stipes is reduced or increased (fig 7.8.2). This is shown well for a specimen of *Palaeodictyota* (also from the Pentland Hills) in fig. 2, pl. 20.

Bull, 1987. Stipes are unlikely to have remained in positions involving in a great deal of torsion in life, the elasticity of the rhabdosome returning the stipes to their stable position.

7.7 Comparison with other groups.

A number of other authors have discussed the biological implications of studying fossil abnormalities for other faunal groups. Fossil abnormalities are considered as possible indicators of pathways to evolutionary change (Gould, 1980:127).

It has been established that trilobite abnormalities provide important data on the biology of an extinct group and should not be overlooked as mere curiosities (Owen 1985:270). The abundance of such abnormalities has been used in the study of trilobite palaeoecology, providing indicators of selection pressures operating at the time, and direct evidence of aspects of trophic structure (Owen 1985:270). Unlike dendroids however, trilobite growth involved regular ecdysis. High mortality rates were associated with the moulting process as trilobites had a very vulnerable period prior to mineralizing of the exoskeleton, consequently many trilobite injuries are associated with this period and include damage caused by the actual moulting process. Similarly, most trilobites were capable of enrollment to protect themselves, and were able to move away. These factors make application of conclusions drawn from trilobite abnormality patterns, not directly comparable with dendroid designs.

Following injury to trilobites, it is thought that their survival was promoted by some degree of healing, expressed by exoskeleton thickening and callus formation (Owen 1983; 1985). Other faunal groups developed their own response to injury. Particularly well known is the ability of crinoids and starfish to regenerate following the loss of arms or even part of the calyx. Also, bivalves and brachiopods with disruption to their normal shell ridge patterns are known. These are all individual animals, and whilst the biological implications of their abnormal features are important, they are not immediately comparable to colonial animals such as dendroids.

A thorough review of fossil Parasitology is given by Conway-Morris (1981), wherein it is clear that the fossilised remains of animals with relatively robust and solid skeletons or exoskeletons, are more likely to preserve the remains of parasitic insects and related borings, galls or tumours. The effects of parasitism at ultrastructural level on graptolites is discussed, but a great deal more evidence is required before graptolite parasitic relationships can be identified fully, and fitted in to evolutionary models.

The effects of disease upon animals now preserved as fossils, has been studied for many years, particularly with respect to human remains. Palaeopathology remains of interest to those studying the evolution of current diseases. In a major work by Moodie (1923) it is noted that 'disease is apparently one of the manifestations of life'. He also noted that not much leaves traces in 'bones'; diseases affect individuals and not the whole race; and diseases can become extinct as well as animal species. He also suggested that early faunas were disease free, and parasitism did not appear until the Devonian period. However, Conway-Morris (1981) gives evidence of parasites from the Cambrian, but comments that the low level of diseases and parasite interaction recorded in these early metazoan faunas seems to be a feature of the relatively simple ecosystems of the Precambrian and early Palaeozoic.

It is difficult in fossil material to differentiate between the effects of change in external conditions and the effects of disease. If every fossil specimen above or below a certain horizon is affected, then a change in external conditions should be suspected. Moodie (1923:31) suggested that an increase of salinity would result in shell thickening, and diminutisation could be caused by crowding, or a change in chemistry such as a decrease in the oxygen content of the water. This does not account for long lived specimens having to cope with rapid fluctuations in conditions. In this study, more than 50 specimens have been considered, from a number of horizons. However even given this large population, no overall trend is seen. Each specimen has a different range of 'aberrant' features. Therefore it is difficult to imagine that any one disease or change in conditions was responsible for all of these aberrant features.

Urbanek (1973:462) described regrowth of monograptids after fracture. He noted that the resultant pattern depends upon the sicula. If the sicula was present in the regrowth fragment, then the growth pattern returns to the juvenile form, if the sicula is not present the regrowth is in the adult form. This is consistent with the pattern observed for dendroids, with the sicula present, the juvenile pattern is returned to (fig. 7.1). Urbanek (1990:336) discussed the viability of the 'regenerative morphoses', which although he was describing planktonic forms, his comments are relevant to the regeneration of dendroids as he suggests that although the regenerated forms were viable, they were, in the normal environment, inferior compared with their parent colonies. Their survival would be constrained by imperfect hydrodynamic stability, feeding depression as a result of the presence of less zooids, and as a direct result of the injury.

The study and comparison of dendroids with their nearest living relatives, the pterobranchs, is as yet in its infancy. Living pterobranchs, although secreting their skeleton from the same material and in a homologous manner to graptolites and dendroids (Rigby 1994), have not yet been described with a strongly ordered growth pattern. The zooids of *Cephalodiscus* can certainly recolonise old tubes, and to some extent mend them. They can either work on (or feed from) many different tubes at one time or all from one tube at the same time. They seem to cooperate to expand the colony into the available space, growing tubes with seemingly no preferred polarity (Rigby & Dilly 1994). The zooids of *Rhabdopleura* generate the material of their own aperture, and if damaged can repair what is within their reach, either from inside or outside of the tube (Dilly 1986). Successive generations of zooid secrete each tube to a precise pattern, and each tube is completed to (and possibly maintained to) a precisely predetermined overall size and shape (Rigby 1994).

Therefore, by comparison it is reasonable to suggest that dendroid zooids were to some extent able to mend their rhabdosome, and this could have been done without formation of calluses for small areas of damage. Some areas of damage may have been out of the range of the zooids. It seems that, unlike pterobranchs however, dendroids were not able to easily reverse the polarity of their growth, and do not seem to have been readily able to regenerate stipe growth in a proximal direction. This may have some bearing on our understanding of whether zooids were concentrated at the outer margin of the cone or whether most of the thecae were occupied at any one time. More information on this will require more detailed work on the dendroid/pterobranch relationships.

One colonial group of animals with known modern and fossil representatives is the bryozoans. The effect of damage, and regrowth capabilities of this group has been studied. This information may give us clues to the response of colonial animals generally to damage, and potentially lead us to models of environmental pressures acting on colonial animals. A few of the observations made about bryozoans are relevant to dendroid abnormalities even though during growth, bryozoan colonies have more complex and more commonly changing colony morphology than the dendroids.

If living bryozoans are intentionally broken they are able to continue growing, and partially to repair the damage (Lutaud 1983:122). The resultant structures depend upon the original degree of damage, but the overall tendency is to cover up any weaknesses and resume the normal growth patterns as soon as possible; it is more usual to leave a much enlarged fenestrule than to effect a perfect repair. Maintenance of physiological continuity by providing intramural links between living zooids, despite mortality of intervening zooids, seems to be a most important factor to the bryozoans (Taylor 1988:541). The same factors probably controlled dendroid regrowth in similar conditions. Like modern pterobranchs, bryozoan zooids can extend the colony with either polarity. Similarly, bryozoan reparative buds clearly can occupy the same sites as the damaged zooids and completely overgrow the original structure (Taylor 1988:541), whereas dendroid growth patterns seem to have been less flexible, with large holes in the rhabdosome being sealed less efficiently.

Clearly as more information from all fossil groups becomes available, fossil abnormalities and their causes and implications have the potential to yield valuable evolutionary, palaeobiological, palaeoecological and palaeoenvironmental information. Study of abnormalities, has implications for workers in other fossil groups, particularly if different fossils with abnormalities were to be discovered in the same sedimentary horizons. Where similar abnormalities occur in other fossil groups, conclusions drawn for one fossil group should be considered for their implications to others.

7.8 Conclusions.

The dendroids figured here and the others described from the Pentland Hills (Bull, 1987), are generally slender forms. They had well developed holdfasts and were able to withstand the effects of some currents, probably requiring the presence of constant current action to bring regular food supplies. The eleven species of dendroid and six graptoloids (Bull and Loydell 1994) preserved, probably co-existed in the same environment, which appears to have suited dendroids particularly well (Bull, 1991). These dendroid specimens have not been transported far or damaged badly on deposition, which is why so many of the growth features of the species can be described.

The mode of preservation and amount of detail remaining, can give much information about the environment of deposition. The conditions the time of deposition of the North Esk Inlier must have been subject to frequent changes, possibly a relatively shallow environment with strong sediment laden currents and frequent storms. Spinosity, large overall size with slender stipes and the ability to withstand injury may be adaptations that allowed this species to survive with an attached mode of life in a harsh environment.

The bulbous, spinose nature of the autothecae of *Dictyonema pentlandica* may have been a form of protection for the zooids. Slender stipes possibly facilitated efficient current deflection through the mesh. Spines may have enhanced zooid feeding strategies, protected zooids from predation, or further directed water currents through the cone.

Each dendroid rhabdosome housed zooids for some time, which secreted the meshwork in a very regular pattern according to a genetic code. It was subject both to mutations, and ever changing and probably often quite harsh external conditions. Consequently fossilised rhabdosomes are rarely perfect (and this fact should not be ignored). For convenience and for clarity of identification, particularly for descriptions of new species, only the most characteristic areas are usually mentioned in systematic descriptions. Descriptions of abnormalities can be used in analysis of palaeoenvironment, palaeobiology and palaeoecology.

Dendroids could rejuvenate after a cessation of growth, probably caused by change in external conditions. They could also regenerate after traumatisation, including injuries caused by predation, natural abrasion, or disease.

Dendroids could repair damage to the rhabdosome, the nature of the repair being dependent on where the injury had taken place. Following injury at the periphery of the rhabdosome the characteristic pattern of growth for each species was returned to as soon as possible, although some stipes may have been too greatly affected to return to the standard pattern. Dendroids appear to have been able, to a limited extent, to patch up holes punched through the side of the rhabdosome. They do not seem to have been able to repair growth in a mature area opened up by damage, such as the sides of a major split in the mesh.

Aberrant growth structures are also observed on a more microscopic scale, tubular outgrowths, probably of the bithecae, could be the result of parasite invasion.

Further comparison of dendroids with modern pterobranchs and other colonial animals, studying their mode of generation and secretion of the normal rhabdosome and their response to environment, trauma, mechanical damage, predation, disease and other changes, may lead to a more complete understanding of the generation of the normal and abnormal features observed for dendroids. Each of the variations from the norm that is observed, can tell us something of the life history of each individual specimen and by implication the environment in which the animal lived.

Chapter 8

8.1 Benthic graptolites

How did the benthic graptolites live? (Bull, 1991).

Through the early years of research, prior to the middle of the Nineteenth Century, graptolites other than dendroids had become well documented and understood, while the branched or shrub like forms (hence dendroid) were being variously described as mosses (Von Brommell, 1727), plants (Hisinger, 1837), corals (Eichwald, 1842), algae (Goeppert, 1859) and Bryozoans (Salter, 1866). The first major statement about the zoological affinities of the dendroids was given by Hall (1865) in his classic memoir of American graptolites. Earlier, Hall (1852) had suggested that dendroids were closely allied to the graptolites, and in 1865 they were formally classified together. He also suggested that dendroids may have had a different mode of life from the "free-floating bodies" proposed for the rest of the graptolites and implied that "dendroid or tree-like" graptolites, were attached to the sea floor.

It wasn't until 1872 that the *Dendroidea* (or colloquially, dendroid) graptolites were recognised as a separate order (Nicholson, 1872). It was not until Gerard Holm (1890) and Carl Wiman (1895) pioneered isolation techniques, that dendroid graptolite thecal structures and their various possible functions could be elucidated. It was another fifty years or so, before there was any further major development in our understanding of dendroids, when Roman Kozlowski (1949) was at last able to publish his major monograph on an amazing Tremadoc graptolite fauna from the Holy Cross Mountains in Southern Poland. Extensive North American and Czechoslovakian dendroid faunas were described by Rudolf Ruedemann (1947) and Bedrich Boucek (1957) respectively. For a while, little more work was done on the dendroids and only recently have more papers started to appear.

Dendroid specimens are not common locally; even on a worldwide scale there are only a few prolific localities, but the fascinating nature of the fossils more than compensates for the extra effort required in locating them. Few specimens are well preserved and few species can be traced and correlated between even nearby localities. Compared with graptoloids, the dendroids appear to be geographically restricted, which accords with the proposed sessile, benthic mode of life.

Dendroids were present in the benthos from the Middle Cambrian to the Upper Carboniferous. The time ranges of individual dendroid genera are generally also extremely long, most ranging through both the Ordovician and Silurian and some (*Dictyonema* and *Callograptus*) existing from the Upper Cambrian to the Upper Carboniferous. Some of this apparent longevity may be an artifact resulting from our lack of detailed knowledge of their morphology. As other graptolites did not appear in abundance until the Arenig and had waned considerably by late Silurian -Devonian times, it appears that dendroids were both ancestral to, and outlived other members of the Class. Dendroids reached a peak of complexity during the Silurian with the *Acanthograptidae*, which are composed of many long thecae twisting around each other, forming stipes that branch and rejoin (anastomose) in complex patterns.

The secret of the success of dendroids seem to have been their adaptability. Some species seem to have been able to tolerate local changes in environment, and some were apparently able to recommence growth after a pause in growth or damage. The debate about evolutionary paths between dendroids and graptoloids is discussed elsewhere (Fortey *et al.* 1991). Dendroids are apparently the most complex of all graptolites. They are certainly very rewarding specimens to collect and study. The overall rhabdosome form and stipe morphology is generally clearly visible with the naked eye and much enhanced by immersion in a thin layer of alcohol. Many specimens may however show an interesting history of burial disruption. Flattened forms, that were originally three-dimensional, can still show a spectacular range of detail. Increased detail can be seen using a microscope, but again internal thecal structures can rarely be seen until exceptionally well preserved material is suitably prepared (Strachan *et al.* 1991). It is on thecal structure and the arrangement or grouping of the thecae, that the most reliable dendroid classification is based. As very few specimens are well enough preserved to reveal details of their thecae, the vast majority of dendroid taxonomy is based on details of external morphology that can be observed and measured from flattened specimens. Consequently much of the classification is still at a fairly crude level of taxonomic resolution, and further refinement will require better preserved material.

Dendroids consist entirely of thecae which twist and curve round each other to form the stipes of the framework of each rhabdosome. It is thought that dendroid colonies grew by adding more and more thecae to the distal periphery of the existing rhabdosome, so that almost every part is made up from thecae. The general mode of skeletal secretion was evidently the same as in the graptoloids. It is thought herein, that each theca housed a zooid which not only constructed the fuselli of the thecae but were also able to strengthen and mend their framework. They were perhaps even able to fasten it more securely to whatever it was attached, by plastering cortical bandages over the surface.

The thecae of dendroids are small compared with those of the graptoloids. Each rhabdosome is composed of thecae of two distinct types, the relatively large autothecae possibly housing female zooids, and the shorter, thinner and generally inconspicuous bithecae, possibly housing the male zooids. These are generally arranged in regular order into stipes, which branch and are linked into the patterns characteristic to each species. This is described more fully elsewhere (Chapter. 9). The bithecae in one rather enigmatic family the Anisograptidae seem to suggest it occupied an intermediate position between the dendroids and the graptoloids. The anisograptids had only a small number of primary branches and their bithecae either grew into and terminated within the autothecae, or were reduced in number and gradually, species by species, disappeared. Thecal structure and the mutual arrangement of the thecae varies between families. Generally dendroid thecae are relatively simple, thin, uniform tubes adapting to the shape of the stipe, unlike graptoloid thecae which are usually repetitions of the same shape, and control the shape of the stipe. Dendroid thecal apertures are, however, very similar throughout a colony, are regularly spaced, and are often denticulate. In both Dendrograptidae and Anisograptidae families, thecae are short and remain in constant contact with the stipe (adnate), reaching to just at, or past, the bud of the next generation of thecae so that stipes consists of only one generation of thecae at any one time. In some genera of *Acanthograptidae* and *Ptilograptidae*, occasionally some thecae may stand off as simple tubes to the side of the main stipe, either as an individual twigs, or as branches. These may gradually thin to twigs and further down to a single theca. In these two families the thecae can be greatly elongated, reaching up to centimetres in length, with many generations overlapping and entwined forming thick branches from many thin thecae.

Bithecal apertures are mostly simple, seen as openings in the side of the stipe, occasionally facing *into* the autothecal tube. Autothecal apertures are usually simple openings at the end of the theca, but the aperture can be accompanied by a swelling of the tube, a spine or an awn (protective shield). All of the apertures are orientated in one direction, which in conical forms is also towards the inside of the cone. Rocks containing fossil dendroid specimens usually seems to cleave along the dorsal or anti-apertural side. It is therefore possible, to have beautifully preserved and intact specimens, that are too delicate to isolate, but which may be equipped with ferocious apertural spines about which we may have no information as all of the apertures point into the matrix of the rock. Only if isolated material is available, or specimens are preserved with their stipes either torn or twisted on deposition, showing the lateral or profile view, can clear details of the thecal structure can be seen.

Given the extreme variations in composition of dendroid stipes, it is remarkable how constant certain dimensions are for each species. The number of thecae per stipe remains constant and because thecal diameter is constant throughout the rhabdosome, then so is stipe width, stipe spacing and angles of branching. The exception to this is when the stipes were secondarily thickened for strength at the proximal end. So, in order for the cone to expand some sort of branching must have taken place, particularly for conical forms which grew by adding more thecae to the peripheral margin of the rhabdosome.

When one main stipe divided, it either bifurcated and formed two new main stipes, or a lateral second order branch formed at an angle to the continuation of the main stipe (lateral branching). For rigidly ordered genera with parallel straight stipes such as *Dictyonema*, the formation of new stipes was usually the result of *bifurcation*, often in recognisable zones an ordered distance from the apex of the rhabdosome. Bifurcation is common to most dendroids. The formation of new stipes does not mean the demise of existing stipes; it was only the expansion of an existing stipe by the splitting of the stolon system. At a stolon node two stolons were produced which went on to produce another node each; one autotheca was produced; but the bitheca was suppressed. Less common are lateral branches, which are a feature of some of the less geometrically arranged genera. These lateral stipes generally caused no diminishing of the existing stipe but often rapidly terminated themselves (*Thallograptus*). The nature of the stipes of each species remained constant, but there was a remarkable variety of shapes of stipe between species, from straight unornamented linear structures (*Callograptus*) to twisted uneven stipes, thinning to lateral branches and twigs (*Acanthograptus*). The re-connection of stipes is observed only for the two families *Dendrograptidae* and *Acanthograptidae* : stipes of the *Anisograptidae* and the *Ptilograptidae* did not reunite. Stipe connection was achieved by one of two methods: anastomosis, or the formation of dissepiments. Anastomosis was the simple process of the merging of two curving stipes at the point where their paths coincided, with the thecae entwining, forming one stipe.

Dissepiments resemble straps, reaching perpendicular to the stipes, bridging the shortest possible distance between two neighbours, and holding them firmly in place. Dissepiments were possibly biologically associated with the bithecae and all that remains are thin tubes of cortical tissue, of constant width and spaced at fairly constant distances for each species. The stipes and dissepiments form four-sided *fenestellae* (holes in the mesh) often of a constant size and shape. Dissepiments should not be confused with autothecal apertural spines which were generally much thinner and were not involved in the process of joining two stipes together. The size of the dissepiment was characteristic to each species and a whole range of sizes existed. Some species had dissepiments that are so very fine they resemble hairs e.g. *Callograptus*. Others, particularly some of the robust species of *Dictyonema* had greatly thickened dissepiments. Unlike anastomosis it is almost impossible to identify the direction of dissepiment growth, even following aberrant growth of one stipe, the next dissepiment will usually have been formed at near normal spacing, without evidence of having grown from one stipe to the other.

Dendroids come in many shapes and sizes. The overall adult rhabdosome size varies from less than one, up to fifty centimetres in axial length. The great range of rhabdosome shapes was based on three distinct patterns, which were themselves controlled by the thecal and branching patterns of each species. *Tree* or *shrub* like forms resulted from freely branched and loosely connected stipes. *Fan* shaped rhabdosomes resulted from slightly more regular arrangements of stipes and forms that were more sparsely branched. The most rigidly regimented species formed *conical* or *funnel* shaped rhabdosomes. The extremes of this case were *disc* shaped, usually arising from a specimen having been squashed into the sediment perpendicular to its axis, its conical form flattened into a disc, although a few species grew in this form originally. In some cases, only one side of a conical form is preserved giving the misleading impression of a fan-like shape.

Fossil dendroids display a great range of stipe thickness, from very robust to slender and delicate. Increases in robustness were due to a number of factors, that in some cases were species specific, such as; increase in thecal size; increases in the number of constituent thecae per stipe; and increases in secondary tissue, particularly cortical tissue around dissepiments, or around the stem and holdfasts. The presence of *extrathecal epithelium* (unfossilised soft tissue surrounding the stipes), if present, may have had some bearing on the strength of the rhabdosome, or the ability of the zooids to direct currents through the mesh. If the sessile dendroid colony could only ensure a regular food supply by positioning itself in a current, then it would have needed to be fairly robust to withstand the buffeting that accompanied such an existence.

Associated with the strength of the whole rhabdosome is the firmness of the basal structure or holdfast. Most benthic dendroids seem to have been attached to something, but since holdfasts and attachment objects are rarely preserved we know relatively little about this important aspect of dendroid growth and form. The majority of dendroid species were benthic and a variety of different holdfast structures were evolved to safely secure the rhabdosomes to the sea floor. Holdfasts do not seem to have been specific to substrate type as one species can exhibit more than one type of holdfast in the same bed. Some forms had simple discs accompanied by either all of the proximal thecae fused into a basal plate, or the stipes forming a stem with the sicula expanding at its base to form the attachment disc. Some species had attachment fibres, that probably spread out across the sediment surface. Other forms had attachment discs wrapped around solid objects such as pebbles. Some colonised and coexisted with other animals such as brachiopods which were themselves secured to the sea floor. So it would seem that larval dendroids, like the majority of living epibenthic invertebrates, had little or no ability to select the sites for their attachment, leading inevitably to some choosing insecure objects with the result that both dendroid and host were washed away.

One difference of dendroids from the graptoloids is that groups of dendroids did not appear to share the same basal attachment structure, although one synrhabdosome of a planktonic *Rhabdinopora* has been described. Whether this implies an ability to have actively inhibited the settlement of larvae of other dendroids on the same site is not known. It seems that one dendroid could from one stem, support a number of separate stocks of individual conical growths (*Thallograptus inaequalis*), although this mode of growth is unusual.

It is tempting to equate very robust small specimens with energetic palaeo-environments. A specimen with the combination of a robust rhabdosome and a substantial holdfast structure (or a delicate rhabdosome with a minimal basal structure), could lead us towards tentative conclusions about the turbulence or tranquillity of the environment that these animals colonised. However, the relationship between robustness and energy of environment is probably not that simple. Both robust and delicate species are often found in the same beds and delicate specimens are often accompanied by very substantial holdfast structures (and vice-versa). It is possible that other factors such as the soft parts of dendroids affected their ability to survive in a particular environment. At present little is known about the microniches occupied by dendroids.

8.2 Faunal Provinces.

"Faunal evidence has the advantage that is is independent of the data base for geophysics and tectonics: good faunas can be collected from small outcrops which are structurally enigmatic, and faunas can be similar over distances through which tectonic styles may change with bewildering frequency. Faunal evidence can be gathered separately from that of other geological sub-disciplines, except that of sedimentology with which it is inextricably involved. It can be used as a check on continental distributions derived from other evidence - and if there are anomalies they deserve further examination."

"That faunas are not everywhere identical at one time is a self evident proposition, and yet, when interpreting ancient rocks, conclusions have often wrongly been drawn by the comparison of like with unlike." Cocks and Fortey (1982 : 465).

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8.2.1. Introduction

The aim of this section is to discuss the nature of oceanic faunal provinces and to outline the latest models of the controls on distribution of faunas, and in particular graptolite faunas in the oceans of the Ordovician and Silurian. The distribution of graptolite faunas within the depth related sediments of the NEI is considered as a control model for testing the depth distribution models of the late Llandovery. The contribution and implications of the graptolite fauna preserved in the NEI to our understanding of faunal provinces is considered.

The development of oceanic faunal provinces as a result of separation of faunas by barriers to true pandemic distribution, such as temperature (Skevington, 1973; 1974; Watkins and Berry 1977), palaeolatitude, palaeocurrent dispersal (Wilde *et al.* 1991), palaeoclimate (Erdtmann 1976) and palaeogeography (Cocks and Fortey 1982), has been discussed at length in the literature (see papers in McKerrow and Scotese 1990). We are only concerned here with graptolite biogeography and faunal provinces.

During the Ordovician, the distribution and relative abundance of many species of graptolite was not uniform throughout the world (Cooper *et al.* 1991:199). Berry and Wilde (1990:134) suggested that there was a general rise in sea level at the beginning of the Llandovery. This means that existing Ordovician provincialism would have been diluted in the early Silurian and much of the of the oxygen poor, nitrogen-rich environment that graptolites seemed to prefer (Berry *et al.* 1987) was lost. There were only a few graptolitic survivors of the end Ordovician near-extinction. Berry and Wilde also noted (1990:134) that early Silurian provincialism is not easily recognised. The early Llandovery is characterised by many endemic taxa, suggesting that the major graptolitic successions were physically separated from one another (see Cooper *et al.* (1991:199) for an extensive list of papers on the extent, composition, and possible causes of graptolite provinciality).

The controls on graptolite distribution were no doubt similar to those of modern zooplankton, and Rickards *et al.* (1990:141) give a review of the complicated and diverse controls on distribution of modern zooplankton. These are primarily temperature, salinity, density, turbidity, ocean chemistry, productivity, and other living organisms. These are

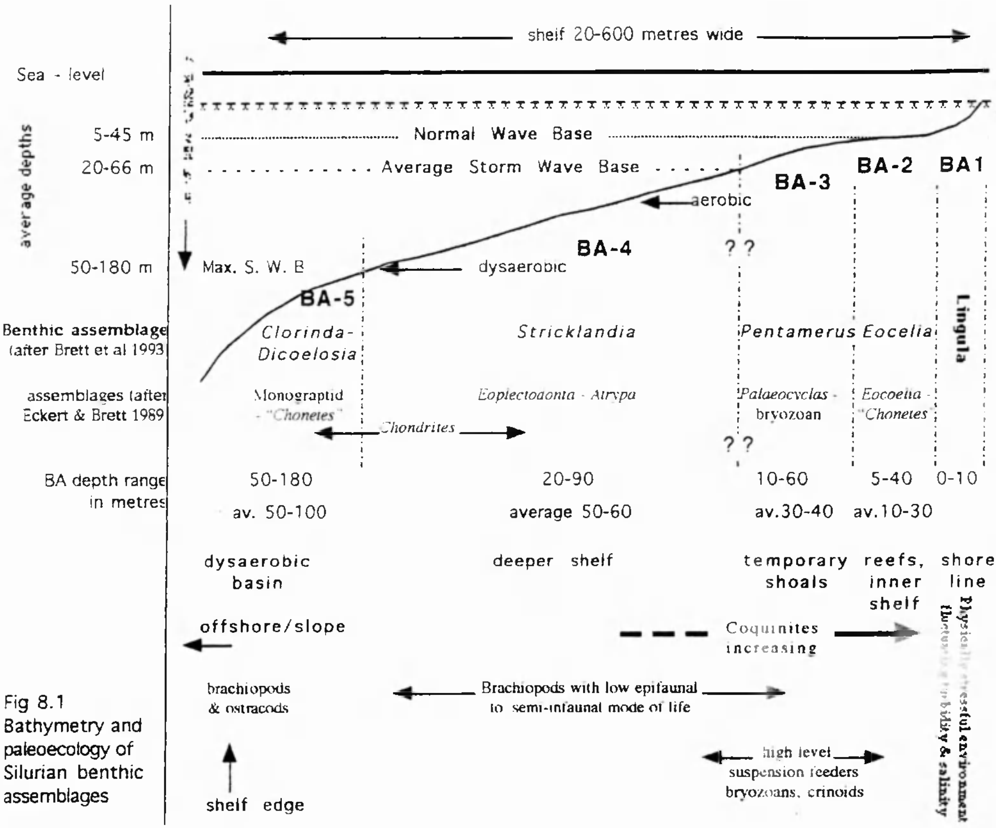


Fig 8.1
Bathymetry and paleoecology of Silurian benthic assemblages

themselves affected by depth, latitude and geography, resulting in the creation of water masses with a unique set of conditions. Water masses themselves can be moved (by currents), retaining their individual characteristics up to thousands of kilometres from source. Some particular species may be limited specifically by depth, latitude, or water mass, whereas others may not be so strictly restricted.

A faunal province can now be defined and identified only from the fossil records of those taxa which originally lived within it. Recognition of a faunal province requires data from many contemporaneous localities, but not all of the living elements from a particular environment, water column or biofacies will necessarily be preserved. Erdtmann (1976) reviewed the controls on provincialism and in particular (Erdtmann 1976:625) noted that existing models of provincialism may be founded partially on unrecognised synonymies. "It may appear preposterous to admit this, but even today there can often be little confidence in the exact definitions, priorities and mutual acceptance of many species from geographically distant localities... [because of] misunderstandings regarding taxonomic judgments" (unfortunately almost as true in 1995 as it was in 1976). Rickards *et al.* (1990) noted that similar morphologies frequently evolved in different lineages, and these morphotypes may have been adapted to occupy particular niches. Berry and Wilde 1990, in discussing environments such as present day deserts, noted that there may be morphological similarities between forms in separated but similar, ecologically challenging environments, that because of a history of physical separation, may be phylogenetically distinct. This stresses the importance of phylogenetically accurate taxonomy.

Recognition of a graptolite faunal province derives from plotting records of "identified" taxa on palaeogeographic constructions, and as noted by Rickards *et al.* (1990:139) these palaeogeographic maps are constantly being updated. The most recently published is not necessarily "correct", hence models of faunal provinces are constantly being modified. Conclusions drawn, for example from comparison of supposed equatorial localities by Watkins and Berry (1977), and models constructed from these results, may well now need revision in the light of more recent palaeogeographical interpretations.

Rickards *et al.* (1990:140) were able to identify a Wenlockian, Rheic (neritic) Subprovince. Future work on currently unresearched Wenlock graptolite faunas, may prove that this Subprovince was more extensive. The late Llandovery graptolite faunas described here may prove to have been an earlier part of this province. There are few British localities where a fauna of the same age as the North Esk Group has been proved, so it will be difficult to reconstruct such a province. However, the Bohemian species *Mcl. geinitzi* and *M. parapriodon*, and dendroid species, have been found in the NEI, and the Bohemian biostratigraphic scheme has been introduced (Chapter 3), and the identification of *Oktavites excentricus* (Bjerreskov 1975) from the NEI (a Baltic form), suggests that these may have inhabited one province that would later become part of the Wenlockian Rheic (neritic) Subprovince (Rickards *et al.* 1990:140).

Attempting to construct graptolite faunal province models for the late Llandovery is possibly premature as not enough information is yet available. There are very few localities in the world where the range of late Telychian biozones have been proved, or updated in the light of recently revised biozonal schemes (see Chapter 3.) Most localities where there is a record of "graptolites indicative of a *crenulata* biozone age" are herein considered worthy of revision. Relevant details as obtained from NEI graptolites are presented here, and it is hoped that as more information becomes available, the graptolite provincialism of the late Llandovery will become clearer.

Rickards *et al.* (1990) noted that dendroids are as yet of no value as indicators of faunal provinces as they are too sporadically preserved, and there is a "monographic bias". As truly benthic animals, details of their occurrences can be considered as part of any depth related association or community, and may add more evidence to palaeobathymetric models (see section 8.2.4.1).

Initial assumptions about graptolites being pandemic, and hence useful for global biostratigraphic correlation have become compromised. More and more papers have been published on graptolite provinciality, water mass specificity, and other factors that described graptolite faunas as restricted, endemic and separated. In this respect the recent synthesis of Cooper *et al.* (1991) is welcomed, whilst they admit some provinciality and some endemicity in their model, they generally record Ordovician pandemicity and very little latitudinal zonation.

In section 8.2.4.4, a comparison of the NEI graptolite fauna with the depth related model is given, and anomalies are discussed in terms of the depositional basin and tectonic situation at the time of deposition. More graptolite bearing, shelf to offshore sedimentary sequences, (regressions and transgression) sections considered in terms of graptolite assemblages, the study of dendroids, where present, with the intention of inclusion in BA- models can only enhance the models of Palaeozoic shelf successions and the anatomy of the continental margins during the Ordovician and Silurian.

8.2.2 Preservation

Any fossil assemblage of planktonic forms, potentially represents a mixture of all living organisms in the water column above at the time of deposition, a taphocoenoses. Erdtmann (1976:626) notes that it is difficult to discern vertically superimposed biocoenoses (or "biotopes" to use the terminology of Cooper *et al.* 1991:200) from such fossil assemblages.

In the same way as today's oceans are subdivided into water masses with relatively unique hydrographic characteristics, inhabited by distinctive planktonic associations (Berry 1977:1106), each region of the oceans of the past was presumably also unique. In consequence the fossils preserved on each bedding surface chart the unique set of conditions based on the actual fauna present in the water column. It must be borne in mind that this would be affected and a distorted picture presented, by the possibility of graptolite blooms (Cisne and Chandlee 1982), of the fauna moving to and fro across the site of deposition with season or climate (Cooper *et al.* 1993: 201), or of the potential for mass graptolite mortality perhaps resulting from overturn or upwelling of anoxic water during storms (Eckert and Brett 1989).

In high-energy shallow water environments graptolites are normally imagined to be broken up beyond recognition before deposition (Erdtmann 1976:629), and increased sediment input in such conditions would in any case dilute apparent specimen densities. Kaljo (1978) found that fewer graptolites were indeed preserved in shallower water, but thought that only a little selective destruction of the more fragile forms would be expected, suggesting that the graptolites lived predominantly at mesopelagic depths. It is here considered that overall, graptolites were distributed evenly through the water column, but in separate niches. This model and the depth associations of Kaljo (1978) are discussed later.

Some authors have suggested that throughout the oceans, graptolites were restricted to the euphotic zone (Erdtmann 1976:629; Bulman 1964). Whereas not all authors agree to what depth that zone extends (Brett *et al.* 1993), it is generally accepted that it would be slightly deeper in clearer mid-ocean water. It is more commonly believed at the present time however, that graptolites were not totally restricted to the epipelagic zone, but extended down into the meso- and possibly the bathypelagic depths (Cooper *et al.* 1991). There would have been some lateral selectivity parallel to the coastline, depending on such factors as temperature, salinity, or water turbidity (Erdtmann 1976).

In deeper water, "defunct rhabdosomes" were well streamlined and would have sunk rapidly (some from the shallowest water). They were also durable, relatively large food items in the water column, taking their decomposers down with them as they sank, or being decomposed and scavenged before they reached the bottom and so contributing to oxygen consumption at depth and throughout the ocean (Cisnee and Chandlee 1982). Specimens of some graptolites that had attenuated periderm, are preserved in sediments deposited in shallow water and also seem well preserved in deep water sediments (Finney 1986). This may be because it was only the zooids and soft parts that were scavenged, the hard parts remaining relatively untouched (Underwood 1993), and the periderm thickness may have had no affect on the scavenging rate. Differential destruction rates of different taxa by benthic decomposers and scavengers does not seem to have been significant (Cisnee and Chandlee 1982). Dead graptolites could have been fed on by other deep water detritus feeders (Erdtmann 1976) or disintegrated by bacteria. Many specimens are preserved pyritised; this may be the result of burial with their soft parts intact, providing a reducant for sulphate reducing bacteria (Eckert and Brett 1989).

Bathymetric differences in graptolite distribution, as with modern animals, would be most marked in the mid-waters of the ocean where fluctuations in natural position of depth restricted species will change regularly in response to small eustatic sea level changes (Cooper *et al.* 1991). Quieter, deeper water deposits are dominated by large, multiramous forms (Erdtmann 1976: 629). Graptolites living closest to the ocean floor at any particular depth, with the least distance to travel before deposition, are the most likely to be preserved and hence will dominate the assemblages preserved at that point (Cisnee and Chandlee 1982).

Our raw data for distribution models, the graptolites collected in the field, are all further affected by burial and post depositional taphonomic processes, lithification and further tectonic processes; surface weathering; and collection bias. Some of the rarer or less well preserved forms may be overlooked (Lenz and Chen 1985) in the field or destroyed by poor sample preparation techniques (Strachan *et al.* 1991).

8.2.3 Water Mass Specificity

8.2.3.1. Specific characteristics of water masses

It has long been known that oceans are usually partitioned into seemingly quite distinct water masses (Berry 1973). The distribution of faunas relative to these water masses is affected by factors that it is extremely difficult to measure in the fossil record such as, temperature, nutrient type, salinity, turbidity, coastal influence and underlying bathymetry. Rapid lateral changes in environmental factors can make neighbouring communities apparently quite distinct (Erdtmann 1976).

Organism - environment relationships are demonstrable in present day marine environments. Plankton in general tend to be less abundant off shore, as the nutrients essential to their growth, are commonly greatest near shore. Different kinds of marine organism each seem to have their optimum conditions and are found there in greatest numbers (elements of a

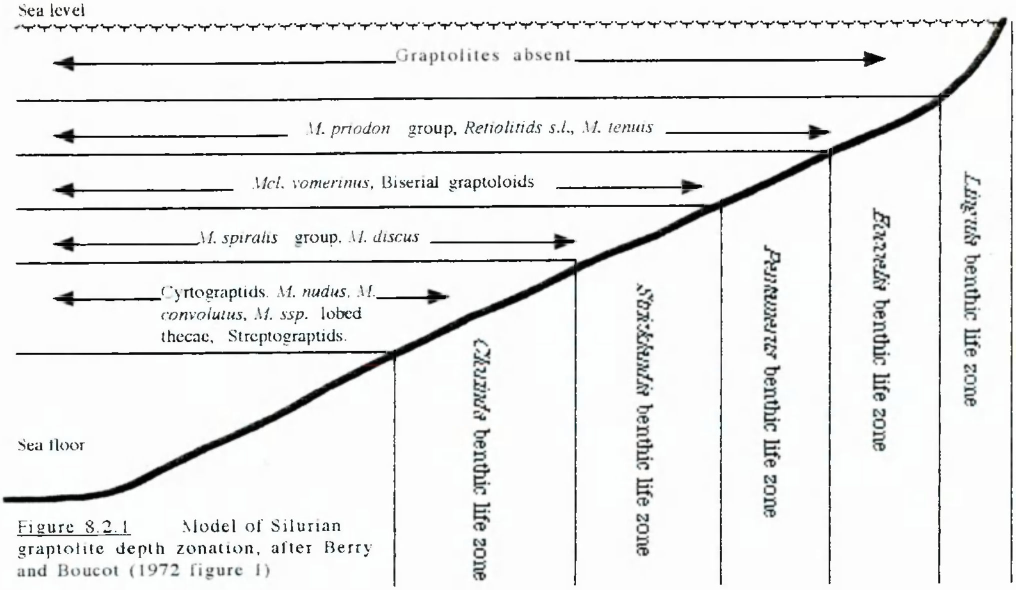


Figure 8.2.1 Model of Silurian graptolite depth zonation, after Berry and Boucot (1972 figure 1)

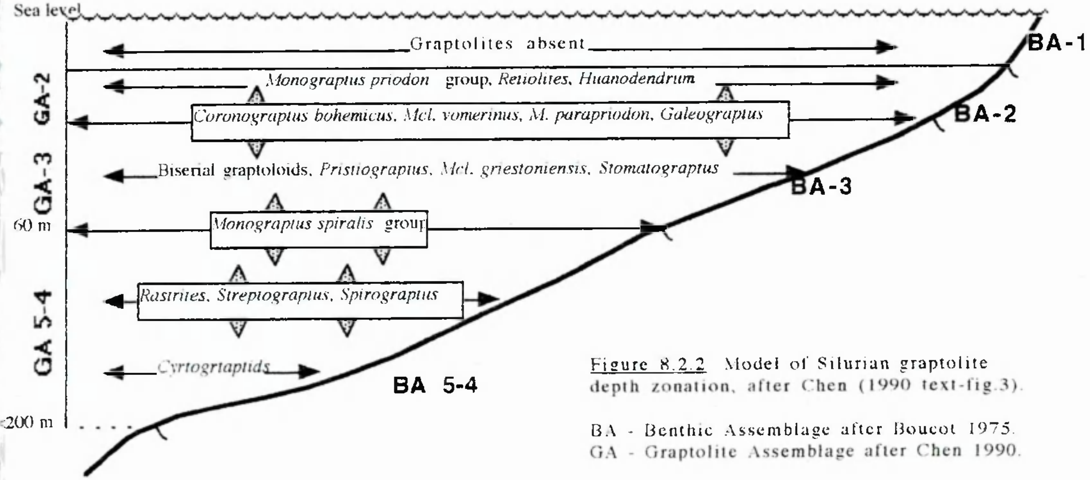


Figure 8.2.2 Model of Silurian graptolite depth zonation, after Chen (1990 text-fig.3).

BA - Benthic Assemblage after Boucot 1975.
GA - Graptolite Assemblage after Chen 1990.

community may be linked by food web), but many species are widely tolerant and not completely confined to their environmentally optimum habitat (Berry 1974:372).

Most stratigraphical work is based on presence/absence studies, and relative abundances of fossils give important environmental indicators. Appearance /disappearance of taxa, basin-wide can depend on both origination and extinction, and changes in water circulation pattern in a changing basin, forming a spatio-temporal mosaic (Cisnee and Chandlee 1982).

It is possible that some faunas were specifically adapted to situations such as a neritic environment (Cooper *et al.* 1991, Rickards *et al.* 1990 and Finney 1984). Undoubtedly some species are specific to certain current controlled water masses, indeed, each water mass may be individually depth stratified. Cool water masses can extend equator-wards at depth, extending the biotope, thereby extending the habitat of a community into deeper water (Erdtmann 1976). Other currents are known to maintain a certain depth for a great distance, then rise to the surface, bringing with them a specific community, and at each level through which it rises, the water mass specific fauna passes other depth specific faunas (Rickards *et al.* 1990). Therefore, depth related faunas, and water mass specific faunas can be found together in the oceans, and hence will be preserved together in the fossil record, .

8.2.3.2 Water Mass Specificity Model

In 1973 Berry attempted to apply depth distribution models (see section 8.2.4) that had been described for the Silurian graptoloids (Berry and Boucot 1972) to studies of Ordovician graptolite ecology. The model failed to fit the available facts, so he made a comparison with plankton distribution today. Berry (1973) discussed how in modern oceans, different plankton associations can be found in different masses of water, and that local water masses have chemical and physical characteristics unique to themselves and also unique plankton associations (water mass specificity).

In 1977 Watkins and Berry published a report on the analysis of a large sample of well preserved Ordovician material from Wales. They developed the concept of graptolite water mass specificity based on the density of specimens preserved per unit area. From this they modelled two "water masses", the "graptolitic water mass" and the "shelf water mass". The deep water "graptolitic water mass" was characterised by a high density of fossil specimens, and the shallow water "shelf water mass" was characterised by a low specimen density. Some species are common to both "deep" and "shallow" samples. From this data they described the migration of the basin northwards through time. They also suggested that like modern oceans, wherein small scale variations within water masses represent population cycles, graptolites were separated in the same way, and that the low density population of the shallow water mass was due to these not being reproducing populations.

The Watkins and Berry (1977) model is based on the assumptions: (1) that graptolites all lived in the relatively shallow water of the euphotic zone, and (2) by comparison with modern oceans wherein there is a barrier between shelf and open ocean, with some shallow water modern plankton preferring to live above deep, and some above shallow water.

According to Cooper *et al.* (1991) no marked continental boundary effect has been observed in the fossil record. Graptolites are now considered to have been able to tolerate depths possibly up to 1000 metres, hence the Watkins and Berry (1977) model is not supported here.

The strongest argument for graptolite water mass specificity, is the absence of specimens of graptolites normally abundant in shallow water taphocoenoses, in sediments preserving deep water taphocoenoses (Finney 1986). Also some species are restricted to being preserved in either shallow, or deep water taphocoenoses. There will always be anomalies known, and our lack of knowledge of graptolite soft parts creates additional problems. For example, petalolithids, which appear when fossilised to be robust graptolites, likely to have survived transport. They may in life, however, have been surrounded by a great deal of edible soft material (lots of juicy soft parts), which may have been highly desirable to predators, and hence were destroyed before reaching the ocean floor, e.g. petalolithids seem common in shallow water but rare in deep water facies (see Loydell 1993: 330).

Some species were undoubtedly specific to a certain water mass, but it is thought here that water mass specificity did not totally control graptolite distribution through the palaeozoic oceans. Kaljo (1978) suggested that there may be some species adapted to and restricted to the neritic zone. Cooper *et al.* (1993) also found some species restricted to a very inshore water mass. The case against distribution entirely dependent on water mass specificity, is given by Cooper *et al.* (1993:206). Their reasons were as follows.

-No "leakage" of oceanic forms to shelf waters, there was a distinct Ordovician deep water fauna or biotope) for 42Ma.

-During transgressions, the deep water biotope encroached on to the outer shelf.

-A large proportion of the total fauna were not restricted to the shelf, so this water mass would have little effect on distribution anyway.

-Fragile multistiped forms were poorly designed for shallow water, and were confined to the deep water biotope.

If graptolites were distributed roughly evenly throughout most of the inhabitable water column, the greater density of specimens per unit area found in deep water sediments (as detailed by Watkins and Berry 1977) would be the result of more graptolites in the water column above to be preserved. Also shallow water has different sedimentary processes and so graptolites had a different likelihood of being preserved in these sediments. Some authors reject as unsatisfactory (Loydell 1993) the model of graptolite depth stratification, and see it as a matter of accepting or rejecting either the depth stratification, or the water mass specificity model (Finney 1986:450). Herein, a combination of both the graptolite depth stratification, and water mass specificity models are acknowledged to have contributed to the fauna preserved on each bedding plane.

8.2.4.1 Palaeobathymetry

A pile of reprints and papers relevant to the subject of palaeobathymetry, stratified by date of publication, makes an interesting prospect, a fascinating glimpse at the evolution of the subject. At the bottom of the pile are two enormously important innovative texts, the foundation of it all. In the first, Ziegler (1965) discussed how lower Silurian marine communities altered with distance from the shore. The second paper (Berry and Boucot 1972) discussed "Silurian graptolite depth zonation". The first dealt with benthic assemblages, the second with planktonic. Both models have been regularly applied to studies of fossil communities elsewhere, supported and/or denied by other authors ever since.

Both the studies of water depth related planktonic assemblages and benthic palaeocommunities (also the Benthic Assemblage approach of Boucot 1975), suffer from the inability to distinguish between *in situ* and sedimentary faunal associations. However, both associations keep being identified in the fossil record, and independent analysis from different areas, keeps on fitting the models. The models have been modified somewhat over the years, and there are those who strongly disagree with them, claiming oversimplification, shortcomings in taxonomic treatments, sampling techniques and interpretations (Finney 1986), or "explained more satisfactorily" (Loydell 1993), by such things as water mass specificity. However, the models keep on being cited and supported.

The fauna fossilised will be unique at any one locality within the ocean, with a combination of factors influencing this. If graptolites migrated (Berry and Wilde 1990:130) through the water column daily, then they will not be restricted to one depth but a depth range. Similarly, currents may carry a fauna to other depths given a large enough oceanic circulation to move within. The chances of the rock record, preserving one fauna in any way intact at two completely different water depths and hence depositional environments are thin (Rickards *et al.* 1990).

Baarli (1988:585) suggested the "Strongest use of multiple palaeobathymetric indications" be employed. We should not consider each fact in isolation. For example, it would be unreliable to ascertain the depth of the water in a palaeo-ocean basin, entirely from the graptolites, information will also be available from factors such as sedimentology, and other faunal elements, e.g. corals and brachiopods. A combination of factors should always be used in preparing a palaeobathymetric model for each locality, taking each piece of evidence in context.

8.2.4.2 Benthic Assemblages

The Silurian Benthic Assemblage scheme (Boucot 1975), was originally proposed by Ziegler (1965), and there are now many papers describing fossil faunal assemblages found in the same relative shoreline position (Boucot and Lawson 1994), and of comparative "communities" and "assemblages" (Eckert and Brett 1991; Calef and Hancock, 1974).

A recent survey (Brett *et al.* 1993) summarised the absolute depth related conclusions of the multitude of previous studies (see fig 8.2.1 for a summary of their main conclusions and the main Benthic Assemblages (BA-1 to BA-5) envisaged today). They detailed various factors such as primarily sedimentary indicators, particularly storm deposit horizons (Brett 1983;

Eckert and Brett 1989). They also discussed proximality trend analysis (Baarli 1988), and geochemical and taphonomic indices, that could suggest depth, and palaeontological evidence including photic zone indicators such as reefs, endoliths, algae and animal vision.

Although certain Benthic Assemblage studies have produced slight variances in estimates of water depth (covered in the range of absolute depths and the averages given in fig 8.2.1) there is remarkable agreement between the various Benthic Assemblage models from around the world. Overall there is good agreement for the Llandovery, with an offshore progression from a nearshore BA-1 lingulid association, followed by *Eocelia, Pentamerus, Stricklandia,* and *Clorinda-Dicoelosia* "communities". All Benthic Assemblages being primarily shelf deposits and in the water depth range 0-200 m (Brett *et al.* 1993) (see fig 8.2.1).

Where a mixture of benthic and pelagic faunas are preserved, Eckert and Brett (1989:303) suggested avoiding the term "community" and using the broader and less genetic term "associations" to describe recurrent groups of fossil taxa.

The Benthic Assemblage (BA) model is primarily based on brachiopod faunas, but is constantly being updated in the light of new discoveries in different BA related fossil assemblages of photic zone indicators (Eckert and Brett 1991), or of comparable associations that are representative of the BA scheme in the absence of brachiopods, such as corals (Cocks and McKerrow 1984; Eckert and Brett 1991). It is possible that fossils of other benthic animals such as dendroids, may contribute further information to this scheme in time (see section 8.2.4.4). The implications of the presence of bioturbation in the sediments to possible water depths is discussed by Eckert and Brett (1989), who also discuss the depth implied by the presence of certain corals, particularly *Palaeocyclus*, the button coral so indicative of the latest Telychian (see Chapter 3). There is still some debate as to the position in the water column (above or below storm wave base) that the tabulate corals occupied, and the absolute depths implied by this, Eckert and Brett (1989) suggesed a depth slightly shallower (fully aerobic, above storm wave base) than Cocks and McKerrow (1984), however both largely agreed with a BA-3-4 association for these fossil corals.

Present day benthic marine communities are distributed in depth zones that are primarily temperature controlled, and within that, communities are substrate related. The presence or absence from a community of a particular organism is dependent on such factors as substrate grainsize, firmness, and chemistry, availability of cracks and crevices, food supply and water motion (Berry 1974).

Cocks and McKerrow (1984) gave a review of the composition of fossil Silurian marine benthic communities, and highlighted the importance of detailing all bathymetric indicators, before correlating between localities. They suggest that the most integrated model for each locality is prepared using all lines of evidence, before correlation with other localities, or extrapolation to larger areas. The apparent absence of a community or faunal element, must be considered in terms of the equivalence of the localities being compared, and the differences between their oceanic or specific water mass conditions.

8.2.4.3.1 Graptolite Depth Zonation

There have been numerous attempts to tie in graptolite distribution with the Benthic Assemblage, depth related models. Outlined below are details of the two distinct models of graptolite depth zonation that are described in the literature. One is characteristic of studies of Ordovician rocks, the other characteristic of Silurian studies. This may represent true differences between graptolite distribution patterns from the Ordovician to the Silurian. It may also be as a result of increased preservation and accuracy in identification of the graptolites from Silurian shelf deposits and their fauna generally, particularly as related to the Benthic Assemblage models (see section 8.2.3.2).

The two models are not mutually exclusive, the "Silurian" model can merely be viewed as a more refined subdivision of the graptolite related bathymetry than the simple "Ordovician" shallow and deep subdivision which is already considered by some authors to be a simplification (Erdtmann 1976: 629).

In homogeneous black shale sequences, typical of deep water sedimentation, zonation by depth and zonation by age generally cannot be clearly distinguished (Cisne and Chandlee 1982). In shallower water, near shore sedimentary deposits tend to be quite distinctive, making water depth correlation easier. Unity of depth zonation models, and in particular the interpretation of what constitutes "shallow" and "deep" water, is improving as models of Lower Palaeozoic benthic marine environments become better defined. It is not yet agreed what absolute depths are indicated by identifiable markers such as the shelf edge (Brett *et al.* 1993). Kaljo (1978) found few graptolites in "shallow" water. He attributed this not to destruction of the rhabdosomes in energetic environments, but suggested that graptolites mostly lived at mesospelagic, not epipelagic water depths. This interpretation depends, however, on where the shelf edge is envisaged to have been (Kaljo has it at BA-3 to BA-4 boundary), and how deep destructive wave action is thought to extend. Reinterpreting the data of Kaljo (1978) on faunal distribution across the East Baltic, in the light of more recent models of storm deposits, and the outer BA-5 positioning of the shelf edge (see fig 8.2.1), may imply that graptolites were more evenly distributed from shallow to deep in the East Baltic ocean during the Silurian.

The existing model of graptolite depth zonation should really be described as "planktonic graptolite depth zonation" as dendroids have not yet been considered in this context, although Eckert and Brett (1989) recorded some dendroids and monograptids in their *Palaeocyclus* - Bryozoan association of the Willowvale Shale of New York, and the information concentrated in certain dendroid localities was discussed by Rickards *et al.* (1990). In section 8.2.4.6, possible benthic forms that can be considered in this way are discussed.

Better details of graptolite depth zonation models will be available as more information emerges about the ecology of the group. Understanding of the degree of automobility of the graptoloids, their ability to migrate up and down through the water column in search of food, or their ability to maintain their position in the water column, obviously have

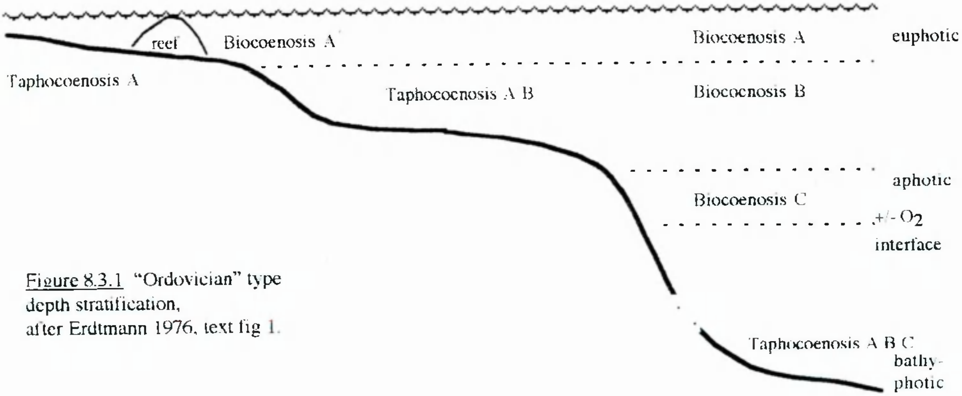


Figure 8.3.1 "Ordovician" type depth stratification, after Erdtmann 1976, text fig 1.

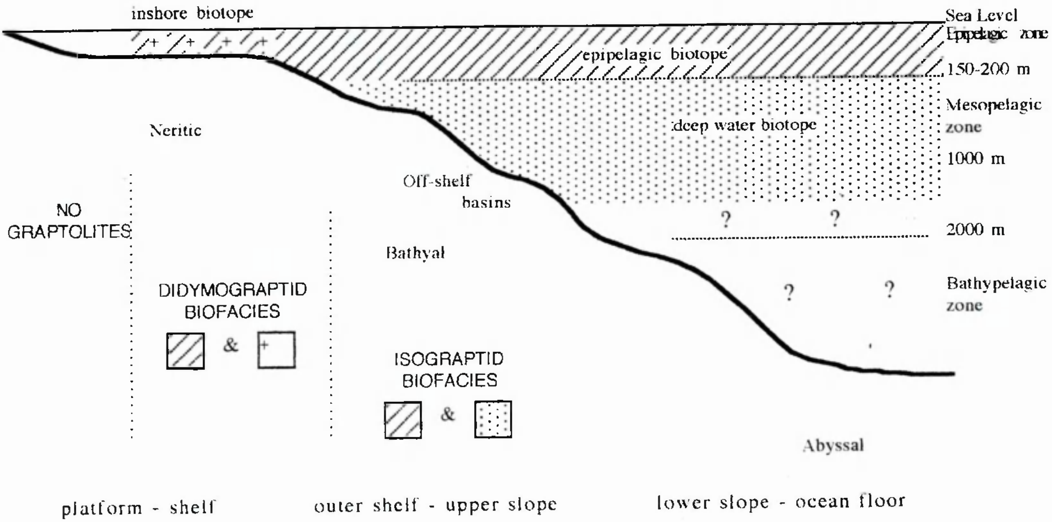


Figure 8.3.2, after Cooper *et al.* 1991, figs 1 and 2. (see original for list of fauna restricted and not restricted to depth facies)

implications to whether or not they could have been restricted to one ecological niche or a certain depth range. Some authors have found other lines of evidence in their studies of the graptolites, to broadly confirm graptolites' ability to maintain a preferred depth, such as the passive drag of nematularia (Mitchell and Carle, 1986:386), or the presence of extrathecal tissue webs on cyrtograptids (Lenz 1974:213).

Benthic dendroids possibly had a planktonic larval stage, but it is unclear how far these larvae could travel, known extant larval life-spans can vary greatly (Cocks and Fortey 1982). Graptolite larvae may also have been greatly affected by water depth, and may have had to remain in the water column for a long time until the optimum conditions were found. Erdtmann (1976) suggested, however, that palaeogeography would have had only limited significance to planktonic forms, and that only severe climatic conditions would have restricted the distribution of larvae. Some suggestion of depth stratification of larvae may account for apparent lack of certain faunal elements in some localities. Eckert and Brett (1989: 313) suggested that some larvae may have been deep floating and prevented from entering areas such as the Appalachian Basin, by surrounding shallow water platforms. In particular this may have affected the graptolites present in the sediments of the Midland Valley inliers, due to their basinal setting (see section 8.2.4.4).

8.2.4.3.2 "Silurian" type of depth stratification model.

Berry and Boucot (1972) were the first to recognise a variation in the graptolites preserved in a progression from shallow to deep water sediments. They based their study on the best documented part of the stratigraphic sequence at that time (not the case now), the Upper Llandovery *sedgwickii* to *murchisoni* biozones data from Britain, Sweden and North America. Their study was based on the "Correlation of marine benthic life zones (Ziegler's 1965 "communities") with co-occuring graptoloid graptolite taxa". Their results are summarised in fig 8.2.2.1, but their main conclusions were as follows:-

- There are no graptolites found in the shallowest water *Lingula* assemblage (BA-1) sediments.
- The shallowest water forms are the *Monograptus priodon* group and the robust retiolitids found with the *Eocelia* group (BA-2).
- These are joined in the *Pentamerus* assembalge by the monoclimacids *(Monoclimacis vomerinus)*, biserial scandent groups, and monograptid forms with lobate and triangulate thecae.
- The "*Monograptus spiralis*" group and *Monograptus discus* appear in the *Stricklandia* assemblage.
- The water depth occupied by the *Clorinda* assemblage, sees the addition of curved thecate groups, cyrtograptids, others of the *M. spiralis* group, *M. turriculatus* and *M. convolutus* type graptoloids.
- The overall trends observed are in the rhabdosomes becoming more curved as water depth increases, possibly also thecal enlargement.
- Those graptolites that lived in the most stressful environment (*M. priodon,* and the retiolitids), are the longest lived in terms of duration of their phyletic stock.

A comparative study of the graptolites associated with shelly faunas from the extensive shallow platform areas of China, was made by Chen Xu (1990:520), who suggested using the term "Graptolite Assemblage" GA-1 to GA-5 as opposed to "graptolite Benthic Assemblages" BA-1 to BA-5. Although the GA and BA ranges are directly correlated, it is felt here that at present, until complete acceptance of the graptolite depth zonation model is made, there is as yet insufficient evidence to erect independent Graptolite Benthic Assemblages.

Chen's findings (see fig 8.2.2.2) largely support those of Berry and Boucot (1972). He found no graptolites in the intertidal zone BA-1, and his main conclusions were similar:-
- "GA-2" is characterised by streamlined and robust *M. priodon,* and retiolitids.
- "GA-3" characterised by compact biserial forms (slightly heavier than the retiolitids hence sinking to greater depths).
- "GA-4" to "GA-5" are indicated by flexible and spiral forms with elaborate thecal apertures.
- Deeper water is characterised by more slender forms, rastritids and spirograptids, and the greatest depths of water were occupied by the cyrtograptids.

Chen also suggested that the "GA" assemblages were probably more complicated in the Ordovician than has as yet been recognised.

Therefore, the Silurian graptolites species are suggested to have been depth stratified in life, the more robust forms occupying the more energetic environment, the more slender, large rhabdosomed forms restricted to the greater depths. This depth stratification is envisaged primarily within the uppermost 200m of ocean waters, and in water above shelf sequences. This depth stratification probably also extended throughout the oceans, with graptolites generally maintaining their preferred position relative to the water surface. This would have been affected by currents and specific water masses that had conditions that did not suit them.

The accuracies of Chinese interpretations are not always fully accepted, and the Berry and Boucot model was erected in 1972, largely in terms of geosynclines rather than current plate tectonic models, understanding of geological processes has moved on since 1972. The interpretation of Ordovician rocks in terms of depth stratification however, has been studied much more recently and with more reliable data sets.

8.2.4.3.3 "Ordovician" type of depth stratification

A number of authors have studied graptolite depth zonation in the Ordovician, and they have reached broadly similar conclusion as summarised in fig 8.2.3.

Erdtmann (1976) suggested that the graptolites in the Ordovician oceans were subdivided vertically into three biocoenoses :-

Biocoenosis A, consisting of surface water, epicratonic graptolites, at or slightly below reef supporting depths. Erdtmann suggested that probably most of the graptolites resided in these surface waters, but were very rarely preserved.

Biocoenosis B was dependent on phytoplankton for food, eumarine, stenohaline and stenothermic. It is suggested that graptolites may have occupied a depth range and had functional automobility to keep up with diurnal phytoplankton rises. This biocoenosis is found in sediments deposited in shelf environments, and equivalent depths within the oceans, but is rarely preserved except in quiet water depressions and basin centres.
Biocoenosis C is envisaged as a very deep water biocoenosis, with very large rhabdosomed forms, long ranging and extremely well adapted to aphotic depths where there was less food and possibly low oxygen levels, but also higher preservation potential. In this biocoenosis, higher endemicity was possible, and graptolites had restricted dispersal potential.

In 1982 Cisne and Chandlee published an accurate, well controlled, study of the relative abundances of graptolite taxa on downslope bentonite bounded sediment transects, correlated with transitions from (shallow) articulate brachiopod dominated to (deep) trilobite fossil dominated faunas. They found that graptolite fossil distribution within the sediments, paralleled the distribution of benthic macroinvertebrates. They also suggested that graptolite distribution recorded structural and topographic features expressed by distribution of sediment types. Cisne and Chandlee (1982) observed zonation by (absolute) depth of deposition, and suggested that the most likely explanation of this was zonation by position in the water column, particularly as graptolite distribution patterns record bed surface topographic irregularities. They concluded that graptolite zonation by depth of deposition, primarily reflects vertical zonation in the water column, rather than onshore-offshore zonation.

The depth related distribution pattern resulting from the work of Cisne and Chandlee (1982), like Erdtmanns's (1976) model, envisaged a three part subdivision, a 50-200 m deep (normal shelf depths) layer characterised by Orthograptus, a deeper Climacograptus characterised layer, found in sediments deposited in water 200-300 m deep, and the deepest Corynoides dominated fauna found in rocks deposited in water of over 300 m depth.

Ordovician depth related graptolite distribution is best characterised by Cooper *et al.* (1991). Here they subdivide the water column into:-
- Shallow water (epipelagic) biotope, the didymograptid biofacies (with a further subdivision of the shallow biotope to include an inshore biotope, which they conclude may be specific to deposition from an inshore water mass).
- Deep water biotope, (which occupied the meso and possibly the bathypelagic zones), the isograptid biofacies.

The maximum depth that the graptolites lived in are suggested to have depended on the oxic/anoxic layering of the oceans (Berry *et al.* 1987), but would not be expected to extend too far into the bathypelagic zone, because of the reduced oxygen levels found therein.

Both of the more recent models (Cooper *et al.* 1991; Cisnee and Chandlee 1982) are characterised by a distinctive fauna, more or less coincident with shelf sediments, and a deeper water fauna characterised by large, slender, multiramous species.

8.2.4.3.4 Overall depth stratification conclusions.

A polarisation of various authors views exist about the relevance of either graptolite depth zonation, or the water mass specificity model. Some authors have suggested that graptolites were either depth zonated or specific to a water mass. This has been detrimental to the interpretation of graptolites. It is suggested here that a certain graptolite species may have been specific to water mass, but that depth zonation was also relevant. Some authors agree in principle with the depth zonation model (e.g. Kaljo 1978) but not in the amount of detail ascribed.

Models of graptolite "water mass specificity", and "depth stratification" are not mutually exclusive. Some species may have been limited by specific conditions to certain water masses, and within a water mass the graptolites may have preferred certain depths. Overall there was a different fauna favouring shallow and deep water. Graptolites are very rarely found in BA-1 sediments. Deeper water (BA-5 and greater), was favoured by larger, more complicated, curved, multiramous, delicate and slender forms. In shallow water deposits (BA-2/3), more robust forms with large, well armoured *priodon* type thecae, and retiolitids are found (see fig 7.2.5 for comparison of the apparent thecal size of forms from different depth zone sediments).

Particularly in the Silurian, when there was rapid radiation of new species, they cannot all have been in direct competition with one another in the shallowest waters of the euphotic zone, some of the species must have specialised (evolved) to occupy the slightly different niches offered by the different water depths.

It is most likely that the preference of certain graptolites for a certain water depth was dependent on food supply, light, temperature, hydrostatic pressure, and competition with other species for the particular depth niche, and was affected by currents, and environment. Some forms may have survived in the physically more stressful shallower waters, as a result of lack of competition from other graptolites just not built to survive in that environment. Absence from a faunal province of certain species may have made less competition for other remaining species, allowing them to occupy an increased depth range. Slight variations may have existed throughout the oceans as certain species may have been specific to water masses or currents and may have interfered with the overall pattern in certain parts of the ocean. However, a depth stratification of graptolites overall within oceans is thought to have existed.

The simplified type of depth stratification identified so far in Ordovician sequences (herein described as "Ordovician type") is thought to be the basic stratification into deep water and shallow water favouring species that can be applied throughout the graptolite record. The "Silurian type" of depth stratification, with the shallower water depths subdivided on a finer scale by the species of graptolites preferring to live there, can be considered as an overprinting of the "Ordovician type", occurring as a result of increased specialisation by Silurian species. Silurian graptolite depth zones can be correlated with the depths of water occupied by different association of benthic animals, which have been recognised and described as Benthic Assemblages.

8.2.4.4. Application to North Esk Inlier of depth stratification model.

" The vertical succession of graptoloids in a basinal shale can depend strongly on the basin's geologic setting and tectonic history. It is necessary to know each basins's setting and history in order to make best use of vertical successions in correlating between basins. A zonation scheme for widespread use should include both temporal zonation and lateral, depth-related zonation patterns." Cisne and Chandlee 1982 .

When developing a depth zonation model, it is much better if you can actually document a sedimentary sequence with recognisable deep to shallow (or vice versa), depositional environments, and then record a coincidence with the discovery of different faunas preserved at the same time at different depths elsewhere.

We are fortunate in NEI to have a deep to shallow regressive transition, resulting from rapid and relatively unbroken (by unconformity or major faulting) sedimentation, recorded within a relatively short period of time, just a few graptolite biozones.

Therefore, for the accuracy that we can expect to observe, certainly for the longer time ranging species, factors such as depth specificity (and preservation potential) may be controlling the fauna preserved in sediments deposited in different depths of water.

The fauna collected from the Pentland Hills presents a fairly unique opportunity to consider depth stratification models. There are a number of faunal elements present that can be compared with existing published "Benthic Assemblage" models, including brachiopods and corals. To this can be added the dendroids, not previously linked to benthic assemblage models, and other interesting elements such as eurypterids, echinoids and starfish. From the same horizons (the Reservoir Formation) and up through the regressive sequence of the North Esk Group, a number of planktonic forms are preserved, including graptoloids that are compared with the graptolite depth zonation models. The documentation of the NEI hopefully will serve to go one step further in recording which graptolites co-existed. Similarly the understanding of the depth and dimensions of the basin will assist in the gradual piecing together of the palaeogeography and graptolite faunal provinces. A graptolite can only be preserved if it was present in that faunal province, specific to the water mass conditions prevailing, and living at a depth where sediment was being deposited at that time (or in shallower water and the remains floating down to the sea floor).

The continental margin position of the Midland Valley terrane, and its shallow sea depositional environment are inherent in a number of palaeogeographic reconstructions (McKerrow *et al.* 1991; Cope *et al.* 1992 (p.51, fig. S7) and Cave 1993 (*In* Cope *et al.* 1992)). It is no longer envisaged that by the end of the Llandovery, deep ocean basin plain conditions would still be persisting at the eastern end of the Midland Valley of Scotland (discussed more fully in Chapter 5). We are concerned here with the independent faunal lines of evidence and the water depth range that these sediments were deposited at, implied from the fossils preserved.

The graptolites are preserved in the following distribution:-
-Deepest water (Shelf edge), Lower Reservoir Formation
New dendroid. Rare *Oktavites spiralis excentricus* & *Mcl. geinitzi.*
-Shallower water, (Middle shelf) Upper Reservoir Formation
Mcl. vomerinus. Oktavites spiralis excentricus, Mcl. geinitzi, M. parapriodon, (M. priodon and *retiolitids) Dictyonema pentlandica, Coremagraptus, Palaeodictyota, Thallograptus* (dendroid species with relatively thick and closely spaced stipes)
-Shallowest water (upper shelf, coastal, lagoonal to shore line) Wether Law Linn Formation. *Mcl vomerinus, M. priodon* (no thin, slender monoclimacids or *priodon* type monograptids). *Thallograptus arborescens* Boucek 1957.

The graptolite succession detailed above is generally consistent with the "Silurian Type" model of graptolite depth distribution discussed above. These results would indicate a depth equivalent to the *Stricklandia* or *Pentamerus* "communities" (BA-4 or BA-3) for the Reservoir Formation. Notable omissions are specimens of *Oktavites spiralis* s.s.. This more robust form, described (Berry and Boucot 1972) as characteristic of the "*Stricklandia* benthic life zone", although normally common in the *spiralis* Biozone, is not preserved in the NEI. Instead the more fragile and rarer *O. spiralis excentricus*, so far only recorded from the NEI and Bornholm (sediments deposited in an intracratonic basin (Bjerreskov 1975: 18)), is preserved.

The absence of *O. spiralis spiralis* may be associated with exclusion from the water mass specific to the remnant of the Iapetus ocean. The presence of both *O. spiralis excentricus* and *O. spiralis spiralis* in Bornholm, within the same intracratonic basin, precludes any model of exclusion by either species being specific to either deep or shallow water masses (section 8.2.3.2), although the NEI basin may have been part of a shallow water mass or small province associated with the remnant Iapetus ocean. The absence of the larger *O. spiralis spiralis* in favour of the more slender *O. spiralis excentricus* may be related to the generally small size of some of the fauna found in the Reservoir Formation, such as the dwarfed crinoids, and reduced average size of the speciemns of the coral *Palaeocyclus porpita* as discussed above.

The emergent Southern Uplands accretionary prism (see Chapter 5), and the remnant Iapetus ocean would have formed barriers to circulation, and certainly some differences between the fauna preserved north and south of these proposed barriers (differences between English and Scottish deposits) are observed. However, similarities between the Midland Valley Inliers (Irish, Scottish and possibly Newfoundland), and similarities of the NEI fauna with Bohemian /Scandinavian deposits are observed. Both the faunal similarities and differences, observed in these sediments, are likely to be associated with provinciality.

The very high deposition rate of the NEI would imply that the water may have been fairly turbid, which may have affected the graptolite population, but again both species are present in Bornholm where deposition rates are fairly slow, with little silt input into the shale sequence, the absence of *Oktavites spiralis spiralis* might be attributable to turbid water conditions. The graptolite faunal provincialism of this area is not yet clear, however, it is suggested that a Rheic neritic province developed in the Wenlock (Rickards *et al.* 1990). This may have extended further, spatially and temporally, and the NEI fauna may yet prove important in defining faunal provinces. The absence of *O. spiralis spiralis* (and other key graptoloids such as *M. discus, M anguinus*) is thought to be due to the limited depth of this depositional basin by late Llandovery times. The conditions are elsewhere described as having been fairly energetic, resulting in the regrowth and other aberrant structures described for *Dictyonema pentlandica* (Chapter 7). Although water depths of the sediments preserved are thought to have ranged from outer shelf to shallow, there may have been slight fluctuations in the water depth prior to deposition, or shallow barriers to open circulation or entry to the basin (Eckert and Brett 1989), excluding the species preferring the greater depths (such as possibly *O. spiralis spiralis*), possibly at the larval stage. It is for this reason that *O. spiralis excentricus* is thought to have been characteristic of slightly shallower water than normally expected for the spiralis group and is considered, along with all of the other graptoloids and dendroids to have been characteristic of BA-3 depths and shallower.

The association of the dendroids with the graptolite depth zonation model, may in future prove to be useful, if more of the (few) dendroid bearing localities were considered in this way. *Dictyonema pentlandica* seems to be characteristic of the deeper water BA-4 to BA-3 environment. It is thought to have been able to withstand fairly energetic conditions, but not as energetic as envisaged for shallower depths than possibly BA-3. Along with *Dictyonema pentlandica*, are Coremagraptids (which also can form very large colonies (see fig 7.3.4.1), delicate species of *Thallograptus* and those forming multiple stocks, and the palaeodictyotids, which also formed large colonies sculpted to a dominant current direction (Chapter 7). In the shallower water, thought to be equivalent to the BA-2 environment, the larger, slender, conical forms are replaced by a small shrubby *Thallograptus,* with thick and quite widely spaced stipes (along with retiolitids and *M. priodon*). Further study is required on the depth distribution of dendroids, but they may well prove to be a useful in depth zonation models.

Faunal associations of the shallower marine sediments from the North Esk Group are discussed in detail in Robertson (1989), wherein they are interpreted as a shallow marine barrier complex, largely deposited by storm and fair weather transport, grading into a lagoonal environment. Various fossil associations are recognised as representing original biocoenoses. Robertson (1989) did not interpret the fauna and sedimentology in terms of the Benthic Assemblage model. However, the amount of storm influenced sedimentation of the Wether Law Linn Formation, the coquinites and the fauna preserved, are highly indicative of upper BA-3 for the lower member, a BA-2 for the middle member. The upper member, with the orthocones, distinctive enormous ostracod *Entomozoe tuberosa,* and grazing gastropods, interpreted by Robertson (1989) as restricted marine coastal embayment or lagoon and shoreline deposits, are considered here to correlate with BA-1.

Robertson (1989) interpreted the Reservoir, Deerhope and the Cock Rig Formations as different lithofacies in a submarine fan, ranging from deep ocean submarine basin plain fan, to submarine slope feeder channel. He interpreted all of the fossiliferous deposits within these Formations as transported and in some cases carried vast distances by turbidity currents. Undoubtedly some of the broken disarticulated remains in some of the "limestone beds" have been transported, but many of the faunal elements are thought to have been buried in situ.

The case for the dendroids being *in situ* has been argued already herein (Chapter 4), the crinoids (Kier, 1973) echinoids (Brower, 1975), starfish (Spencer, 1914-1940) and Eurypterids (Waterston, 1979) are also thought here to have been buried *in situ*, all of which indicate deposition within the euphotic zone, further confirmed by the presence ofthe calcareous alga *Ischiadites* in both the "Limestone Bed locality" sediments, and in the Deerhope Formation. *Ischiadites* as an indicator of the photic zone has been discussed by Eckert and Brett (1989).

Many of the brachiopods found in the Reservoir Formation are common elements of shelf successions of the late Llandovery. Most of the very distinctive brachiopod Benthic assemblage indicators, such as *Clorinda, Stricklandia, Pentamerus* and *Eocelia* are missing, which may partially be due to the reasons discussed above, that of possible earlier fluctuations in basin depth or restricted access to the basin of very depth specific forms. A comparison with the fauna recorded by Eckert and Brett (1989) from New York (see fig 8.2.1), is considered highly appropriate here due to the similar models of deposition in a basinal setting (see chapter 4). Some of the faunal elements and associations are different between the two areas, as would be expected given their palaeogeographic and provincial separation, but the Reservoir Formation shelly faunas can be correlated well with the upper BA-4, lower BA-3 assemblages of Eckert and Brett (1989), particularly the recorded presence in the Willowvale Shale of dendroid remains. This in turn makes an interesting correlation with the Charlestown Inlier in Ireland. Parkes (1993) also compared the faunas of the Charlestown Inlier with the results of Eckert and Brett, and agreed an assignment to BA-3 or BA-4. There are a number of faunal elements that the Charlestown Inlier and the North Esk Inlier have in common, particularly the presence of abundant *Palaeocyclus* corals, and most importantly the presence of the large brachiopod *Megastrophia (Protomegastrophia) undata* (M'Coy). This brachiopod is only known from the North Esk Inlier, Charlestown Inlier and from the Oslo region (Cocks and Worsley 1993), and may prove to be an important indicator of both biostratigraphy and bathymetry. This brachiopod (referred to the genus *Erinostrophia* by Cocks and Worsley (1993)) is to be the subject of further work. Another Midland Valley Inlier that has been considered in terms of Benthic Assemblage models is the Craighead Inlier near Girvan (Ward 1989), where considerable agreement with a depth related distribution of the brachiopods was also observed.

During the course of this work, numerous new brachiopod specimens have been found from the "Limestone Bed Locality" in the upper part of the Reservoir Formation. Some are stricklandiide ventral valves (?*Costistricklandia*) and one specimen of ?*Meristina* sp. has been identified (Fig 10.20), all of which are indicative of a mid-shelf Benthic Assemblage 3-4 environment (M. G. Bassett pers. comm. 1992). The lower part of the Reservoir Formation, although only very sparsely fossiliferous, is considered to have been deposited in conditions not greatly different from the later Reservoir Formation (see Chapter 4), and hence not at vastly greater depths than the other sediments.

The North Esk Group records a regressive sequence (Robertson 1989). Evidence presented here suggests that the range preserved is from fully marine shelf conditions, with the deepest sediments deposited at depths consistent with those normally associated with BA-5. The majority of the Reservoir Formation sediments were deposited at mid shelf, BA-4 to BA-3 depths. The overlying sediments of the upper formations were deposited in gradually decreasing depths and record the development of shoreline structures, barriers and lagoonal deposits as described by Robertson (1989). The important difference recorded here being that at no point is sedimentation considered to have been in a deep ocean basin environment, the deepest water depths envisaged are equivalent to an outer shelf environment. This may have been because there was no continental slope present in this part of the ocean, but just a shallow continental marginal basin, a remnant of the Iapetus Ocean and possibly part of an inter-arc / fore-arc basin complex (Cope *et al.* 1992:50).

8.5 Chapter summary.

A degree of provinciality is suggested to have controlled the distribution of graptolites within the oceans of the past, and some are thought to have been specific to certain water masses with particular characteristics. these factors are not always readily identifiable but must not be ignored when considering the fauna preserved. Additionally, certain graptolites are thought to have preferred to live in water of particular depth and hence are more likely to be preserved in sediments deposited at these specific depths.

The regressive sequence of the marine sediments of the North Esk inlier, deposited in environments ranging from outer shelf to nearshore conditions are confirmed by a study of the depth related graptolite faunas preserved within the sediments.

Chapter 9

Taxonomy.

This chapter contains the taxonomic work completed during this project. The first section is a general introduction, particularly applicable to graptoloid taxonomy. There then follows a section of graptoloid taxonomic descriptions, and then dendroid taxonomic descriptions. Finally, a more thorough review of terminology is given in section 9.4., which follows largely that of Bulman (1970); Loydell and Palmer (1991) and Bates (1990).

Included in the first section of this chapter is a description and examples of a new technique developed during the preparation of this thesis, that of constructing graptolite "profile plots". This is a method that can be used to distinguish between different species with similar thecal structure, and may eventually become the basis of computer generated taxonomic profiles.

(9.1) Measurements and Terminology

(9.1).1.1

Figure 9.1.1 illustrates the most important morphological features and biometric terms (see also Loydell 1992:25). The abbreviations 2TRD (Two thecae repeat distance) and DVW (Dorso-Ventral Width), are used throughout this thesis.

If measurements are made at predetermined levels along a graptoloid stipe, then meaningful comparisons of thecal-spacing and stipe width can be made. Common usage (Loydell 1993; Zalasiewicz 1994) has resulted in measurements made at 5 thecae intervals becoming standard. The first measurement is usually taken at th. 1-2, the second at the. 5, then th. 10, th.15 and so on at 5 thecae intervals. If no major changes are observed beyond a certain thecal level then sometimes one reading is given, say th. 20+. Sometimes with well preserved material or where major diagnostic changes are observed in the proximal portions, then readings are taken for th. 1, th. 2, th.3 and th. 5.

(9.1).1.2 Two thecae repeat distance (2TRD)

In the earlier texts (Lapworth 1876), thecae per inch were recorded, which was followed by thecae per 10 mm (Elles and Wood 1901- 1918) or dendroid stipes per 10 mm (Ruedemann 1947; Boucek 1957), for proximal and distal portions of the stipe. Howe (1983) introduced the concept of 'Two Theca Repeat Distance', this is "defined for th.*n* as the distance in millimetres between two equivalent points (for example, the junction of the free ventral wall and the interthecal septum) o th.*n* -1 and th.*n* +1". 2TRD is measured over two thecae to iron out some of the minor differences caused by diagenetic flattening, inhomogeneous deformation, imperfect preservation, or abnormal growth of one theca (see figure 9.1.1 for illustration of the measuring points). In practice, measurements are taken at the standard intervals (discussed above) of *n* = 1-2, 5, 10, 15, 20, etc, although measurements can be made and plotted in a meaningful way on a graptolite profile plot (see section 9.1.2) using the first well preserved theca of the specimen as the unknown *n*, and measuring *n*+ 5,10, etc, when the sicula is not preserved and *n* cannot be identified.

The measure of 2TRD is usually quite accurate, but can be subject to problems such as when it is too literally interpreted, particularly if one of the thecae is enlarged by abnormal growth. Also, as noted by Loydell (1992:25) 2TRD is far more accurate for distinguishing between straight stiped forms than it is for curved or coiled forms. Inevitably some element of subjectivity is introduced as to how far from the ventral margin the 2TRD reading is taken. The point of measurement should be clearly stated in all taxonomic descriptions of curved forms (see description of *Oktavites excentricus*), which has not always been the case (Loydell and Cave 1994). 2TRD is also considerably more time consuming to measure than simply placing a rule alongside the specimen and counting the thecae in 10 mm.

This technique has not been accepted by all authors. Some (Loydell 1993; Loydell and Cave 1994; Zalasiewicz, 1994) quote this parameter in all of their taxonomic descriptions, others (Lenz 1988; Lenz and Melchin 1991; Rickards *et al.* 1994) do not. And obviously all taxonomic descriptions published prior to the introduction of 2TRD in 1983, will not include a record of this parameter, yet the descriptions remain absolutely valuable. Loydell (1991a) gives a conversion table of 2TRD to th/ 10mm.

Rickards *et al.* (1994:127) do not use 2TRD, instead they "...prefer the thecal spacing of Packham (1962) in which spacing for two or three thecae is translated into "thecae per cm"; this most closely measures change in spacing along stipe, yet enables easy comparison with thecae per measured 10mm, the traditional measure". The usefulness of 2TRD is also not immediately apparent to non-graptolite workers. Thecae per 10 mm is easily understood and interpreted by someone trying to read or use a taxonomic description for the first time, as it is easier to visualise or imagine.

It is clear therefore, that although some authors will continue to use 2TRD, some will not, and comparisons will always have to be made with existing (pre- Howe 1983) literature. Therefore the taxonomic descriptions contained herein also contain a record of the thecae in 10 mm, so that easy comparison can be made with published taxonomic descriptions not recording 2TRD.

The possible advent of computerised aids to specimen identification will eventually focus on accurate parameters that can easily be measured or scanned by machine and plotted in meaningful interpretive ways (see below for the introduction of graptolite profile plots). The use of 2TRD as such a parameter, will inevitably increase with time.

(9.1).1.3 Dorso-Ventral Width (DVW)

Dorso-Ventral Width is a more instantly recognisable concept. It is measured from the dorsal margin (i.e. the straight or curving edge of the rhabdosome), to the outermost ventral margin of the theca (see figure 9.1.1.). This should incorporate both the protheca and the metatheca. It is the greatest width that any part of the graptolite theca reaches, measured perpendicularly from the dorsal margin of the stipe (excluding any spines). It is not a measure that involves the position of the thecal aperture in any way. The measurement is

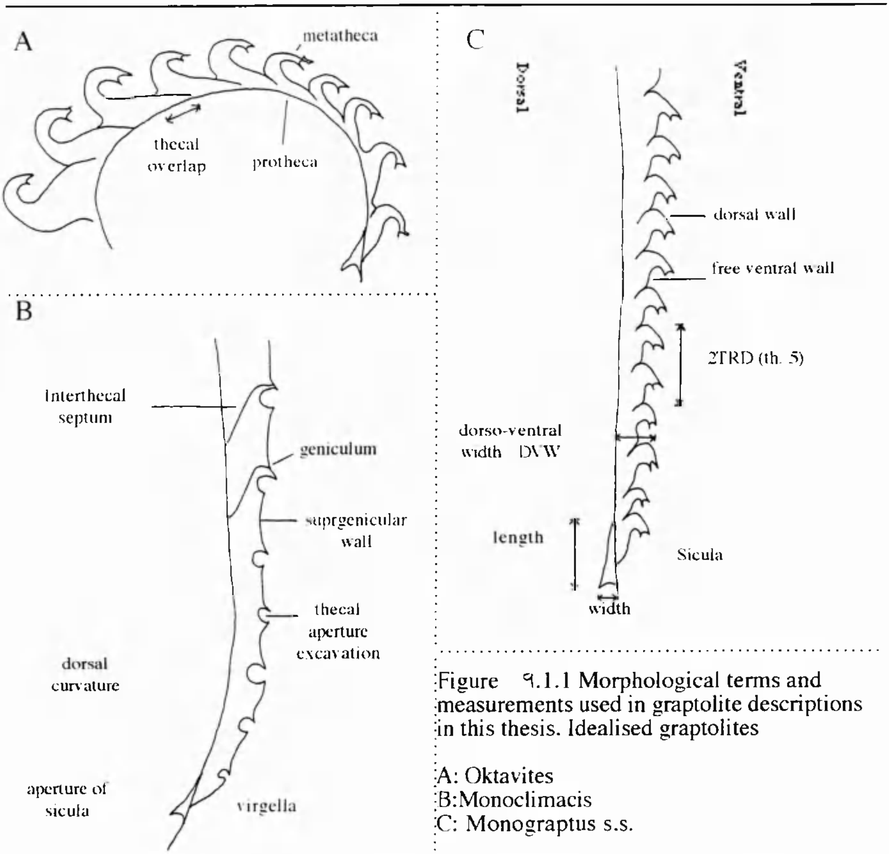


Figure 9.1.1 Morphological terms and measurements used in graptolite descriptions in this thesis. Idealised graptolites

A: Oktavites
B:Monoclimacis
C: Monograptus s.s.

taken at the level of the widest part of th.*n*., and *n* is counted along the ventral margin of the stipe, not the dorsal.

When species with elongated thecae and a large degree of thecal overlap are considered, then a measurement of DVW taken at th *n* may include the earliest parts of theca *n*+1 (or even *n* +3). Care must be taken that the measurement is of the true DVW, taking into consideration the tectonic deformation, completeness of preservation, individual theca with growth abnormalities, and whether or not the true dorso-ventral profile view is encountered. Very often, particularly for spirally coiled monograptids (Loydell 1992:26), a scalariform, or intermediate view is seen and inaccuracies can be introduced. In practice the DVW at the level of the three thecae incorporated in the measure of 2TRD (th.*n* -1, th.*n* , and th.*n* +1) is considered (provided that a full dorso-ventral view can be found), and either an average of the three, or the most representative reading is recorded. Also readings are taken at the standard levels as discussed above.

This measurement is greatly subject to the effect of flattening. The true DVW is the cross sectional profile of an uncompressed specimen. Assuming simple flattening of the periderm, the width of the graptolite could be increased by up to 30% (Packham 1962:499), and sometimes more if the concave supragenicular wall of a monoclimacid were folded outwards on compression. The specimens from the NEI are only partially flattened and not noticeably tectonically deformed. Any flattening would probably only cause the DVW measurement to be inaccurate to about 5%, which is possibly has less of an affect than than the inaccuracies introduced through magnification, and the difficulties of measuring such small animals.

(9.1).2 "Graptolite profile" plots.

A new technique has been developed during this study, which facilitates accurate differentiation between graptolite species of similar thecal shape. The procedure involves measurement on each specimen of two taxonomically significant parameters and plotting them graphically against one another, resulting in a characteristic array, particular to each species.

Measurements (on each graptolite specimen) are taken of two thecae repeat distance (2TRD), and dorso-ventral width (DVW) at regular points along the stipe, spaced at 5-thecae intervals (th.2, th.5, th.10, th.15, th.20 etc.) (see section 9.1). This is already standard taxonomic procedure, as these are taxonomically significant parameters. These values are than plotted against one another all the way along the stipe of each specimen, and the points may then be joined together for convenience. The measurements of a second and subsequent specimens are similarly plotted. If all of the specimens known to be of one species are superimposed in the same way, the resultant graph contains an array of points, through which the best fit curve should be the ideal profile for that species, ideally the type specimen should conform to this ideal profile.

If all specimens of two species that are difficult to distinguish because of having the same thecal shape are plotted on the same graph, then it is possible to identify the two separate

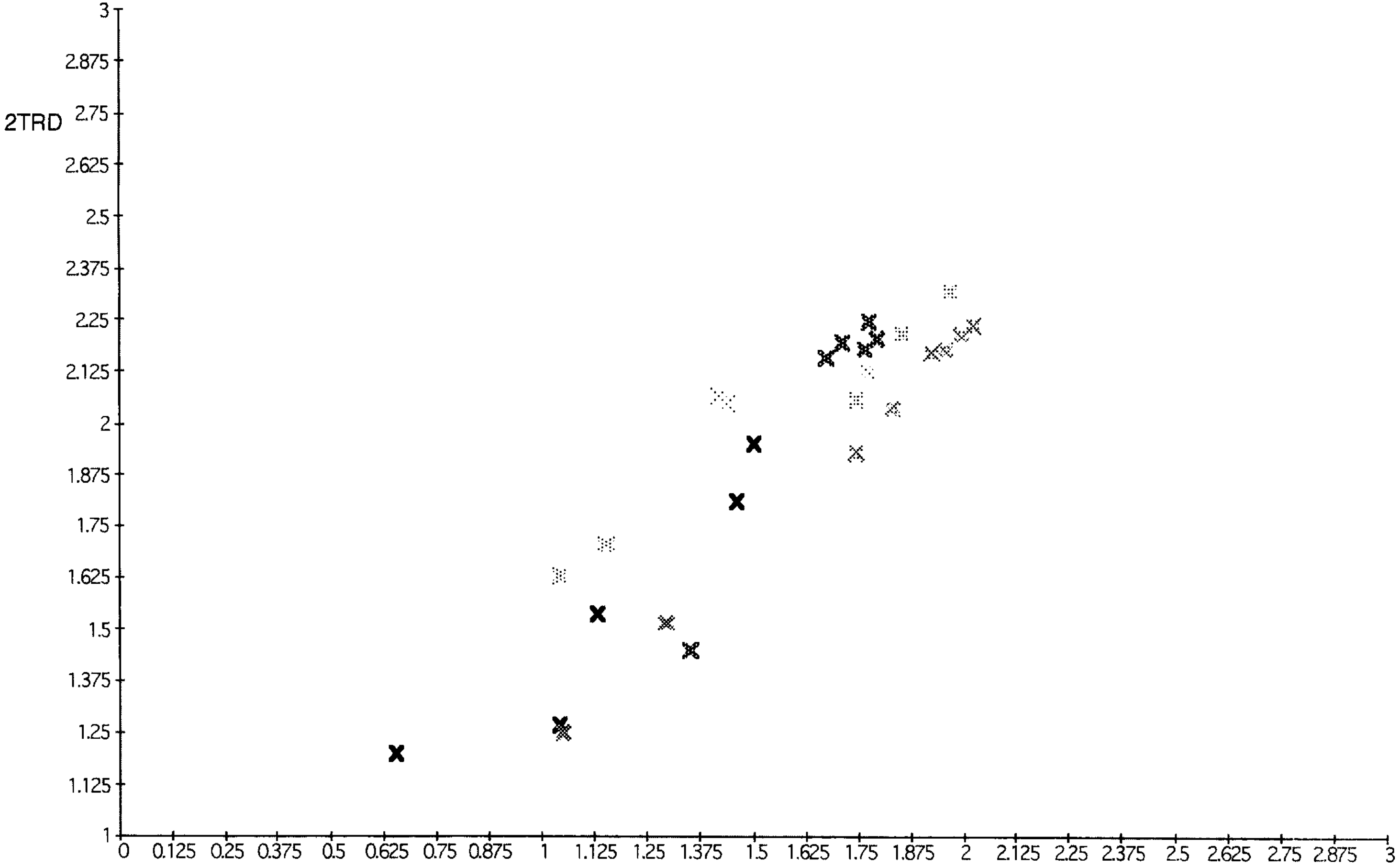


Fig 9.1.2.a *M. priodon*

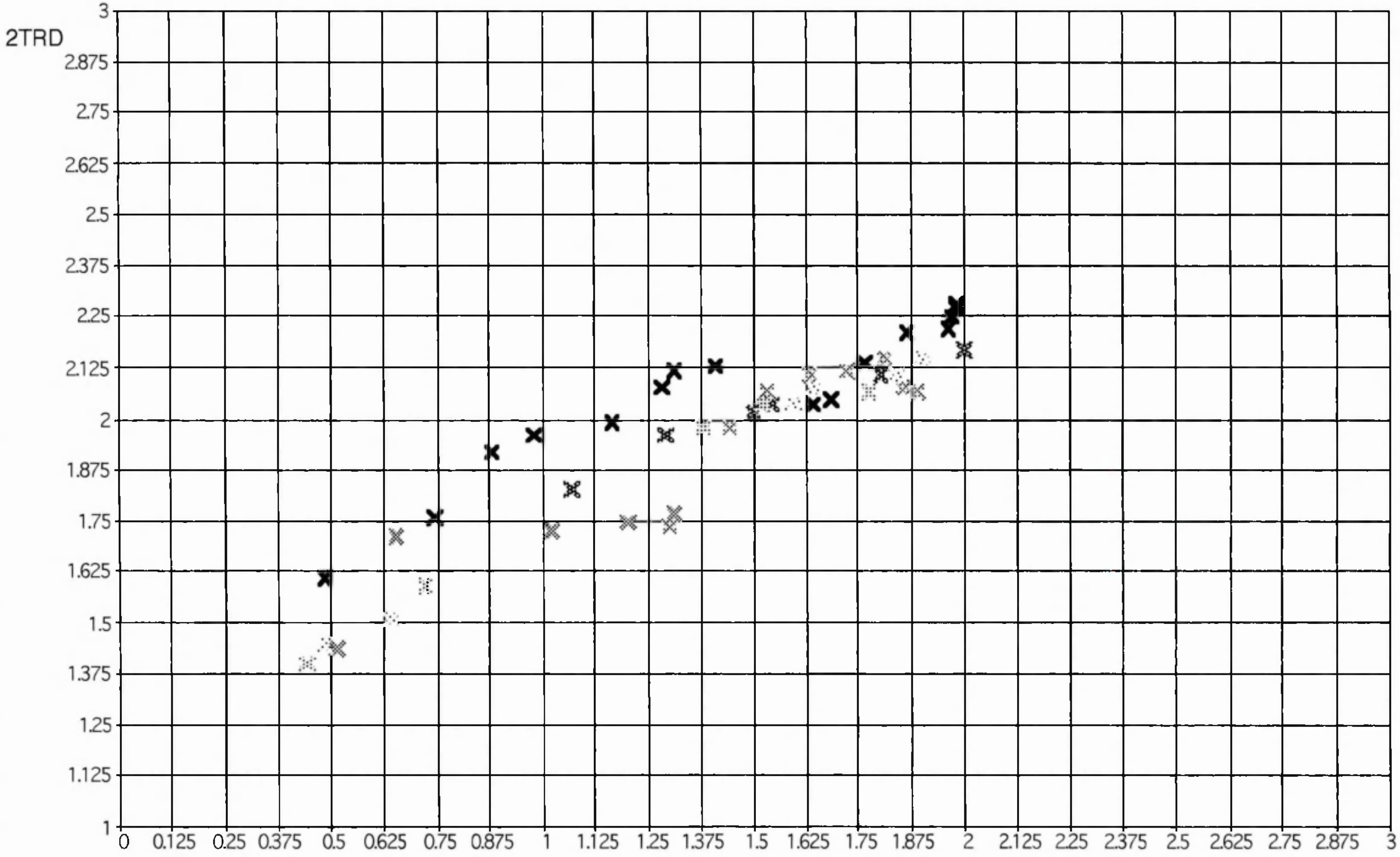


Fig 9.1.2 b *M. parapriodon*

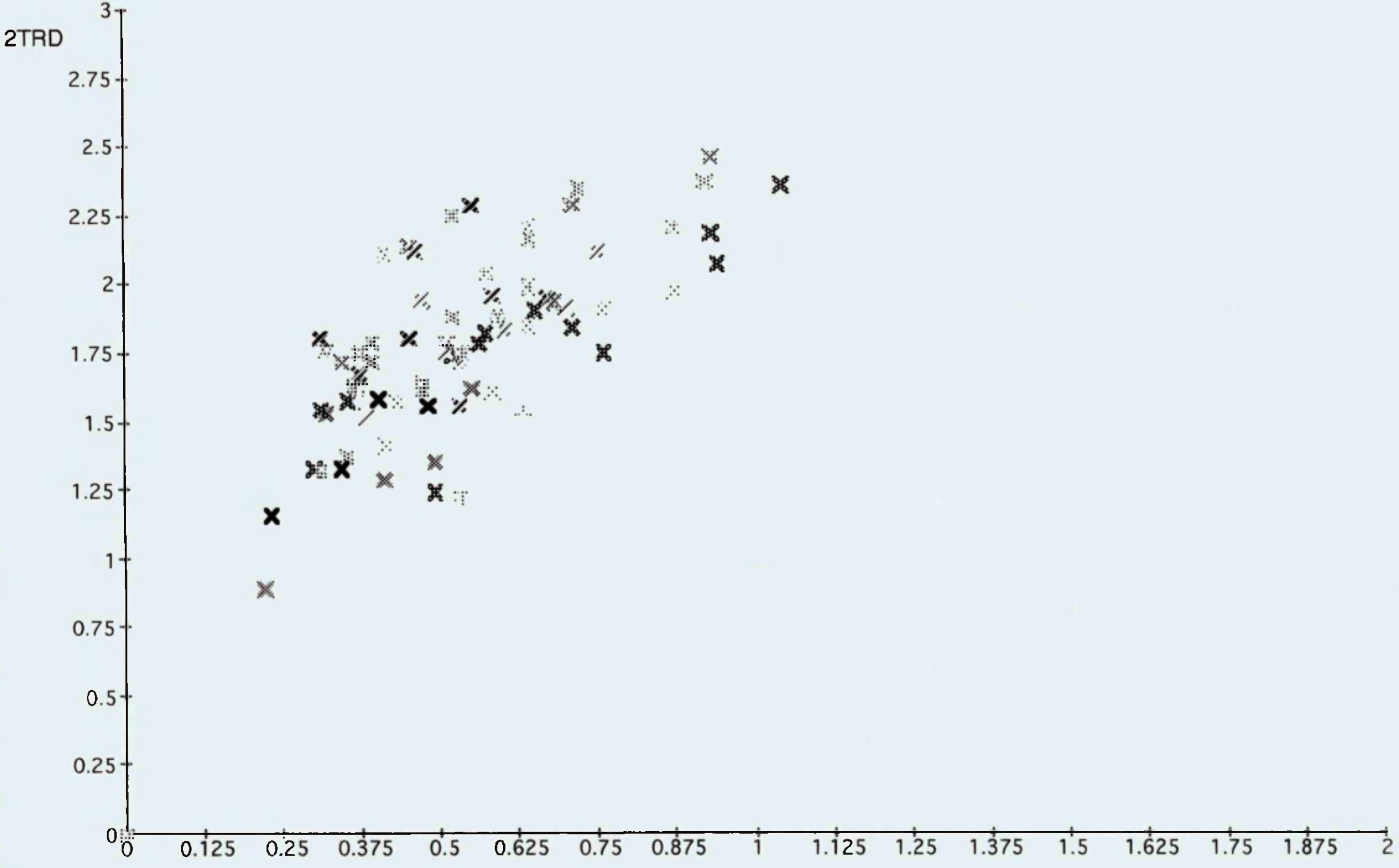


Fig. 9.1.3 a *Mcl. geinitzi*

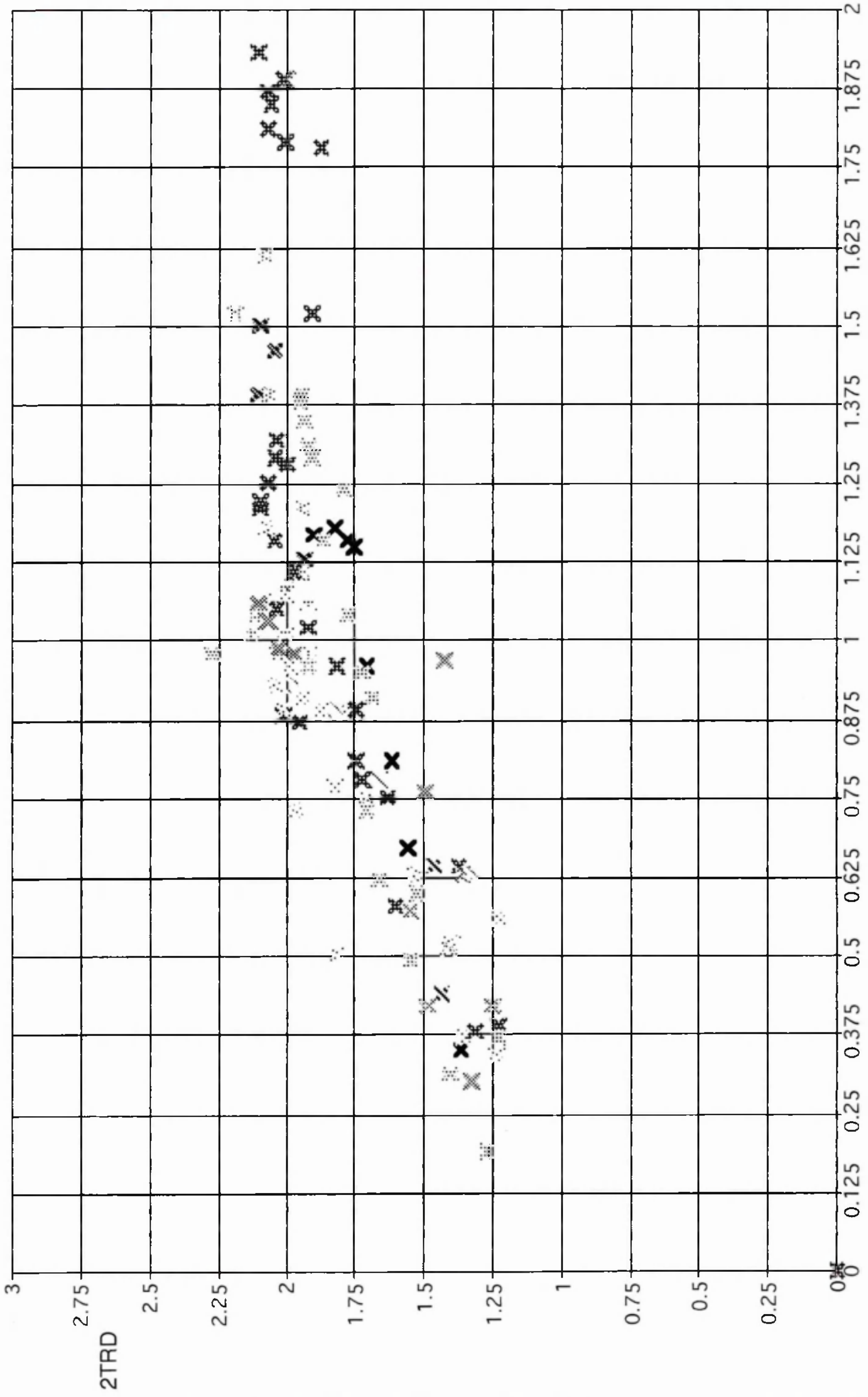


Fig. 9.1.3.b *Mcl. vomerinus*

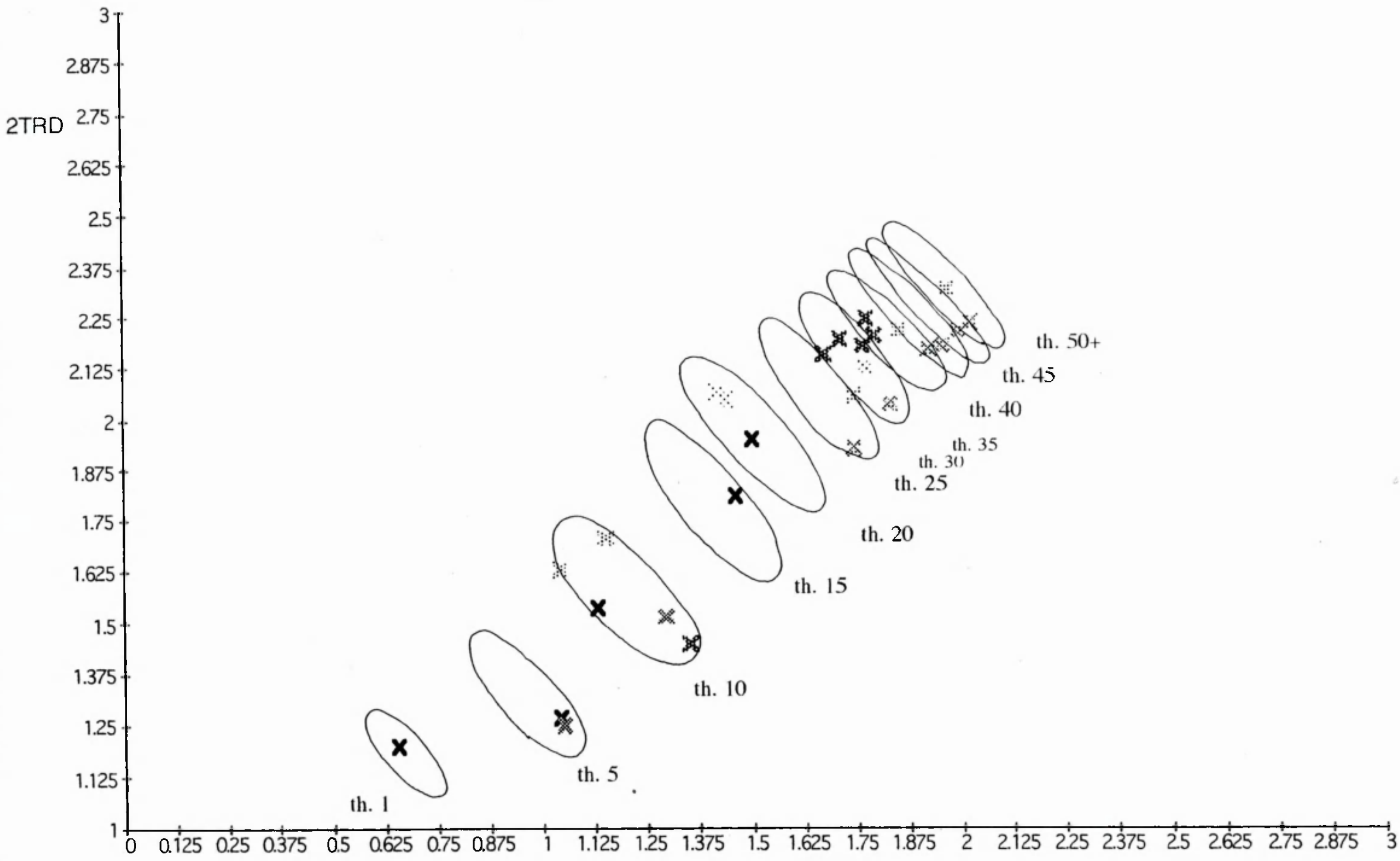


Fig 9.1.4 *M. priodon*

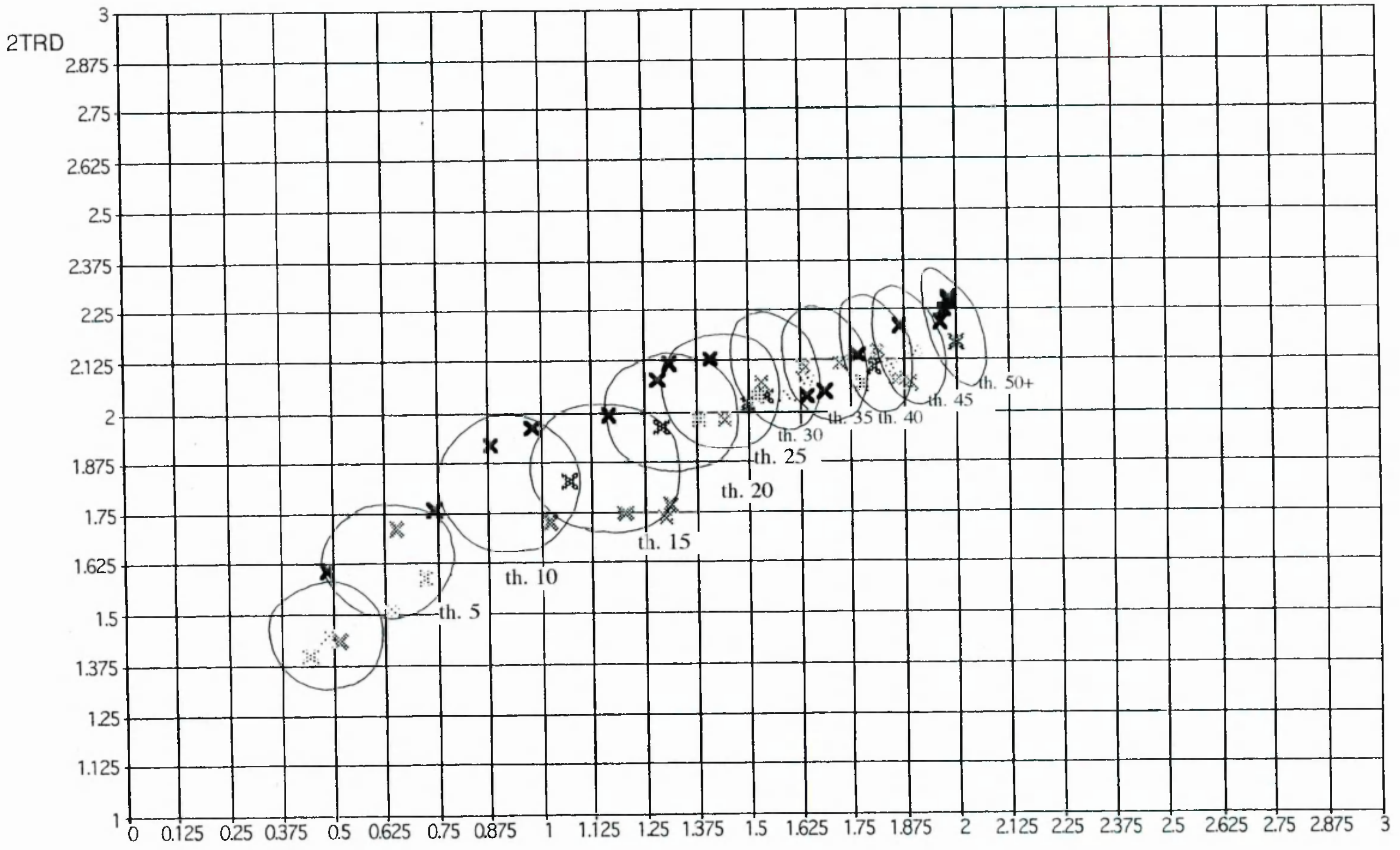


Fig 9.1.5 *M. parapriodon*

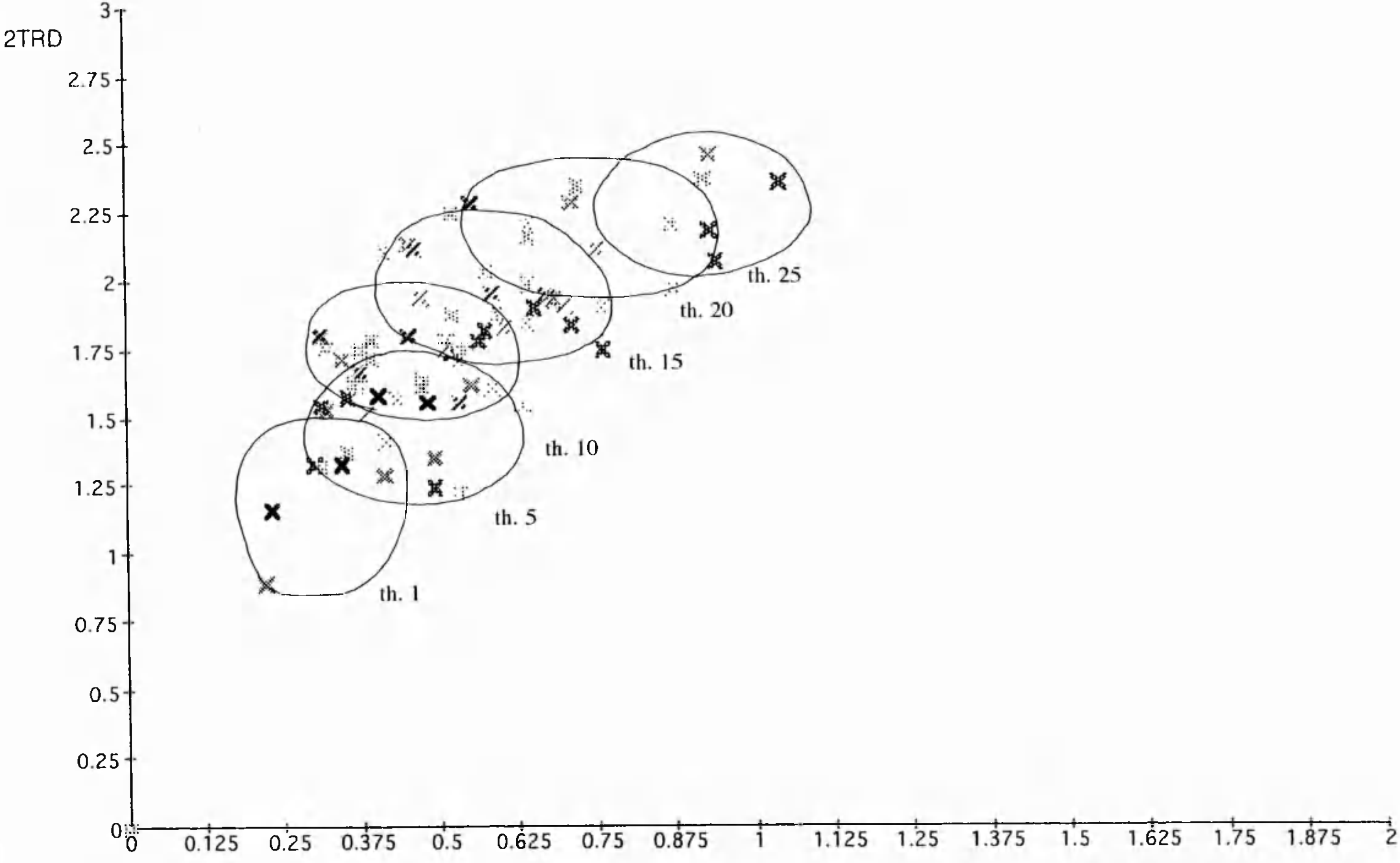


Fig. 9.1.6 *Mcl. geinitzi*

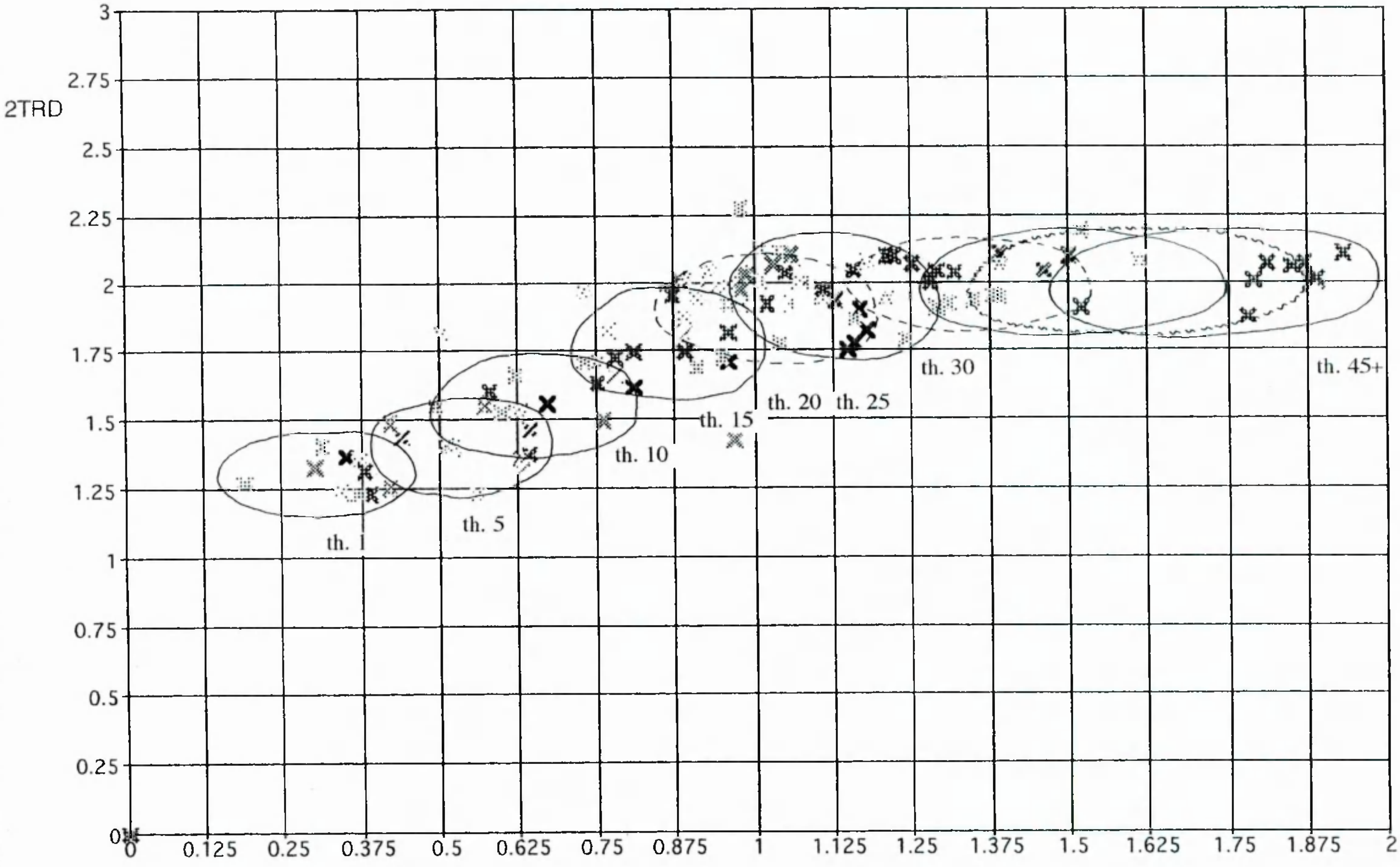
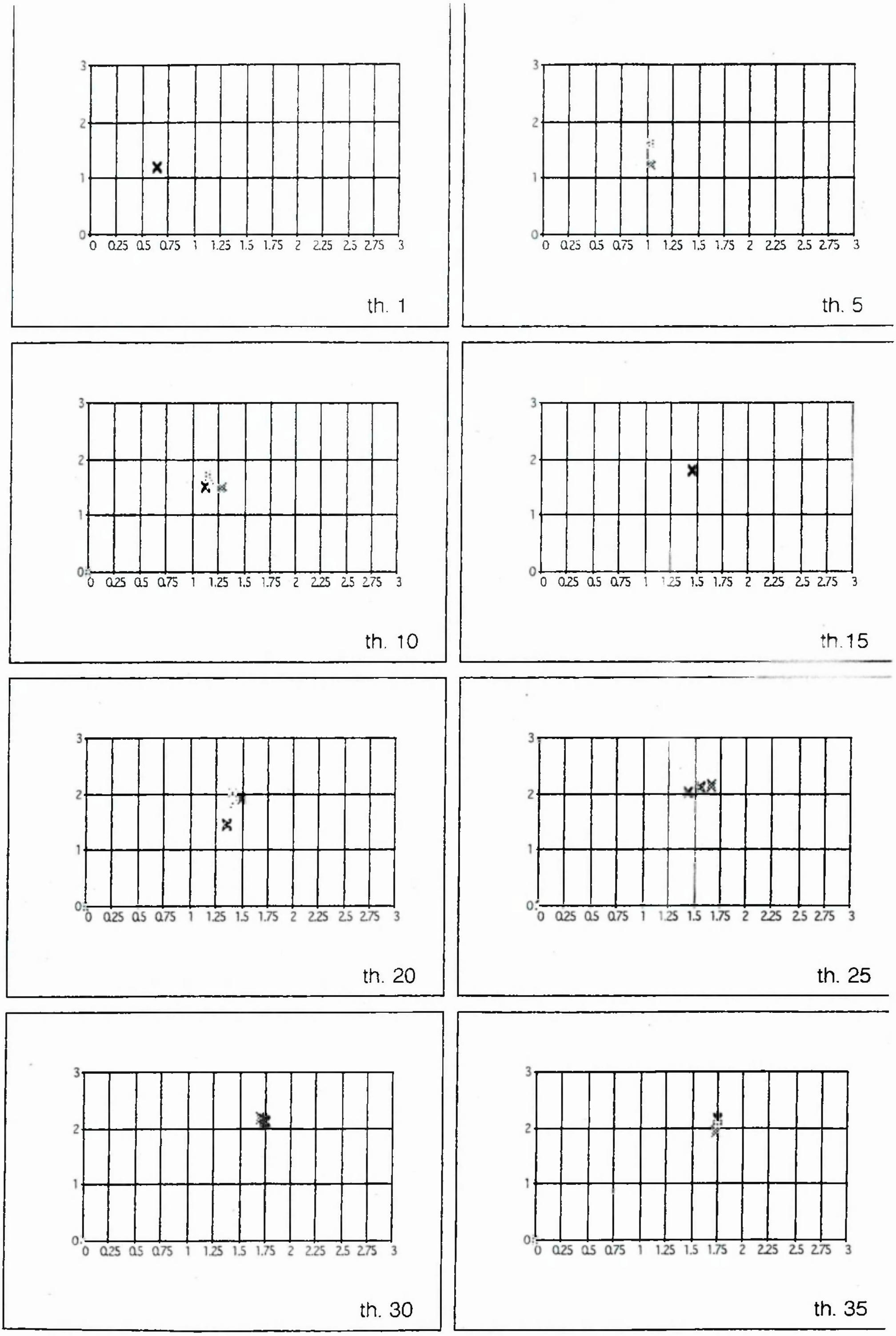
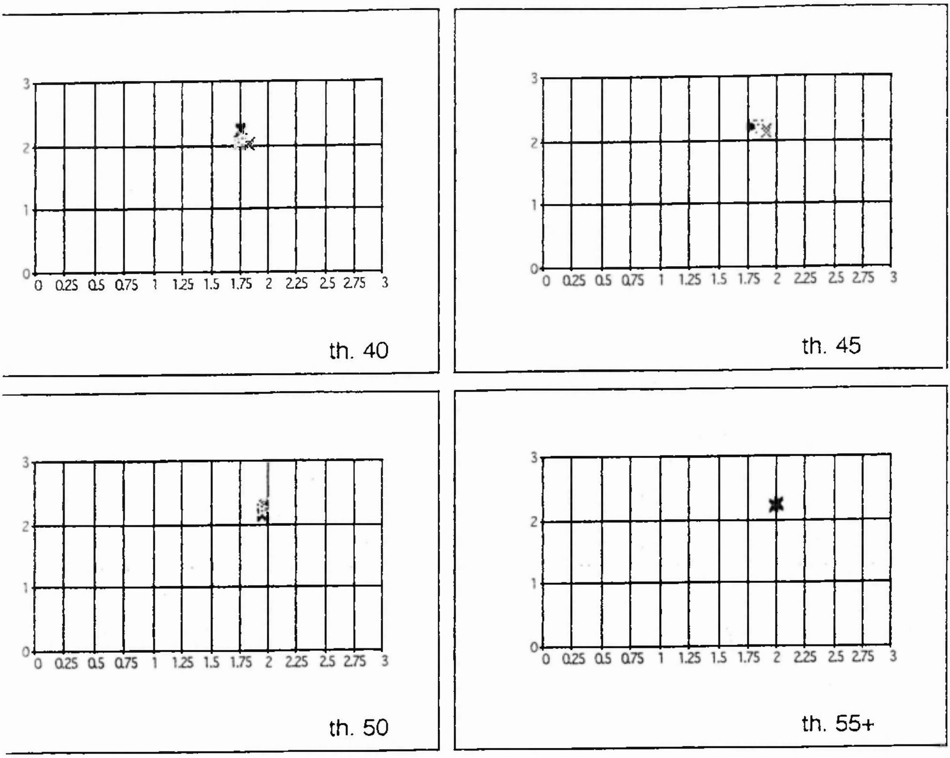


Fig. 9.1.7 *Mcl. vomerinus*



th. 1
th. 5
th. 10
th.15
th. 20
th. 25
th. 30
th. 35

M. priodon DVW/2TRD at each thecal level



th. 40

th. 45

th. 50

th. 55+

Fig 9.1.8. cont. *M. priodon* DVW/2TRD at each thecal level

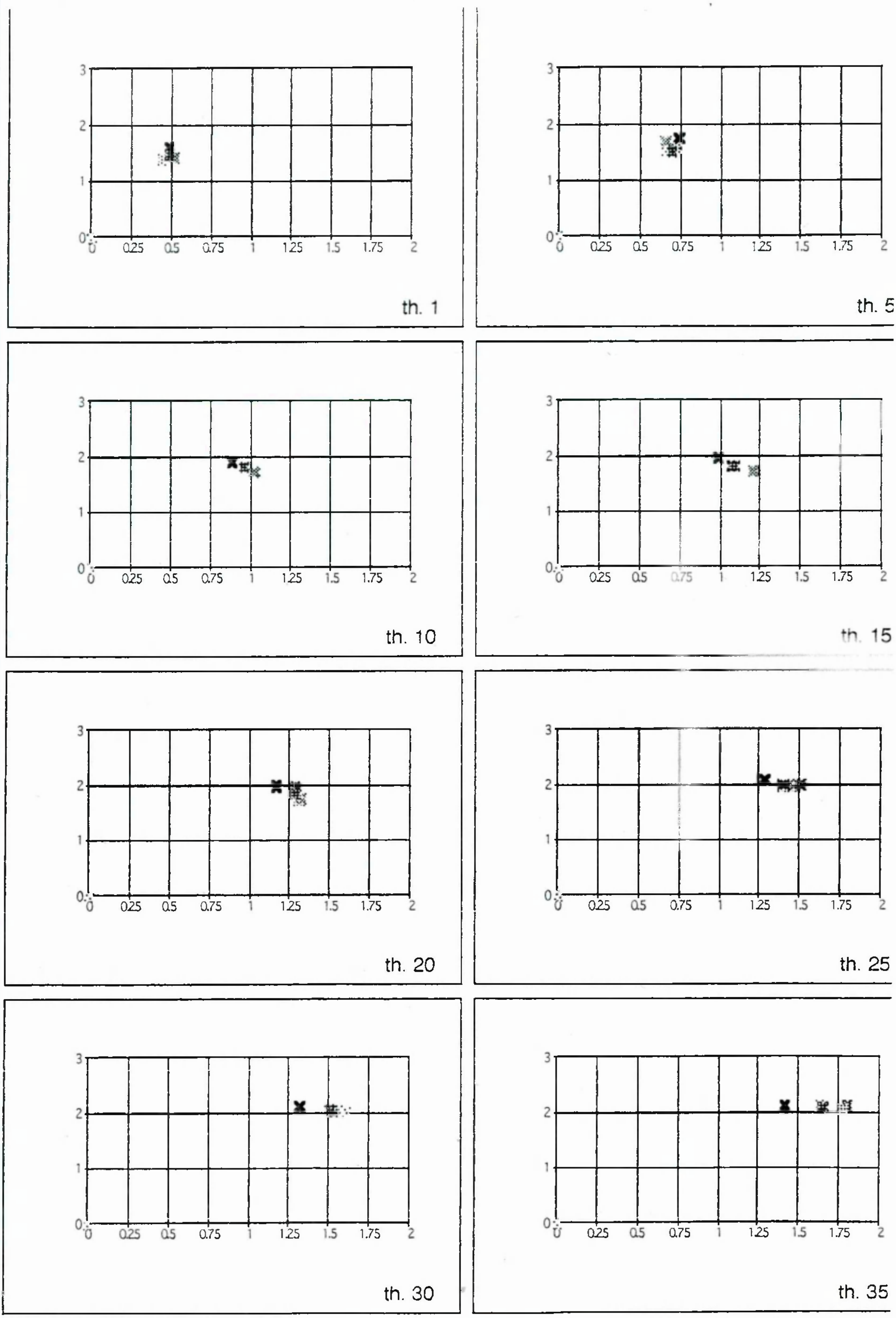


Fig 9.1.9 *M. paraprionodon* thecal arrays at each thecal level

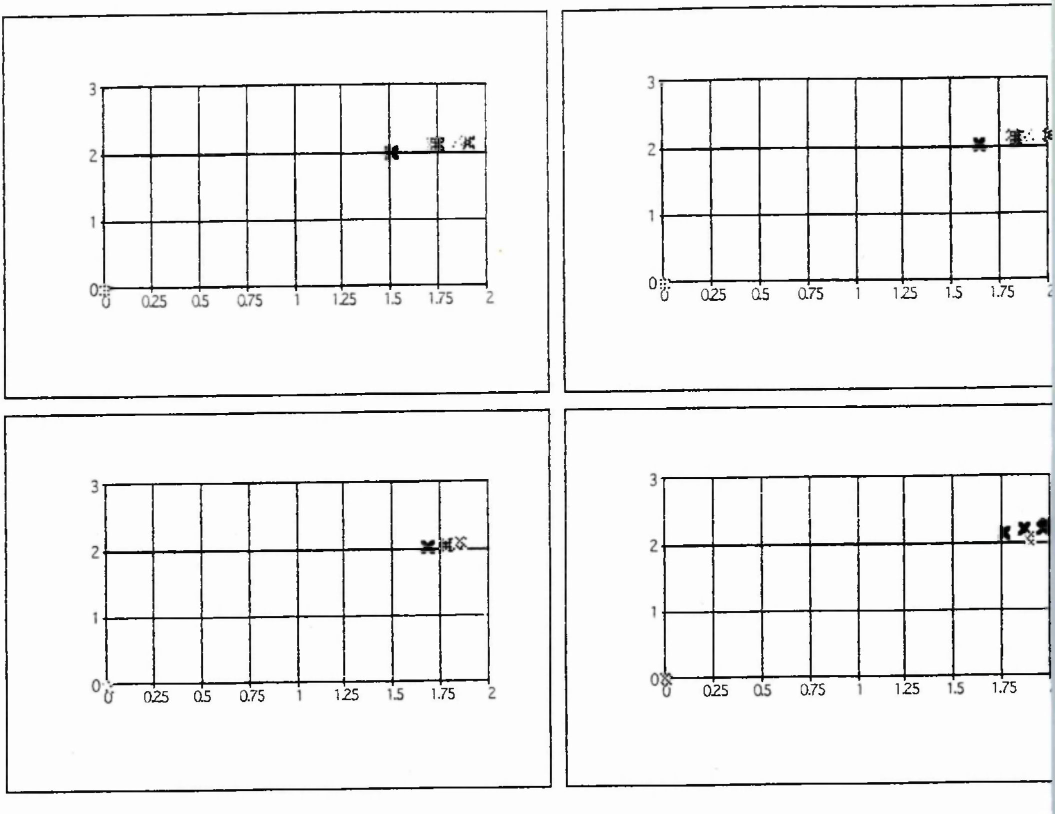


Fig 9.1.9 cont. *M. parapriodon* thecal arrays at each thecal level, continued

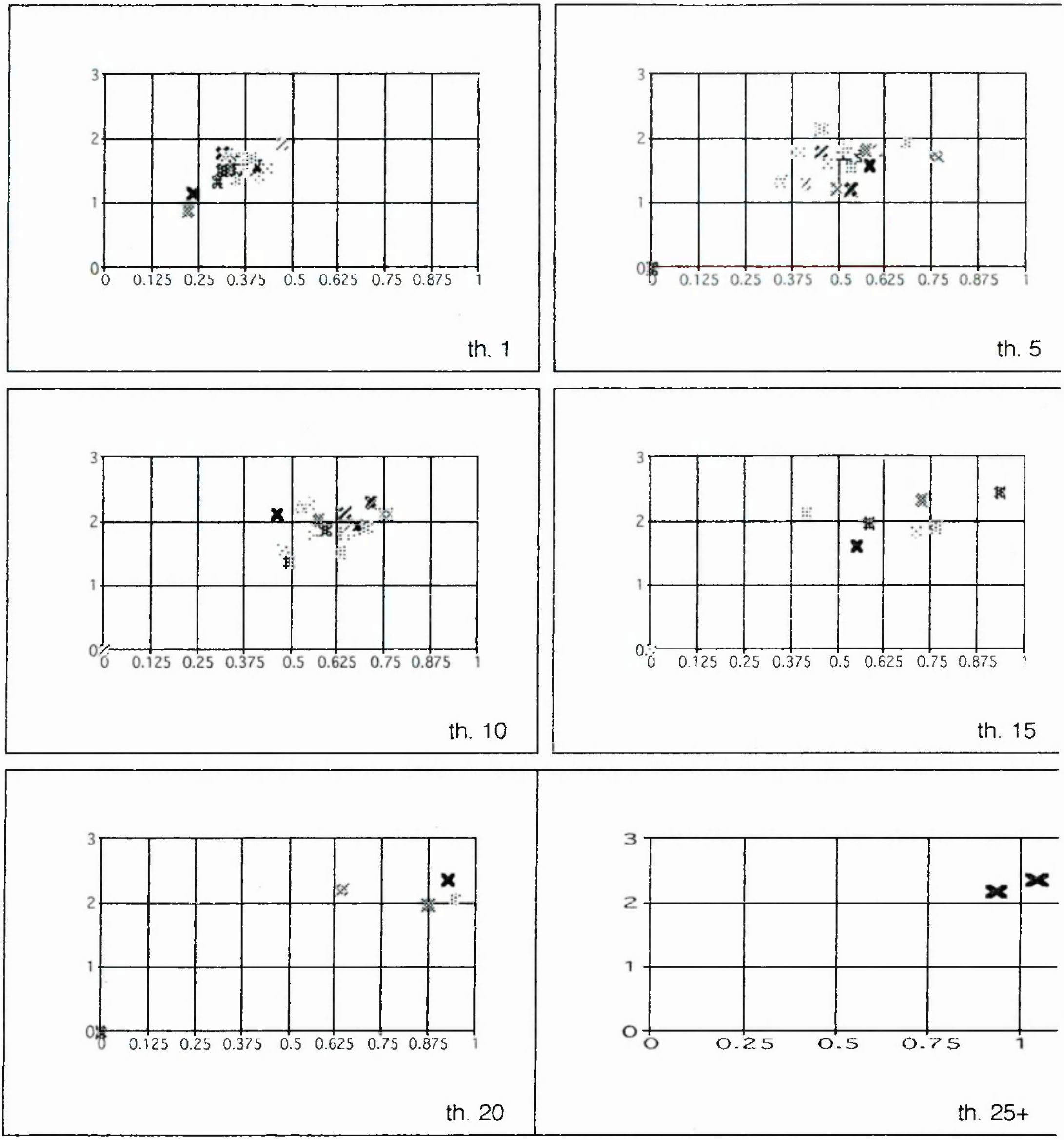
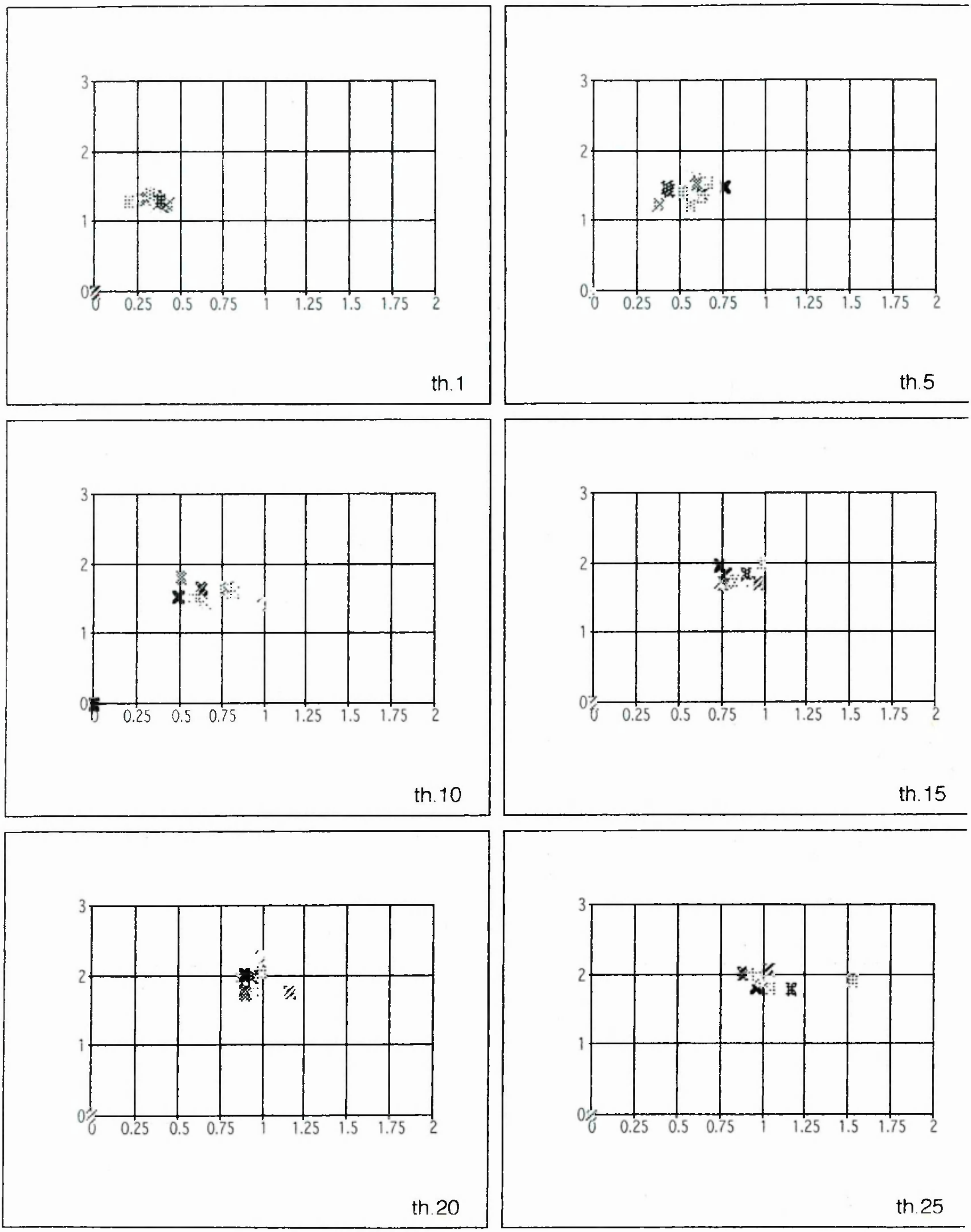


Fig 9.1.10 *Monoclimacis geinitzi*
arrays of points corresponding to each thecal level.



th.1

th.5

th.10

th.15

th.20

th.25

9.1.11 *Monoclimacis vomerinus*
array corresponding to each thecal level along stipe

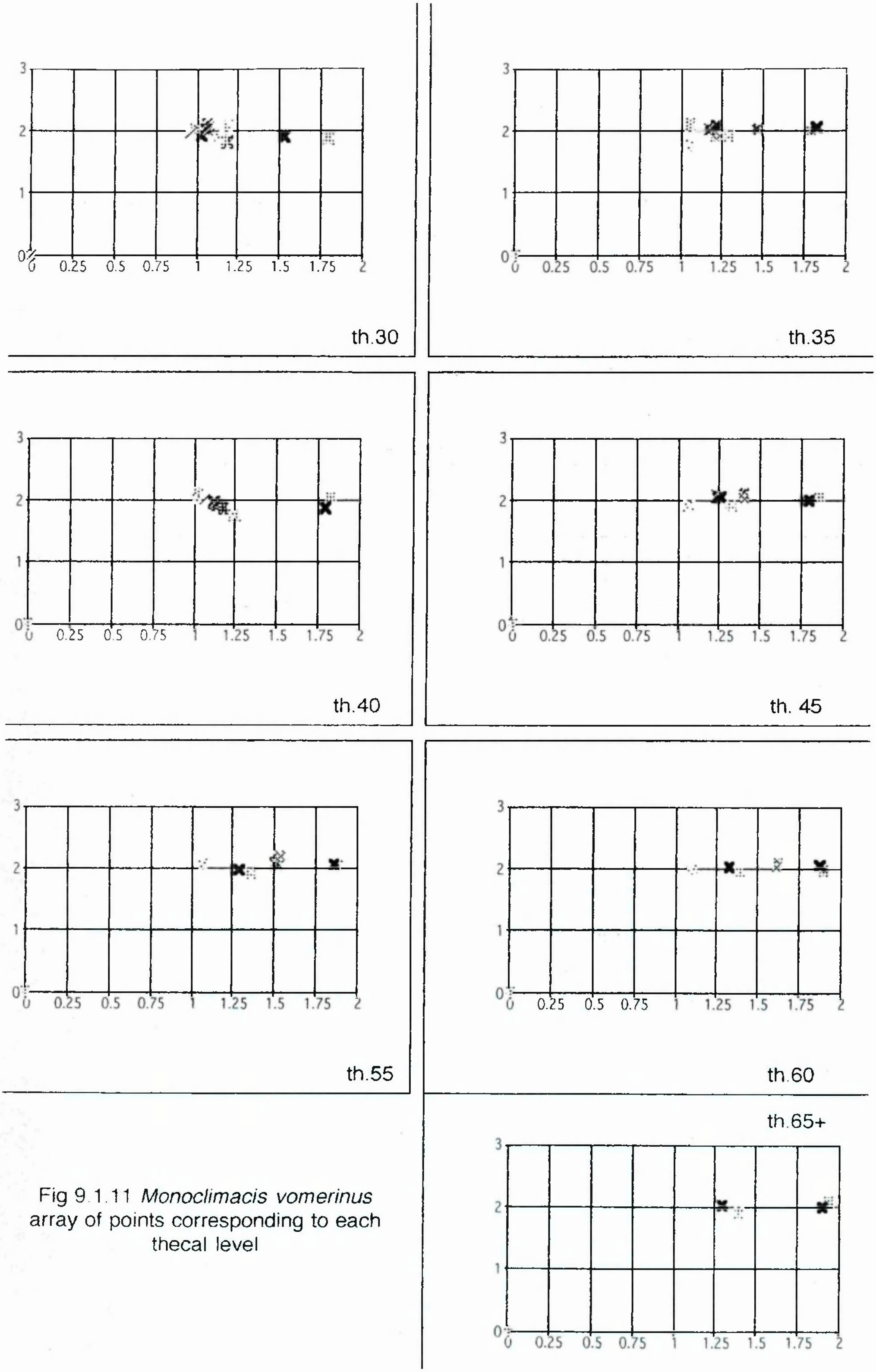


Fig 9.1.11 *Monoclimacis vomerinus* array of points corresponding to each thecal level

arrays, even though they may cross at one point or merge. Furthermore, if specimens in which the sicula is not preserved are considered, measurements can be made at th.*n*, th.*n*+5, th.*n*+10, th.*n*+15 etc. If this data is then plotted in a similar manner and compared with a known array for specimens with the same thecal shape, then a preliminary identification can be made of the specimen, along with an estimate of the original total thecal number of the specimen and also the length.

Examples are given in figures 9.1.2 and 9.1.3. Only two species are plotted on each graph, fig. 9.1.2 involves two "priodon" thecal -type species (a,*Monograptus priodon* and b, *Monograptus parapriodon*). Fig. 9.1.3 involves two monoclimacids (a, *Monoclimacis geinitzi* and b, *Monoclimacis vomerinus*). It can clearly be seen that the array of points corresponding to each species is quite distinctive.

This technique has the advantage that specimens thought to be of the same species, from different areas, can be compared with the known array for that species, resulting in a standardised scientific representation of what would otherwise be presented in descriptive terms. If arrays for the type material of each species were available, then each new specimen found could be compared against type arrays for improved identification.

This technique is not applicable to all species, probably only those with relatively straight rhabdosomes. This is due to the approximations inherent in measuring 2TRD and DVW for tightly curved or spirally coiled specimens.

Accurate illustration of thecal shape is very important so that subsequent authors can clearly compare further specimens, as it is quite possible for two distinct species with slightly different thecal shapes to have the same rhabdosome size and shape, therefore plotting as the same array using this graphical representation, whereas the differing thecal shape would distinguish them as separate species.

The further plots (figs. 9.1.4-9.1.7) are of each species. In some, lines have been omitted and only points plotted. Clusters of these points have been identified corresponding to the level of measurement (e.g. th.10) (figs. 9.1.8-9.1.11 are the preparatory plots for each species at each thecal level). If a specimen without a proximal end and measured at th.*n*, th. *n*+5 etc, is compared with this array, then a first order approximation to what thecal level is represented by "*n*" can be made.

A careful study of the relevant spacing of clusters of points characteristic of each thecal level, can yield more information, and the pattern of these clusters can be characteristic of a particular species. In particular, it is important for the distal clusters to be identified because, if the species reaches a maximum width and thecal spacing, and consists of a length of stipe of constant size, then all of the measurements made at further 5 thecal spacings, will plot close to one point. Once identified, this becomes a distinctive, easily identified, part of the species description, not to be confused with a short species which terminates abruptly on reaching certain dimensions. Similarly, it is important to study the clusters in the correct order, otherwise trends typical of the species, such as either parameter decreasing, remaining constant or increasing rapidly at a later point, may be masked. These trends however, are easily identified from such plots.

Ideally each cluster of points corresponding to a specific thecal level of each species should be centred on the measurement of DVW and 2TRD for the type specimen, and the cluster should represent the margin of error acceptable for identification as that particular species, based on the plotting of a large number of syntype material. Preparation of this basic database would be a major undertaking; further work in this field was therefore considered to be beyond the scope of this project. "Stipe expansion" diagrams (plots of dorso-ventral width against thecal number), were convincingly used by Cooper and Fortey (1982) to differentiate between Ordovician graptolites. As suggested above, the combination with 2TRD gives a far more accurate profile of the species.

The author has recently become aware of a similar technique by Dr. M. P. A. Howe (Howe, 1982; 1983). Some results were published (Howe 1983:636) but the graphs presented were not a convincing representation of the power of this technique. A computer programme was developed (Howe 1982) and the three measurements, DVW, TRD and thecal number (measured at single thecal spacing not 5 thecal intervals or two-thecal repeats) were plotted against one another on a 3-D graph, requiring stereoscopic glasses to view. Similar profiles were obtained, but this approach has not been widely accepted, perhaps because of the difficulties of seeing the images in 3-D. The convention adopted by Howe (1983:637) of plotting DVW on the x-axis and (2)TRD on the y-axis has however been followed here.

It is possible that with advances in computer technology, eventually it will be possible to scan individual specimens automatically and compare them with a database of 3-D images, allowing computer identification. The present 2-D approach records a unique profile for each species and further analysis of the distribution of clusters of points at measurements levels from the same 2-D graph produces the same information as Howe's (1982) 3-D plot, in a more readily usable form.

Considering identification in this way, it may be possible in the future using the technique outlined above (if a sufficiently large number of specimens were available) to introduce statistical tests on the accuracy of identification.

(9.1).3 Generic splitting.

The 'Monograph of British Graptolites' (Elles and Wood, 1901-1918), is a very major text containing clear scientific descriptions and good figures of many hundreds of species. It also has the first main indication of a graptolite zonal scheme. Unfortunately, although the figures are clear, and most are excellent, some are composites of material from many different localities. Some illustrations figure rhabdosomal sections that are not representative of the graptolite under description, such as distal sections with thecae turned into the rock. The Synoptic supplement to Elles and Wood's (1901-1918) monograph (Strachan, 1971), goes a long way towards rectifying ambiguities and updating the original identifications; this text itself is currently under revision (Strachan, pers comm.). Even so, Elles and Wood's (1901-1918) monograph remains the most influential publication on graptolites so far published.

Graptolite classification is currently unsettled. There is not universal agreement at any level in recent systematic works (Rigby 1986; Fortey and Cooper 1986; Mitchell 1987; Loydell 1992,1993b). Many new genera have been introduced, often in non-English language journals, which are less accessible. One thing is agreed, however, that more, accurate taxonomy is required (Loydell 1993a:332).

The majority of graptolite specimens studied (worldwide) are silhouettes. Flattened silhouette material is not good for the erection of genera (Rickards 1989). Genera must however, be sufficiently broadly defined that well preserved, flattened material can be identified, or else the whole idea that graptolites are useful biostratigraphic tools, is negated if the majority of specimens become difficult to identify to even a generic level. Thecae have a very great range of form, but in silhouette only a rough approximation of the true thecal shape can be seen. More delicate, twisted or spinose details are not easily apparent, particularly lateral features. Phylogenetic linkages in the evolution of thecal shape can be identified, therefore this can be used a criterion for defining genera (Rigby, 1986:6). For description of species, graptolite rhabdosomal form, the shape (curved, coiled, convexity) and dimensions (width, length) are important. However, for the description of graptoloid genera, rhabdosomal form has little influence on phylogeny, with similar rhabdosomes having widely different thecal shapes. Greater regard for phylogenetic and phyletic lineages is now recognised as important (Rickards (1989:274).

The reluctance of "western" graptolithologists (Rigby, 1986) to subdivide monograptid genera (a process seemingly favoured by "Eastern" workers) had resulted until recently in relatively few 'new' genera being introduced. In the last few years, some authors have come round to using established monograptid genera such as Bjerreskov's current usage of *Monoclimacis crenulata sensu* Elles and Wood (Bjerreskov 1981:24). Previously there was a reluctance to assign species to the genus *Monoclimacis*, maintaining assignation to *Monograptus aff.. crenulatus sensu* Elles and Wood (Bjerreskov 1975:54). Other genera too have started to become regularly used.

Many Chinese and Russian workers have assigned species to the genus *Oktavites* (Levina, 1928), some with limited success, such as Lin (1989), who described *Oktavites tullbergi* (Boucek), and *Oktavites tullbergi spiraloides* (Pribyl), from the Llandovery of Southern Shaanxi, China. In the plates the thecal shape illustrated shows clear *Oktavites* -type thecae, and although the rhabdosome shape is similar to *tullbergi*, the thecal shape precludes this from being *tullbergi* , which is a species of the genus *Torquigraptus*.

The best work will always come from isolated material. However, descriptions based on such specimens must be applicable to flattened material and at least "well preserved" silhouettes must be identifiable from the descriptions, otherwise the descriptions become only valid for isolated material and no realistic stratigraphy can be based on the resulting graptolite biozones. Furthermore the literature must not become impenetrable to non graptolite specialists, precluding identification to even generic level by non specialists. Further subdivisions of the Family *Monograptidae* (Lapworth 1873) are likely to prove counterproductive.

The classification and list of genera introduced by Loydell (1993b) is used in this study, including *Oktavites*, and in addition, recognising *Monoclimacis* Frech 1897. Following this classification (Loydell 1993b), *Monograptacea* Lapworth 1873, has been raised to the level of Superfamily, and Family *Monograptidae* Lapworth 1873, has been subdivided into a number of genera. Limited comments are made on dendroid classification in section 9.4. I would prefer to retain a broadly conceived idea of genera, particularly *Monograptus*, like Rickards *et al.* (1993:129)

Acceptance of the subdivisions of monograptid genera is growing. There is one factor that contributes to this, is that two of the authors most in favour of the generic subdivision are among the most prolific authors (Loydell and Zalasiewicz), and their opinions and specimen identifications are regularly sought by non graptolite workers (e.g. Parkes *in* Parkes and Palmer 1994), leading to the publication of the new generic names.

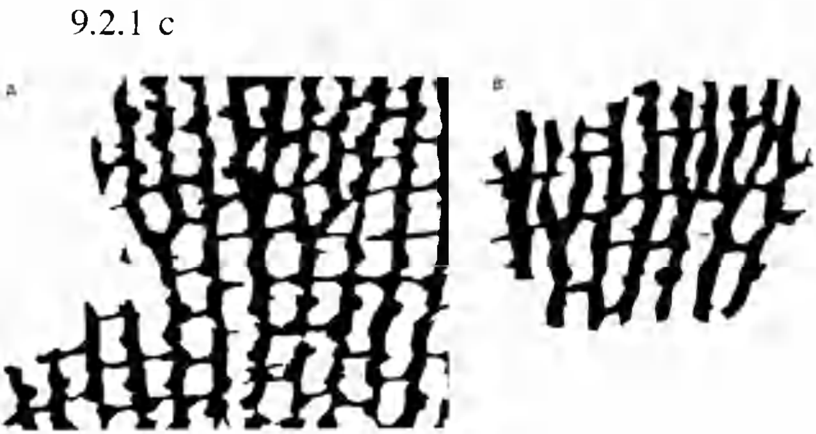
9.2.1 a

Dictyonema pentlandica sp. nov. EDNCM 20237, conical proximal end; the rhabdosome is preserved gently folded and reaches a length of 200 mm; superimposed on this specimen are two fragments of *Coremagraptus imperfectus*, × 0 75.

9.2.1 b

Dictyonema pentlandica sp. nov. Modes of attachment. A. RSM GY.1985.29.4, showing secondary thickening of stem and base region, and root fibres for securing stem within sediment. B. RSM GY.1985.30.1, attached to brachiopod shell securely anchored in the sediment (boxed area is shown on text-fig. 8A). Scale bars 10 mm.

9.2.1 c



Dictyonema pentlandica sp. nov. RSM GY.1985.30.1. A, knobbly appearance of stipe is caused by presence of large bithecae, × 10. B, dissepiments associated with each bifurcation, × 10.

9.2 Dendroid Taxonomy.

The majority of this section was published as Bull (1987). Text contained herein has been revised and updated and some new descriptions and comments added. The original illustrations have been retained and renumbered in the text.

Localities. All specimens were found in the North Esk Inlier, Pentland Hills, Scotland and, unless otherwise stated, they originate from the 'Gutterford Limestone' bed locality in the Gutterford Burn (see fig. 1).

Comments. A revised systematic diagnosis of Order DENDROIDEA Nicholson 1872 was given by Rickards, Baillie and Jago (1990:211), wherein they retain the Bulman (1938) diagnosis of Dendroidea rather than following Fortey and Cooper (1986) and placing the Anisograptidae within the Graptoloidea. Rickards et al. (1990b) follow the definition of the Acanthograptidae given by Bull (1987), which is also followed here.

One poorly preserved specimen has been discovered from the east shore of the North Esk Reservoir, which is considerably lower in the section than all previously collected dendroid material. This new specimen has dissepiments and some anastomosis and a conical rhabdosome shape, and is tentatively considered to be a reticulograptid. Further work is required to confirm this identification.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. RSM GY, Department of Geology, Royal Museum of Scotland, Chambers Street, Edinburgh; EDNCM and GI and EEB, Grant Institute of Geology, King's Buildings, West Mains Road, Edinburgh; GSE, British Geological Survey, Murchison House, West Mains Road, Edinburgh; BU Birmingham University; SM A. and A. Sedgwick Museum, Cambridge; NMW National Museum of Wales, Cardiff; P Nicholson collection, British Museum (Natural History), London.

Class GRAPTOLITHINA Bronn, 1846
Order DENDROIDEA Nicholson, 1872
Family DENDROGRAPTIDAE Roemer in Frech, 1897
Genus DICTYONEMA Hall, 1851.

(9.2).1

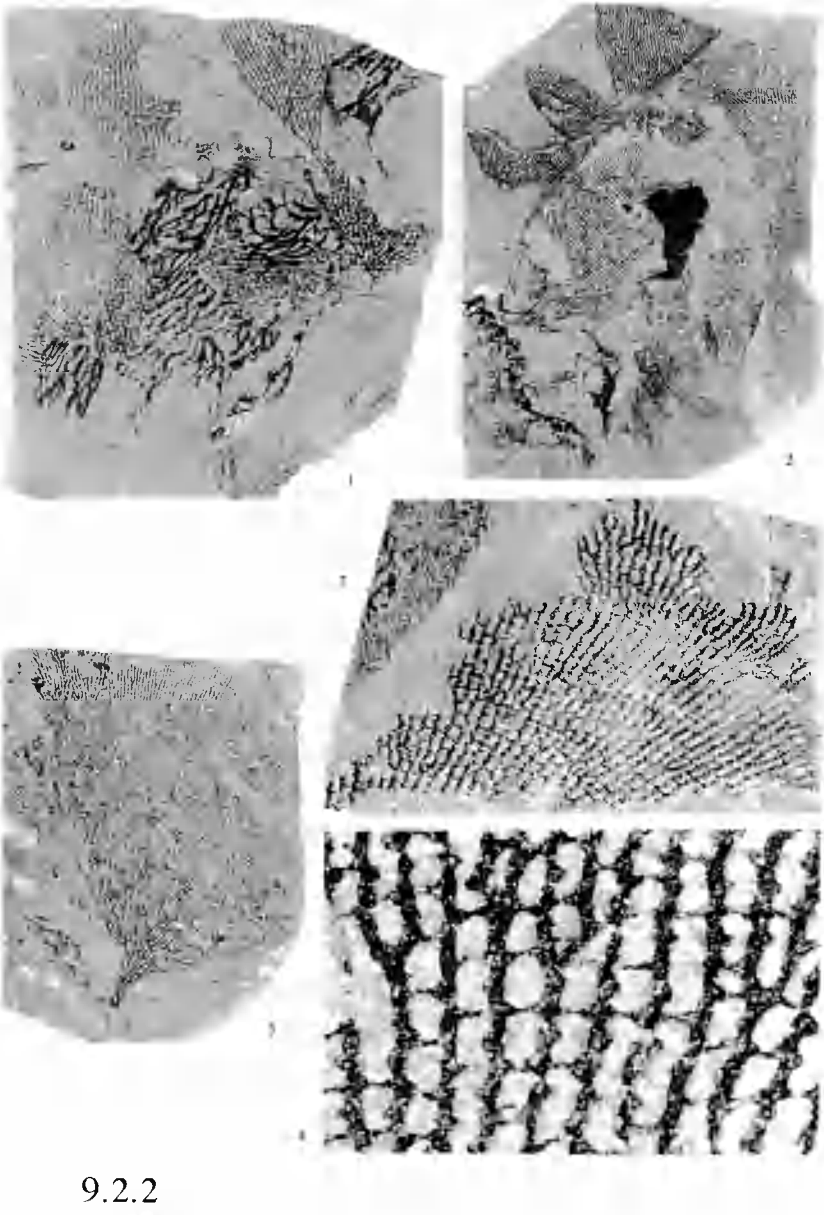
Dictyonema pentlandica Bull, 1987.
figs. 9.2.1 - 9.2.3.
(Also figs 7.2-7.9)

1987 *Dictyonema pentlandica* sp. nov. Bull, p. 122, pl. 17, fig. 1-5, text-figs 5-8.

Emended diagnosis. Rhabdosome broadly conical, up to 500 mm axial length, terminating proximally with a short stem 5-10 mm long, either attached to a solid object or accompanied by fine root fibres. Some proximal secondary thickening. Stipes slender, 0.22 mm wide, spaced 0.29 mm, 17-22 per 10 mm. Dissepiments regularly arranged perpendicular to the stipe and very thin, 0.06 mm diameter, 11-13 in 10 mm. Autothecae closely spaced, 0.67 mm apart, 28-30 in 10 mm, forming distinct swellings of the stipe, with single 0.4 mm long ventral, sub-apertural spine. Bithecae slender tubes with constant width of 0.03 mm looped over swelling at the ends of the autothecae. Rhabdosome capable of regeneration and regrowth in response to trauma.

Type material. Holotype RSM GY. 1985.30.1. Paratypes RSM GY. 1985.29.4 and EDNCM 20237.
Other material. RSM GY.1980.51.5, 1985.29.1, 1985.29.2, 1985.30.2, 1897.32 and thirty-four unregistered specimens in 'Drawer 61' of RSM; and three unregistered EDNCM specimens.

Description. The rhabdosome grew as a broad cone but, due to the extremely large size of this species, it is not possible to tell how wide the cone became. It is commonly preserved with the walls forming broad undulating folds, and this may reflect the original form of the



9.2.2

Figs. 1–5. *Dictyonema pentlandica* sp. nov. Reservoir Formation, Gutterford Burn . upper Llandovery. 1, RSM GY.1985.29.1, numerous fragments superimposed, associated with *Coremagraptus imperfectus* Kraft, 1982, × 0·5. 2, RSM GY.1985.29.2, several rhabdosomes showing basal attachment and rejuvenation of meshwork, × 0·5. 3, RSM GY.1985.30.1*p*, holotype, part of mesh showing an area of rejuvenation, × 3. 4, RSM GY.1985.30.1, part of mesh where thecal structure is preserved; note that a pair of dissepiments is associated with each bifurcation, × 10. 5, RSM GY.1985.29.4, showing secondary thickening of basal region and root fibres, × 1.

cone (figs. 9.2.1a&b). The base of the cone is sometimes secondarily thickened, up to double the thickness of the normal stipe, and has a short stem up to 10 mm long (fig. 9.2.1.b).

This species had a number of methods of benthic attachment, an organic apical disc, with or without associated attachment fibres, secured by attachment fibres alone or by firm attachment to shells (fig. 9.2.1.b) such as *Leptaena* (which lived partially buried in the sediment) or less well-anchored forms of shell, when the stem is accompanied by many small attachment fibres.

Autothecae preserved as regular swellings of the stipe (fig. 9.2.1.b) giving the stipe its distinctive knobbly appearance. Autothecal apertures simple, opening inside the cone of the rhabdosome and adorned with simple (unforked) autothecal apertural spines (described in more detail in chapter 7). Bithecae simple tubes opening into the side of the stipe. 2TRD approximately 0.35 mm throughout the rhabdosome. Stipes straight and evenly spaced, bifurcating regularly every 6 mm; this interval does not become appreciably larger distally. Bifurcation is concentrated on certain stipes, while others are continuous, straight, and unbroken.

Dissepiments are of constant length, perpendicular to the stipes, and often form continuous chains across the rhabdosome. Each point of bifurcation is directly associated with two dissepiments one on either side of the zone of bifurcation (fig. (9.2).1.b). The fenestellae formed by dissepiments and stipes are of fairly constant size (0.6 x 0.4 mm), and generally rectangular. When dissepiments grow from the swelling of a bitheca the fenestellae may appear ovoid. Zones of mesh rejuvenation occur, similar to those described by Bulman (1950) for other species of Dictyonema, and are probably related to regrowth after damage (see chapter 7).

Discussion. The presence of a holdfast structure confirms the attribution to *Dictyonema.*. *Dictyonema pentlandica* is subject to aberrant structure growth on both microscopic and macroscopic scale, including tubular outgrowths of the bithecae and large scale regrowth or mending of the rhabdosome following changes in growth patterns or predatorial attacks, or other environmental factors. Details of these aberrant structures are discussed in chapter 7.

Dictyonema pentlandica shows considerable resemblance to both *D. delicatulum* Lapworth, 1881 (see Boucek 1957 and Kraft 1984b) and *D. elegans* Bulman, 1928. It is distinguished by the very distinctive swollen or knotted appearance of the stipe, due to the thecal morphology; the large, very elongated nature of the rhabdosome; and the thinness of the stipes, which are slightly wider spaced (17-22 in 10 mm, rather than 22-23 or 20-24 respectively). The general outline of the stipe, caused by the thecal type, closely resembles *D. geniculatum* Bulman, 1928, but is easily distinguished from it by the smaller size and spacing of the stipes. Kraft (1984a) noted the close similarity of *D. delicatulum* and *D. elegans*, particularly in poorly preserved specimens; he stressed that 'their stratigraphic distribution must be taken as the fundamental criterion', *D. delicatulum* being limited to lower Llandovery and *D. elegans* limited to Wenlock. Care should be taken in limiting dendroid faunas to particular stratigraphic horizons; it is uncertain at present whether these three species are stratigraphically useful, as *D. pentlandica* appears to be intermediate both structurally and temporally. It is also possible that *D. pentlandica, D. delicatulum* and *D. elegans*, are all ecophenotypic variants of the same species.

(9.2).2

Family ACANTHOGRAPTIDAE Bulman, 1938

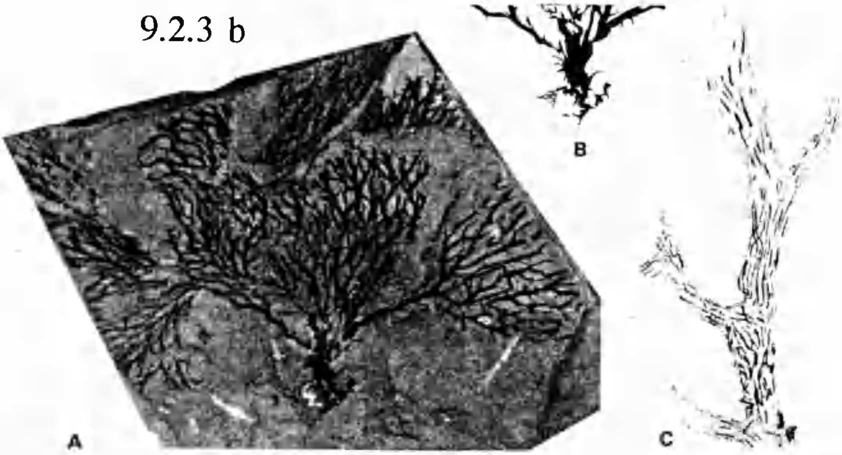
Included genera. I follow the classification of Boucek (1957; after Bulman 1938) and distinguish the genera *Acanthograptus* Spencer, 1878, *Thallograptus* Ruedemann, 1925, *Coremagraptus* Bulman, 1927, and *Palaeodictyota* Whitfield, 1902. Holland et al. (1967) referred only *Acanthograptus, Coremagraptus,* and *Palaeodictyota* to this family and assigned*Thallograptus* to the family *Inocaulidae.* The evidence presented below shows that *Thallograptus* is much more closely related to the *Acanthograptidae.*

Discussion. Boucek (1957: 86) grouped *Acanthograptus* and *Thallograptus* as forms with 'Rhabdosome composed of individual branches or completely ramified; branches mostly free, not uniting with each other'. Similarly, he grouped *Coremagraptus* and *Palaeodictyota* as forms with 'Rhabdosome infundibuliform, branches more or less flexuose and regularly united by anastomosis'.

Acanthograptus and *Palaeodictyota* are considered here to be the two morphological extremes of the family, no subfamilies (*sensu* Boucek) are defined here; since

9.2.3 a *Dictyonema pentlandica* sp. nov. Reconstruction showing the broad conical form; clusters lived attached by a short stem with root fibres to a solid object.

9.2.3 b



Thallograptus inaequalis Bouček. RSM GY.1985.28.7. A, at least six stocks attached to single stem, which is attached to a shell and associated with some root fibres (boxed area shown in C), × 1·5. B, attachment area, × 1·5. C, thecal structure, outline of thecal thickness, and thecal distribution are clear; branches taper to single theca, × 15.

9.2.3 c

Coremagraptus plexus Počta. RSM GY.1985.28.1*p*, showing regular anastomosis and many short side branches, associated with a short section of *Monograptus spiralis* Geinitz. Scale

Acanthograptus is not found in the North Esk Inlier, it is only considered for the sake of completeness. Acanthograptus is composed of relatively few tube-like thecae that regularly and continuously branch off from the main stipe in bundles of two autothecae and two bithecae to form very many small twigs, of approximately the same length, along the main stipes and usually ventrally or subventrally. It is possible that all thecae terminate by turning away from the stipe and forming a twig, and that none terminate as pores on the surface of the branch. Boucek's diagrams (1957, e.g. fig. 37f) show some anastomosis of main stipes, but this is probably due to one branch being superimposed on another; indeed the lack of anastomosis seems characteristic of this genus.

Thallograptus is an intermediate form. Like *Acanthograptus*, a major distinguishing feature is the lack of anastomosis, but *Thallograptus* has much less regularity in the arrangement of its twig-like side branches. The main stipes maintain a constant thickness. They bifurcate and also form lateral branches, but the latter gradually become thinner, consisting of fewer and fewer thecae until only one or two remain (fig. 9.2.5.a.B); this gives the rhabdosome a very spiny appearance (fig. 9.2.5.b). In some species the thinning begins abruptly, giving the branch a swollen appearance (fig. 9.2.5.c) at the base of the terminating twig. *Coremagraptus* also has many side branches that thin as the constituent thecae successively reach their full length, although in this genus most thecae terminate together abruptly without individual thecae becoming distally isolated. *Coremagraptus* shows quite frequent but not always very regular anastomosis. Sometimes two stipes are connected by a number of lateral branches from one joining with another. Side branches are increasingly less abundant in *Thallograptus* and *Coremagraptus*, and not all thecae terminate as discrete twigs (as in *Acanthograptus*). In both genera thecal apertures appear also as pores on the surface of the stipe (fig. 9.2.8.c).

Palaeodictyota is characterised by complete anastomosis, and represents the other morphological end member of the family. All thecae terminate within the stipe or as pores on its surface; none form twigs or discrete branches. The main stipes are fairly continuous and rarely bifurcate; the meshwork is formed by lateral branches joining other stipes, creating regular fenestellae with a distinctive and constant size and shape.

The more or less continuously variable morphological series from *Acanthograptus* through to *Thallograptus* and *Inocaulis*, towards genera with increasingly compound stipes and a lack of twigs was also accepted by Rickards Baillie and Jago (1990:226).

(9.2).2.1

Genus THALLOGRAPTUS Ruedemann, 1925

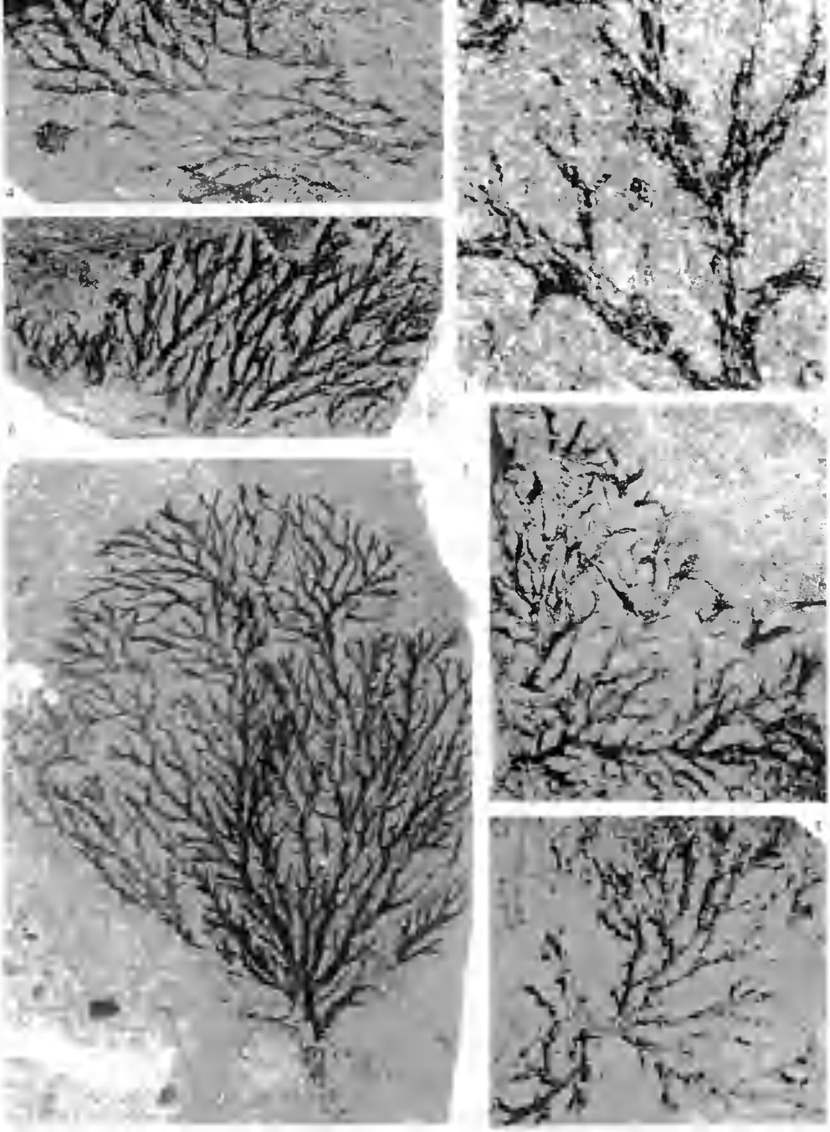
Type species. *Thallograptus succulentus* (Ruedemann, 1904). Lower Ordovician of Deep Kill, New York and Point Levis, Quebec, Canada.

Emended diagnosis. Rhabdosome shrub-like, stipes bifurcating and forming lateral branches irregularly; branches discrete, no anastomosis; thecae tubular, adnate throughout their length, opening as pores on the surface; branches taper to a single theca distally.

Discussion. Ruedemann (1947) assigned *Thallograptus* to the family *Inocaulidae*, together with the genera *Inocaulis*, *Medusaegraptus*, and *Diplospirograptus;* I follow Boucek (1957:88) in abandoning this classification. Neither the diagnosis by Bulman (1938) nor Ruedemann (1947:230) adequately summarised all of the features of the genus. Ruedemann's reference to 'hair-like filaments' (see Boucek 1957:97) appears either to be a misidentification or to refer to a different genus. Boucek (1957:97-98) discussed the lack of branch connection by cross-bars or anastomosis, and noted the intermediate nature of this genus between *Acanthograptus* and *Coremagraptus* without formally emending the diagnosis.

Thallograptus is recorded from both the Ordovician and Silurian. Boucek (1957) considered it to peak in numbers during the Ludlow, but it is now known to be common also in the Llandovery (Kraft 1982; Bull 1987). Numerous species have been described (Boucek 1957; Ruedemann 1947; Kraft 1982, 1984a), and these are distinguished by thickness of stipe, length of branches, whether branches appear inflated before termination, angle of stipe, bifurcation, and branching.

It is thought possible that a number of synonomies exist within the Thallograptids. It appears that this genus would benefit from a thorough review, including an inspection of all of Boucek's Bohemian material, and Ruedemann's collection, in conjunction with the NEI material.



9.2.4 BULL, *Thallograptus*

Figs. 1–4. *Thallograptus arborescens* Boucek, 1957. 1 and 4, Reservoir Formation, Gutterford Burn 2 and 3, Unit D of Tipper (1976), Wether Law Linn Formation; all *crenulata* Zone, upper Llandovery. 1, EDNCM 1984.87.3, branches show traces of thecal structure; fine lateral branches taper to a single theca, × 25. 2, EDNCM 1984.87.3, part of rhabdosome with regular branching, × 3. 3, EDNCM 1984.87.4, attached to a pebble and growing out in two directions, × 3. 4, GSE 14161, sparsely branched specimen, × 3.

Figs. 5 and 6. *T. inaequalis* Bouček, 1957. Reservoir Formation, Gutterford Burn *crenulata* Zone, upper Llandovery. 5, RSM GY.1985.28.10, compressed rhabdosome, × 1·5. 6, RSM GY.1985.28.9, distal portion of rhabdosome, × 2.

(9.2).2.1.1

Thallograptus arborescens Boucek, 1957

fig. 9.2.5.a-b; fig.9.2.4:1-4.

1865 *Chondritis versimilis* Salter: Haswell p.42, Pl. 4:20.
1957 *Thallograptus arborescens* Boucek, pp. 106 107, pl. 23, fig. 4.

Emended diagnosis. After Boucek (1957). Rhabdosome up to 30 mm wide, partially flabellate and shrub-like in form. Main branches approximately 1 mm thick, bifurcating regularly at 30-70°, thinning gradually to 0.5 mm. and nowhere perceptibly inflated. Lateral branching frequent, terminal branchlets 0.4-0.5 mm long, thinning to single theca, and separated by about 2 mm. Branches entirely free without anastomosis or dissepiments.
Material. RSM GY.1985.28.2-1985.28.4 and nine unregistered specimens all located in 'Drawer 62' of the RSM collections; CSE 14161 and two unregistered specimens; and EDNCM 1984.87.3 1984.87.5 and one unregistered specimen.

Description. RSM GY.1985.28.2 is undoubtedly *Thallograptus arborescens* and has terminating branchlets tapering from a maximum thickness of 0.2 mm to a single theca thickness (fig. 9.2.5a) of 0.04 mm. but exceptionally elongated up to 3 mm long. Branchlets curve out at progressively increasing angles from the stipe, which is not straight but changes course slightly at each branching episode. The mean angle of stipe bifurcation is 70°. Other specimens examined, such as RSM GY.1985.28.3 and 1985.28.4 (fig. 9.2.5 b), GSE 14161, and EDNCM 1984.87.3 1984.87.5 (pl. 9.2.4, figs. 1-3), are distinguished by a slight thickening at the base of some of the branchlets. All other dimensions are very similar to T. arborescens s.s., including main stipe thickness of 0.6-0.8 mm, stipe divergence angle of 45-60°; branchlets 1-2 mm apart and greater than 15 mm long; overall rhabdosome size up to 40 x 40 mm.

Discussion. Boucek noted only four specimens of this species (the holotype and three fragments), gave a diagnosis (emended here), and provided a clear figure (1957, pl. 23, fig. 4) from which it has been possible to identify the specimens figured here. All the present specimens are similar enough to be considered one species. Boucek noted that the branching pattern and lack of inflation of the branches made *T. arborescens* quite unmistakably distinct. Even allowing for a very slight inflation, this species is unlike any other. Some of the specimens figured here bear previous identification labels. GSE 14161 carries a label by 0. M. B. Bulman stating '*Koremagraptus* sp. B'; his identification is undated (possibly 1957) and incorrect. Hardie identified RSM GY.1985.28.4 as *Callograptus* cf. *salteri* Hall, while Lamont identified RSM GY.1985.28.2 as *Calyptograptus digitatus* Lapworth, 1881. However, *T. (=Calyptograptus) digitatus,* as currently recognised, has a much smaller rhabdosome and thinner branches, despite the resemblance of RSM GY.1985.28.2 to one of Lapworth's figures.

(9.2).2.1.2

Thallograptus inaequalis Boucek, 1957

Pl.9.2.4, figs. 5 and 6; figs. 9.2.3b and 9.2.5c

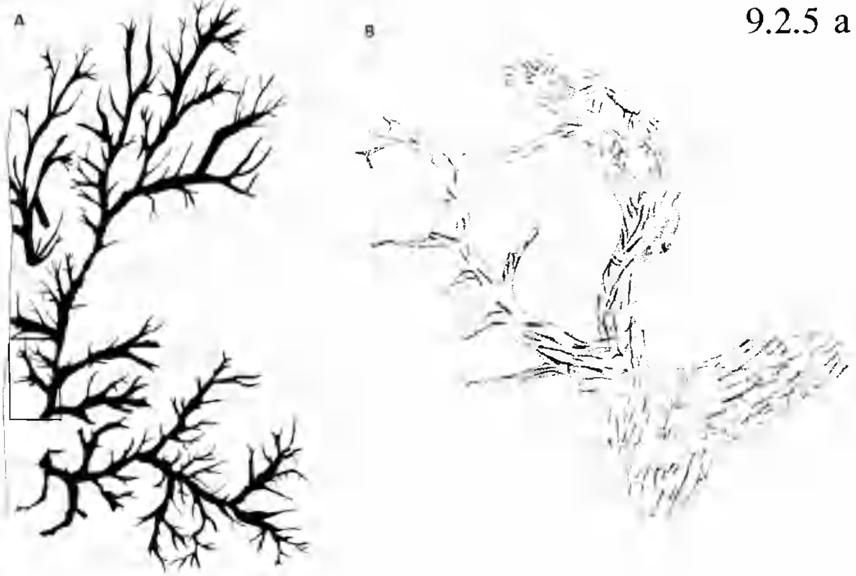
1957 *Thallograptus inaequalis* Boucek, p. 107, text-fig. 47b; pl. 21, figs. 4 and 5.

Emended diagnosis. After Boucek 1957. Rhabdosome of medium to large size, composed of separate flabellately shrub-like stocks attached by individual stems to a central stem. Each stock composed of unequally ramifying main branches and thinner lateral branches, forming a dense network. Main branch width 0.7-0.8 mm. Lateral and terminal branches decrease in thickness from 0.5 to 0.2 mm. Branches rarely irregularly inflated. Nine to ten branches in 10 mm.

Material. RSM GY.1985.28.5, 1985.28.7, 1985.28.9, and 1985.28.10, and GY.1897.32 from the Hardie Collection, all located in Drawer 62' of the RSM.

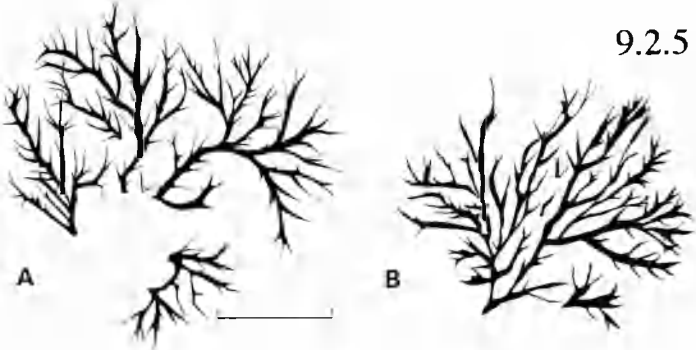
Description. The main central stem is sometimes attached to a shell (fig 9.2.3.b.A); secondary stems attach separate stocks to the central stem. Individual stocks number up to six per specimen and are preserved compressed above one another. Branches taper to a single thecal thickness (fig. 9.2.5.a.B) and are not perceptibly inflated.

9.2.5 a



Thallograptus arborescens Bouček. RSM GY.1985.28.2*p*. A, rhabdosome with well spaced, tapering branches, ×2. B, enlargement of boxed area on A, showing preservation of thecal tubes and branches tapering to a single theca, ×25.

9.2.5 b



Thallograptus arborescens Bouček. A, RSM GY.1985.28.3*p*, showing some complete, well-preserved branches, sometimes superimposed. B. RSM GY.1985.28.4, specimen displaying branching pattern and apparent swelling of branch before end. Scale bar 10 mm.

9.2.5 c

Thallograptus inaequalis Bouček. RSM GY.1985.28.5, single isolated stock. Branches appear to anastomose but were merely compressed and superimposed at deposition. Scale bar 10 mm.

Discussion. Boucek (1957) suggested that specimens may differ due to the irregular growth of the branches. As each stock arises from an individual stem, they must have been vulnerable to displacement on deposition (fig. 9.2.3.b.A), so producing a misleadingly irregular appearance.

(9.2).2.2

Genus COREMAGRAPTUS Bulman, 1927

Type species. C. onniensis Bulman, 1927. Upper Llandovery, Shropshire, England.

Description. The stipe consists of many generations of tightly packed, elongate thecae twisted into a rope-like form. Each theca is about 0.04 mm wide and average side branch width (preserved compressed) is 0.3 mm.

Coremagraptus can develop quite large rhabdosomes, at least 130 x 70mm. Anastomosis is common but irregular, and usually only the lateral branches are involved. Sometimes two stipes are united by unidirectional lateral branches from one stipe joining another.

Numerous species of *Coremagraptus* have been described (Bulman 1927; Boucek 1957; Kraft 1982). Distinguishing features are thickness of stipe, degree of anastomosis, thickness, length, and abundance of lateral branches, and overall size.

Discussion. The nature of the thecae has been discussed at length (e.g. Bulman 1955, p. V27; Boucek 1957:87;114). Thecae are not normally observed in unsectioned material, but specimens figured here are preserved as partially 3-D, internal moulds, and thecal structure is discernible in the stipe walls. The ends of the side branches are detectably thinner, consisting of a smaller bundle of thecae than the main stipe (although considerably more than the three or four thecae mentioned in Bulman's original diagnosis). Where a pair of stipes are united by unidirectional lateral branches they act as one branch, and are quite often found superimposed on another pair.

(9.2).2.2.1

Coremagraptus kalfusi Boucek, 1957

Pl.9.2.7, fig. 1

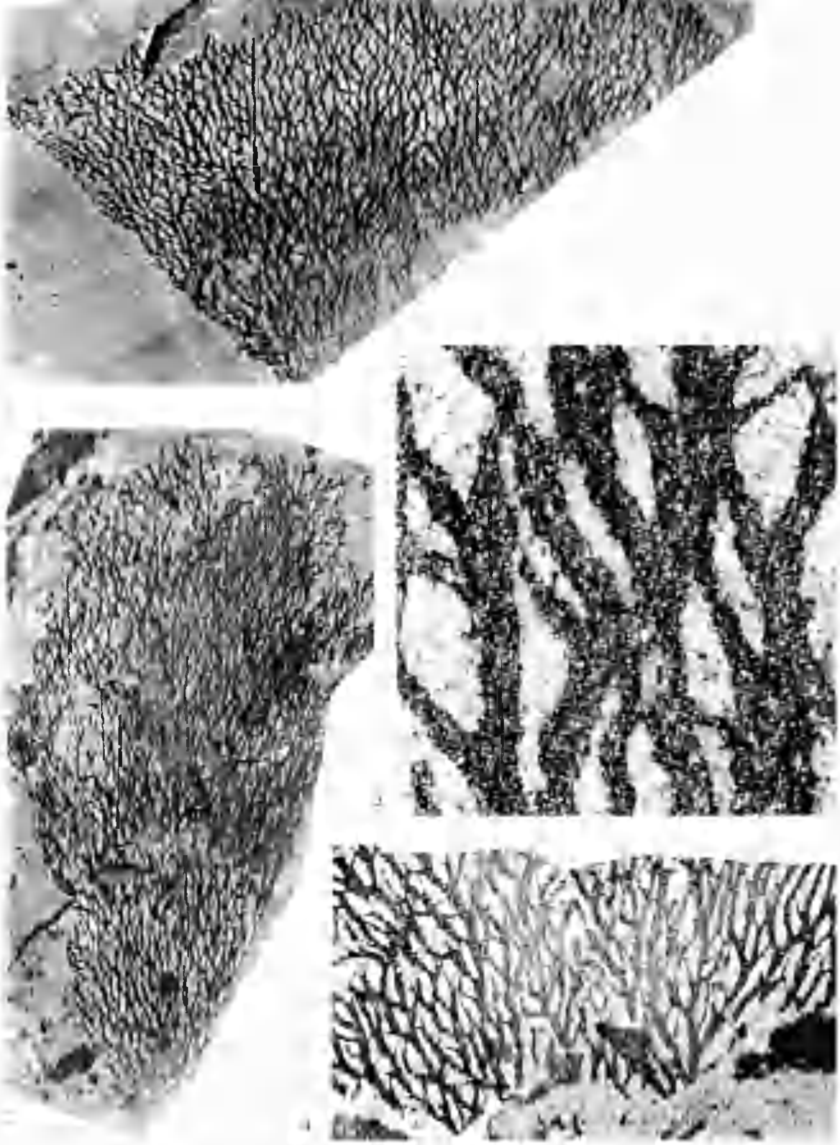
1931 *Callograptus* sp. Boucek, pl. 22, fig. 2a.
1957 *Coremagraptus kalfusi* Boucek, p. 124, text-fig. 57b; pl. 26, fig. 3.

Diagnosis. See Boucek (1957:124).

Material. One specimen on RSM GY.1985.28.1. Only one other specimen is known, the holotype figured by Boucek (1957) from Lochkov, Bohemia.

Description. The specimen shows distinctive secondary thickening in the basal regions, up to three times normal stipe thickness of 0.4-0.6 mm. New stipes are formed by both bifurcation and lateral branches. Most main branches form dichotomously; most side branches form laterally. Six to seven side branches occur in 10 mm and the angle of bifurcation is 30-40°. Side branches reach a mean length of 1 mm before terminating and are more common proximally; they often have blunt ends, and it appears that all thecae ceased to grow when a certain length of branchlet had been attained. Anastomosis is more common distally, with fenestellae of a fairly constant sized, elongated oval (27 x 10 mm). Overall rhabdosome size, 60 x 40 mm.

Discussion. This specimen and a specimen of *C. plexus* are on slab RSM GY.1985.28.1 which has been mislabelled '*Acanthograptus cf. multispinus* (Bassler)'. It is well preserved; such features as blunt branchlet ends are unlikely to be the product of damage to the colony during or after deposition.



BULL, *Coremagraptus*

9.2.6

Figs. 1–4. *Coremagraptus imperfectus* Kraft, 1982. Reservoir Formation, Gutterford Burn *crenulata* Zone, upper Llandovery. 1, RSM GY.1985.28.8, distal region of large, fan-shaped rhabdosome, × 1. 2, RSM GY.1985.28.11, sheared, incomplete fragment, × 1. 3, GSE 12093, showing anastomosis, side branches, and traces of thecal structure, × 10. 4, GSE 12093, showing anastomosis and many terminating side branches, × 2·5.

(9.2).2.2.2

Coremagraptus imperfectus Kraft, 1982

Fig. 9.2.6; Fig. 9.2.1.a

1982 *Coremagraptus imperfectus* n. sp. Kraft, p. 90, pl. 11, fig. 1; pl. 12, fig. 2.

Emended diagnosis. After Kraft (1982:90). Rhabdosome conical, of medium to large size, up to 120 x 70 mm. Stipes irregularly curved but continuous and 0.4-0.8 mm thick. Stipes occasionally bifurcating, lateral branching at 45-50° common, forming both new stipes and thinner branches. Six to nine stipes in 10 mm. Anastomosis frequent; other branches thin (thecae cease to form), terminate with rounded ends, and are up to 2 mm long. Fenestellae irregular ovoids pointed at each end, 1.0-1.5 mm wide and 2.5-5.0 mm long. Thecae tubular, adnate throughout their length with mean thickness of 0.08 mm.

Material. RSM GY.1985.28.8, 1985.28.11 and eight unregistered specimens, all located in 'Drawer 62' of the RSM, GSE 12093 and its counterpart. One other specimen is known, the holotype figured by Kraft (1982) from the Zelkovice Formation, Hyskov, Czechoslovakia.

Discussion. Kraft's original figured specimen is incompletely preserved but is unmistakably conspecific with the material described here. Both have long sections of stipe between each branching or anastomosing episode, and both show a tendency for the lateral branches of one stipe to arise in one direction. These may then join (anastomose) with another stipe that is not at that point producing any branches, so that a 'step-ladder' appears, which is often free to move independently and can be found superimposed over other stipes (fig.9.2.8.a). *C. imperfectus* is fairly similar to *C. spectabilis* Boucek, 1957 (a common species of *Coremagraptus* from the Lochkov beds of Lejskov, Czechoslovakia). *C. spectabilis* has much stouter, thicker stipes, which do not thin towards the ends of the branches, and *C. imperfectus* does not show secondary thickening. Hence *C. spectabilis* is not an adult form of *C. imperfectus*.

(9.2).2.2.3

Coremagraptus plexus (Pocta, 1894)

Fig 9.2.3c

1894 *Desmograptus plexus* Pocta, p. 188-189, pl. 5, figs 1 and 2 (non figs. 3 and 4)
1894 *Desmograptus textorious* Pocta, pl. 4, fig 9 (non fig. 8, 8a)
1957 *Coremagraptus plexus* (Pocta) Boucek, 117-119, fig 54 a-d; pl. 27:2,3; pl. 28:1; pl. 33:3

Material. One well preserved specimen , RSM GY. 1985.28.1, a fragment of a larger form.

Description. This species is distinguished by the presence of many short processes on the stipe walls, or very many short side branches 0.2-0.4 mm long. These appear to be bundles of thecae turning away from the stipe together when they have nearly reached their total length; this feature is very much more common in C pseudoplexus Boucek 1957. The present specimen is also from a much older horizon.

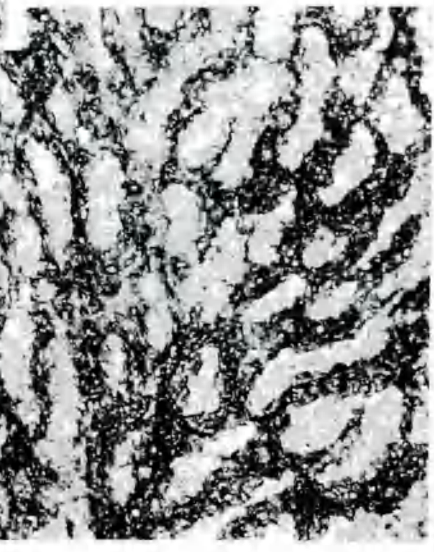
The specimen figured is on the same mislabelled slab as a specimen of *C. kalfusi* (see above). It is a broken fragment but still quite large (20x50 mm). Most branches form through bifurcation of others. Anastomosis is quite common, although some branches were superimposed during compression to appear anastomosed.

(9.2).2.3

Genus *PALAEODICTYOTA* Whitfield, 1902.

Type species. Palaeodictyota anastomotica (Ringueberg, 1888) from the Ordovician and Silurian of New York, Ontario and Kentucky. Figured by Ruedemann (1947:269).

Diagnosis. (Emended Rickards *et al.* 1990b) Rhabdosome fully anastomosed except at growing tips; no projecting thecae, which open on ventral side of stipes, closely adpressed; numerous tubes present in any stipe cross section; presumed several stolonal chains; compound.



BULL, *Coremagraptus*, *Palaeodictyota*

9.2.7

Fig. 1. *Coremagraptus kalfusi* Bouček, 1957. Reservoir Formation, Gutterford Burn *crenulata* Zone, upper Llandovery. RSM GY.1985.28.1, showing basal secondary thickening, a distal increase in anastomosis, and branches abruptly truncated; associated with *Monograptus spiralis* Geinitz, 1842, × 2.

Figs. 2-4. *Palaeodictyota pergracilis* Hall and Whitfield, 1872. Location as fig. 2, GSE 14163, showing shape of fenestellae and distortion of mesh, × 3. 3, GSE 14164, × 3. 4, showing thecal structure and thecae terminating as pores on the surface of stipes, × 10.

Discussion. The presence of tubular thecae and compound stipes (a characteristic of the *Acanthograptidae*), distinguishes *Palaeodictyota* from the otherwise morphologically similar *Desmograptus*. Ruedemann (1947) separated this genus from the *Acanthograptidae* and referred it to '*Dendroidea Incertae sedis*".

Occurrence. Most common in the Wenlock to upper Ludlow of Bohemia; recorded from Ordovician to uppermost Silurian rocks.

(9.2).2.3.1

Palaeodictyota pergracillis (Hall and Whitfield, 1872)

Pl. 9.2.7, figs 2-4, figs 9.2.8b.

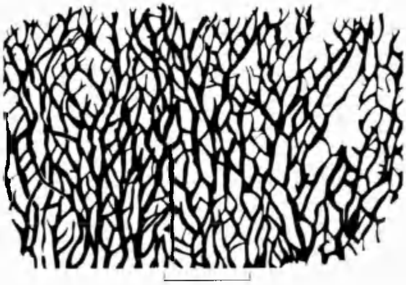
1872 *Dictyonema pergracile* Hall and Whitfield, p. 181, figs.
see Ruedemann (1947:272) for synonomy.
1908 *Desmograptus pergracillis* Ruedemann p.2
1915 *Desmograptus pergracillis* Bassler p. 403
1947 *Palaeodictyota pergracillis* (Hall &Whitfield); Ruedemann: 212, pl. 23:10, pl. 30:10,11

Emended diagnosis. Rhabdosome of medium to small size, 30x40 mm, narrowly conical, extending from short stems. branches thin and continuous, 0.2-0.5 mm. Bifurcation rare, lateral branching common. Anastomosis complete, branches do not terminate separately. Branches of constant thickness, forming a flexible meshwork with sixteen to eighteen stipes in 10 mm. Fenestellae rounded rectangular, 1.7-4.0 mm long by 0.3-1.6 mm wide. Thecae tubular, adnate throughout, opening as pores on the stipe surface.

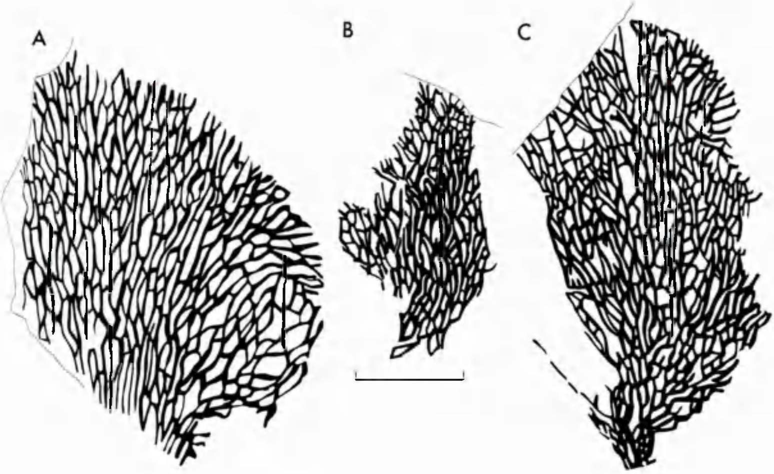
Material. GSE 14163-14165, and 12040; unregistered RSM specimens in 'Drawer 62' of the museum.

Description Stem about 3 mm wide and 4 mm long, with stipes branching out from it (fig. (9.2.8.b.C). Branches usually remain straight but are pulled around fenestellae as if it were more important for the fenestellae to maintain a constant shape. The meshwork is also prone to being preserved stretched out at the edges, or compressed (fig 9.2.8.b.A). Branching and anastomosis follows no regular pattern. branches maintain a remarkably constant thickness. Thecae open as pores on the surface, but do not protrude from the stipe and are not seen in profile view.

Discussion. This species is very similar in general morphology to *P. undulatum* (Pocta 1894) (see Boucek 1957:131), but is distinguished by its much finer branches (less than 0.5 mm compared with over 1.0 mm). *P. raymondi* Ruedemann, 1947, has similar meshwork dimensions, but a much smaller rhabdosome. *P raymondi* also encompasses extreme variation in mesh shape and size, and shows some secondary thickening, which is not seen in *P. pergracillis.*
GSE 14164 and GSE 12040 were identified on specimen labels by O.M.B. Bulman as *Koremagraptus* sp. A (undated).



9.2.8 a *Coremagraptus imperfectus* Kraft. GSE 12093, showing unilateral anastomosis, the superimposing of neighbouring stipes, and the presence of short side branches. Scale bar 10 mm.



9.2.8 b *Palaeodictyota pergracilis* Hall and Whitfield. A, GSE 14163, showing the mesh stretched at one edge but continuous elsewhere. B, GSE 14165, specimen greatly compressed on deposition, causing mesh to close up. C, GSE 12040, showing usual distribution of mesh, extending from stem region. Scale bar 10 mm.

9.2.8 c

Thecal structure of *Palaeodictyota pergracilis* Hall and Whitfield. GSE 14163, showing thecae terminating as pores on surface of stipes, × 15.

(9.3.1).1

Order GRAPTOLOIDEA Lapworth, 1873
Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily MONOGRAPTACEA Lapworth, 1873
Family MONOGRAPTIDAE Lapworth, 1873
Genus MONOGRAPTUS Geinitz, 1852 *sensu stricto.*

Type species. Subsequent designation; Bassler 1915:822; *Lomatoceras priodon* Bronn, 1835:56, Pl.1:13, from the Silurian of Germany.
Diagnosis Rhabdosome straight or with curvature, usually proximally. Theca are hooked, with or without apertural spines or processes. Thecal apertures face proximally or proximo-dorsally. Thecae overlap, often for half their length or more distally.
Remarks. When used in the strict sense, the genus *Monograptus* unites a number of mostly robust species. From the *Sp. turriculatus* Biozone onwards *Monograptus* was one of the dominant Silurian genera.

(9.3.1).1.1

Monograptus priodon (Bronn, 1835)
Fig 9.3.1 E-G and H; 9.3.4. E-F; Fig. 9.3.5.K

1865 *Graptolites priodon* Geikie: Haswell p.41.
1962 *Monograptus* cf. *priodon* : Mykura and Smith, p.14.
1974 *Monograptus priodon* : Tipper
1989 *Monograptus priodon* : Robertson p. 138.
(see Loydell 1993:107, for extensive list of synonomies including 148 references).

Holotype. By monotypy; the specimen figured by Bronn 1835, pl. 1:13, from the Silurian of Germany.

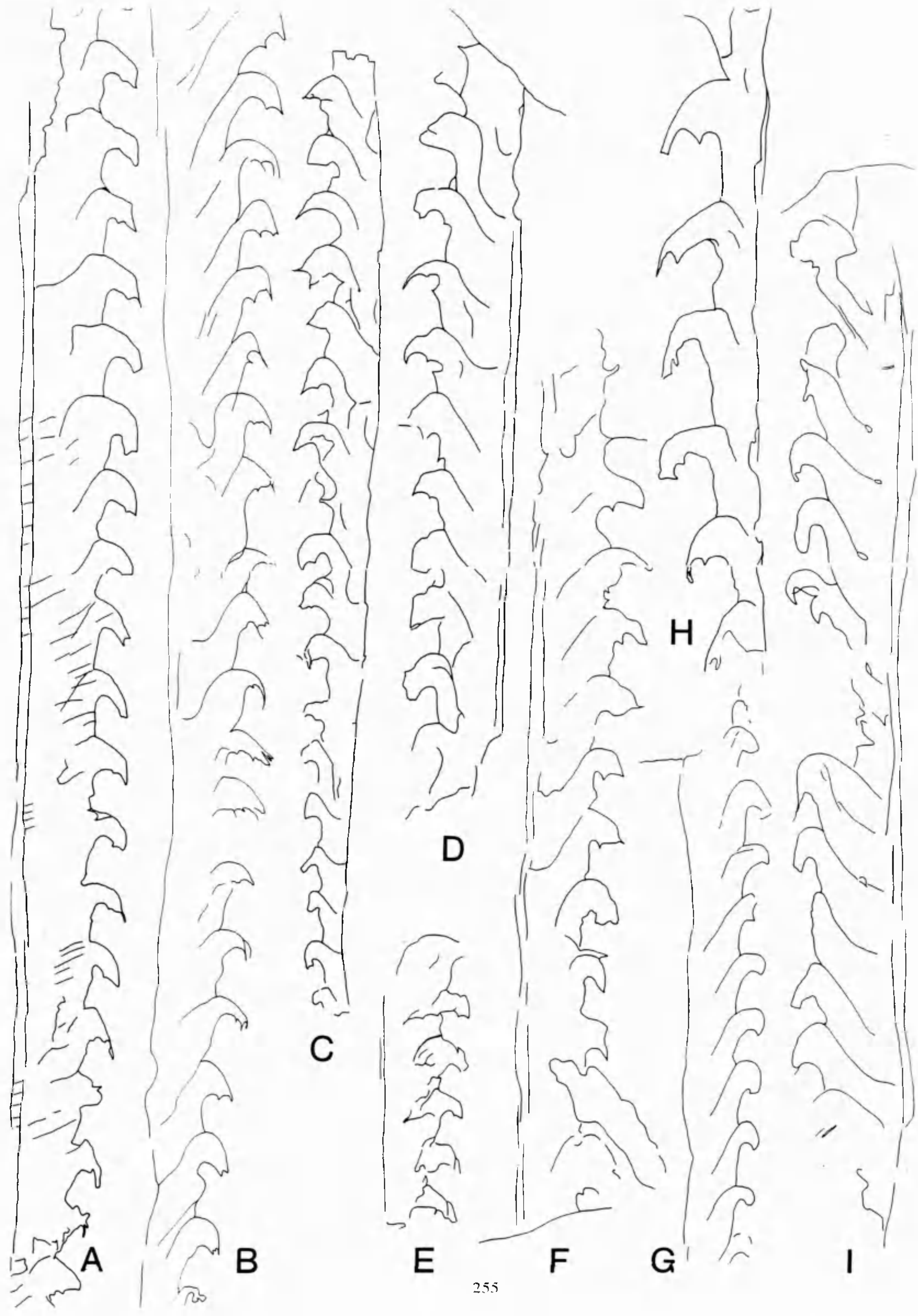
Material. 7 specimens and numerous fragments, preserved in partial to full 3D relief, some partially pyritised, from Reservoir, Deerhope and Wether Law Linn Formations, rocks of the *Oktavites spiralis* graptolite biozone age, and ranging up to the Llandovery / Wenlock boundary (possibly ranging through *grandis* and *insectus* biozones).

Diagnosis. Rhabdosome generally straight, bearing hooked thecae. Rhabdosome width increases rapidly from c. 0.6 mm at th1 to c. 0.9 mm at th5, and then to a distal maximum of 3 mm. 2TRD's are low 1.05 to 1.4 mm at th1, 1.5 to 1.9 mm distally.

Description. The rhabdosome is generally very straight, with uniform robust thecae. The prothecae are triangular, overlapping consistent with that recorded by Loydell (1993:110) as one-fifth proximally to one-half distally. Metathecae hooked, with some small spinose apertural ornamentation proximally, hooked portion of metatheca occupying one-third of the overall stipe width (see figure 9.3.1). Metathecae that are simple tubes of constant width, not tapering towards the simple aperture. The metathecae are hooked abruptly, turning through 90°, so that the aperture faces proximally. Sicula about 1.5 mm long.

Remarks. M. priodon is one of the most ubiquitous Silurian graptolites, recorded as common from rocks of *turriculatus* to *riccartonensis* Biozone ages (and possibly later), although its true range may be only *griestoniensis* to *riccartonensis* Biozones (mid Telychian to mid Sheinwoodian), and has been used to revise the known range of successions such as the Dalradian of Scotland (Skevington, 1971).A thorough review of this species (and methods of distinguishing this species from other similar species) is given by Loydell 1993:107-112, and the specimens from the NEI agree broadly with this description. This species is recorded as common from shallow water deposits (Berry and Boucot 1972) worldwide.

Figure 9.3.1 All from the Reservoir Formation, Gutterford Burn, North Esk Inlier, except I, from the Wether Law Linn. A-D, and H, *Monograptus paraprioidon* Boucek 1931; E-G and I, *Monograptus priodon* (Bronn, 1835). **A**, GI 22223 distal section X 14; **B**, GI 47566, distal section with clear thecal spines X 14; **C**, EEB 212, proximal section X 14; **D**, EEB 214, distal section X14; **E**, R82, X14; **F**, EEB 211, X 14; **G**, GI 1886, X14; **H**, JCT 79:0127, very proximal few thecae with spines, X 27; **I**, EEB 225, distal section X13.


A
B
C
D
E
F
G
H
I

When specimens of this species are preserved with the aperture and hooked portion turned away from the rock plane (lateral view) or the specimen is badly damaged so that the hooked portions are removed, then at first glance this species can resemble *Monoclimacis*, and is probably the cause of many misidentifications in the field.

Graptolite "profile plots" (see section 9.1.2) for all of the *Monograptus priodon* group specimens from the NEI have been made. It can be seen from fig 9.1.2 that the material from the Pentland Hills is clearly divisible into two species, (*M. priodon and M. parapriodon*). Similarly this technique is used to distinguish between other species from published data (see section 9.3.2).

Size ranges of NEI material (see Chapter 10 for full data listings).

Monograptus priodon

theca	DVW	2TRD
1	0.55-0.75	1.07-1:27
5	0.75-1.12	1.14-1.43
10	1.02-1.37	1.39-1.75
15	1.25-1.56	1.62-1.94
20	1.33-1.63	1.83-2.19
25	1.58-1.82	1.89-2.24
30	1.62-1.87	2.11-2.27
35	1.68-1.97	2.06-2.37
40	1.75-2.04	2.13-2.42
45	1.80-2.07	2.19-2.45
50+	1.82-2.12	2.22-2.50

Distinguishing from other species. M. priodon has a greater DVW proximally (0.6 to 0.8 mm.) than *M. parapriodon* (0.4 to 0.7 mm). However *M. priodon* has a much lower 2TRD proximally (1.1 to 1.3 mm) than *M. parapriodon* (1.4 to 1.8 mm). The rate of increase of 2TRD per unit increase in width of *M. priodon* , is much higher than *M. parapriodon*, resulting in a much steeper curve on a profile plot, although for *M. priodon*,. This tails off distally as DVW goes on increasing with 2TRD increasing much less or remaining constant distally. For distal sections, the species are easily distinguished, as *M. parapriodon* does not reach the same DVW as *M. priodon* , with a maximum of about 2 mm, whereas the recorded distal width of *M. priodon* can be 3 mm. The sicula length of 1.5 mm and DVW at th. 5 accord well with those recorded for British *M. priodon* Uppermost Llandovery (*crenulatus* biozone) specimens by Lenz (1974:270) in his study of evolution of *M. priodon.*

The lower 2TRD and greater DVW proximally, and the gradual increase in both measurements resulting in higher 2TRD and in particular, larger DVW for this M. priodon (see fig. 9.3.2), enables it to be distinguished easily from all other '*M. priodon*' group species.

(9.3.1).1.2

Monograptus parapriodon Boucek 1931

Figs 9.3.1. A-D and H; Fig. 9.3.4.C-D; Fig. 9.3.12.E

1931 *Monograptus parapriodon* n. sp. Boucek , p. 17, fig. 4 a, b.
?1966 *Monograptus kovalevskyi* n. sp.: Obut and Sobolevskaya, p.X
non1971 *Monograptus (Monogr.) priodon parapriodon*. Boucek 1931. Schauer p. 56, Pl. 36:12-13.
1974 *Monograptus* cf. *rickardsi* : Tipper
1981 *Monograptus ?parapriodon*. Boucek, 1931. Bjerreskov: p.41, Pl. 4:2

Type material. Specimen figured by Boucek 1931:17, specimen no. 157, from Vyskocilka, Gothlandian of Bohemia, housed in the collections of the Charles University, Prague.

Material. More than 50 specimens, mostly incomplete. Six full proximal to distal specimens, preserved in partial relief. All from the Gutterford Burn, Reservoir Formation of the NEI. Specimens collected recently now housed in the Grant Institute of Geology, Edinburgh. Some specimens housed in the Royal Scottish Museum also from the same locality

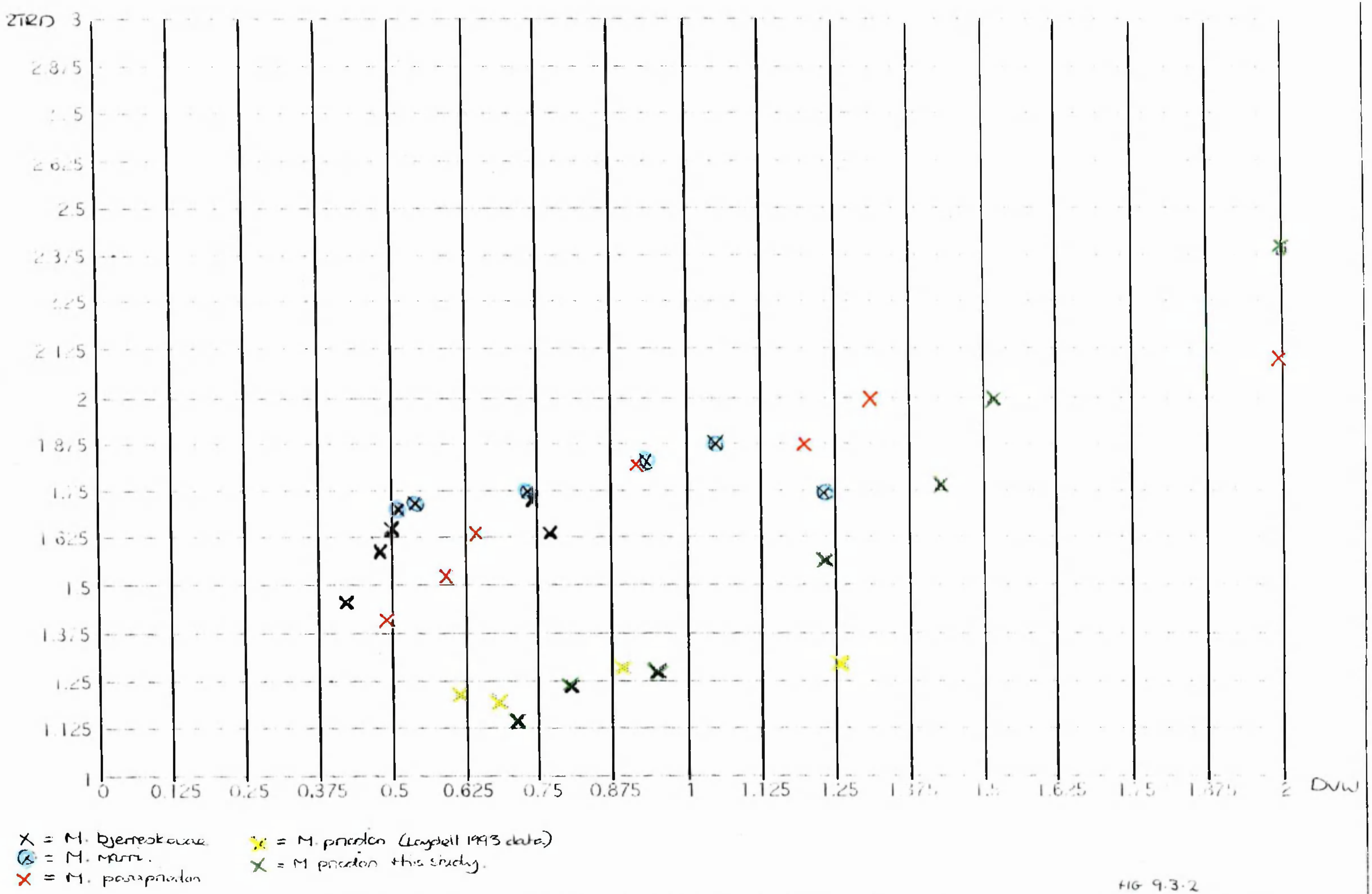

ZTRD
3
2.875
2.75
2.625
2.5
2.375
2.25
2.125
2
1.875
1.75
1.625
1.5
1.375
1.25
1.125
1
0
0.125
0.25
0.375
0.5
0.625
0.75
0.875
1
1.125
1.25
1.375
1.5
1.625
1.75
1.875
2
DVW
X = M. bjerreskovae
⊗ = M. mum.
X = M. parapriodon
X = M. priodon (Laydell 1993 data)
X = M priodon this study.

FIG 9.3.2

Original description. "Hydrosome très long, parfaitement droit et assez mince - depuis la sicula il s'élargit peu à peu pour atteindre une largeur de 1.2 mm. Il y a 10 hydrothèques du type priodon par 10 mm. Vyskocilka - zone représentant probablement un terme de passage entre la zone à *M. greistoniensis* et la zone à *M. subconicus* . Associé à *Mon. largus, praecedens, speciosus, Ret. geinitzianus angustidens, Diversograptus ramosus* et autres."

Translation: Rhabdosome very long, perfectly straight and very thin - from the sicula it enlarges little by little until attaining a width of 1.2 mm. There are 10 thecae of priodon type in 10mm. Vyskocilka - zone representing a timespan between the M. griestoniensis zone and the *M. subconicus* zone. Associated with.......

Description. Rhabdosome long, thin and very straight, sicula may be displaced to lie displaced behind dorsal margin of rhabdosome. Sicula 0.9 mm long, reaching to base of th2, with virgella present. Thecae of *priodon* type, with triangulate prothecae overlapping up to one third proximally (usually one quarter) and one third distally. Metatheca sharply hooked, turning 90° to face proximally, with distal section lying at about 50° to the stipe axis. Metathecae simple tubes, not narrowing appreciably towards aperture. Aperture ornamented with two short spines on the upper surface. These spines can be better preserved than the rest of the thecae, and sometimes are the only part of the thecae preserved (see fig 9.3.5.K), suggesting they may have been more robust than the remainder of the thecae, having the appearance of rods originating from the protheca, and running the length of the dorsal margin of the metatheca.

Measurements taken from NEI material (see appendices for full data listings).
Monograptus parapriodon

theca	DVW	2TRD
1	0.32-0.61	1.32-1.59
5	0.47-0.79	1.50-1.81
10	0.75-1.09	1.64-2.00
15	0.98-1.31	1.72-2.04
20	1.16-1.46	1.83-2.19
25	1.31-1.58	1.92-2.22
30	1.43-1.69	1.94-2.25
35	1.61-1.79	1.95-2.26
40	1.73-1.88	2.00-2.28
45	1.83-1.93	2.02-2.27
50+	1.93-2.08	2.06-2.28

Measurements of NEI material compare well with measurements taken from the original illustrations (Boucek 1931:4,a,b), which are:-
Sicula 1.4 mm long, reaching to base of th2, stipe 0.4 mm wide proximally, reaching 0.85 mm by th15 and 1.2 mm wide distally. 2TRD proximally 1.4 mm, distally 1.6 to 2.0 mm. Specimens in original illustration do not have spines on thecal aperture. Common usage indicates this species to be spinose (Loydell 1993:107), however, few taxonomic descriptions are available for comparison.

Material of this species was donated by Boucek to Dr. Palmer and then on to the collections of the National Museum of Wales. The following measurements were obtained from specimen no. NMW: 91.53G.26 identified by Boucek as *M. parapriodon*

Theca	1	5	10	15	20	30	40	50
DVW	0.47	0.71	0.85	0.95	1.01	1.05	1.28	1.42
2TRD	1.82	1.91	2.03	2.17	2.25	2.31	2.38	2.41

Dimensions are quite similar in proximal portions which does not readily conform with measurements from the PH distally.

Distinguishing from other species. The principal feature distinguishing *M. parapriodon* from other *priodon*-group species is the spinose apertural ornament. *Stimulograptids* also have prominent paired apertural spines, but they do not show any appreciable thecal overlap, even distally. Differentiated from *M. bjerreskovae* Loydell 1993 by *M. parapriodon* having greater DVW, proximally and distally, due to the slow increase in DVW of *M. parapriodon*. Proximal portions of these two species, with sicula absent are best distinguished by the greater proximal thecal overlap of *M. parapriodon*. The introduction of graptolite profile plots may also help distinguish these two species (see below). Differentiated from *M. marri* by the greater thecal overlap proximally of *M. parapriodon*, and by greater 2TRD proximally and distally of *M. marri*. Distinguishing from *M. priodon*, see above (9.3.1.1).

(9.3.1).2 Comparison of *Monograptus* s.s. species using profile plots.

Data for 2TRD and DVW at specific thecal levels for four species (data averaged from that published by Loydell (1993) and also data from this study), has been collected (see fig 9.3.2.a), and plotted using a graptolite profile plot. It was hoped that it would be possible to identify the profile of each species and hence graphically illustrate the differences between the species.

As can be seen from figure 9.3.2, plotted measurements given by Loydell (1993) for *M. priodon* agree very well with those for *M. priodon* from the NEI, and plot within the same area of the graph. This species is also quite easily distinguishable from other species by its much smaller 2TRD and greater DVW, particularly distally.

	th. 2	th. 3	th. 5	th. 10	th. 15	th. 20	th. 50	
M. bjerreskovae DVW		0.42	0.48	0.5	0.74	0.77		
M. bjerreskovae 2TRD		1.46	1.59	1.65	1.73	1.64		
M. marri DVW		0.51	0.54	0.73	0.93	1.05	1.23	
M. marri 2TRD		1.7	1.72	1.75	1.83	1.88	1.75	
M. priodon DVW		0.61	0.68	0.89	1.26			
M. priodon 2TRD	1.22	1.2	1.29	1.3				
M. parapriodon DVW E		0.49	0.59	0.64	0.92	1.2	1.31	2
M. parapriodon 2TRD E		1.41	1.53	1.64	1.82	1.87	2	2.1
M. priodon DVW E	0.71	0.8	0.95	1.23	1.43	1.52	2	
M. priodon 2TRD E	1.15	1.24	1.28	1.57	1.77	2	2.4	

Figure 9.3.2.a.
Monograptus profile plots, data.
DVW against 2TRD at various thecal levels of different species.
Data taken from Loydell 1993 for *M. bjerreskovae, M. marri, and M. priodon*

Data marked with E, taken from NEI material
Used to plot figure 9.3.2.

M. bjerreskovae has very similar 2TRD measurement to *M. parapriodon* but much smaller DVW (Loydell does not give distal measurements for *M. bjerreskovae* , but states that *M. parapriodon* is much broader distally). *M. bjerreskovae* has smaller 2TRD and DVW than *M. marri* , and positioning of all of the points plotted for *M. marri* is much further to the left of the graph than *M. bjerreskovae* clearly showing that *M. marri* has a much greater DVW all along the stipe.

M. parapriodon has similar DVW proximally to *M. marri* , and possibly *M. parapriodon* is slightly larger than *M. marri* , but *M. marri* has much greater 2TRD and according to Loydell 1993:106, *M. marri* has slightly greater 2TRD distally with similar DVW to *M. parapriodon* (These are stratigraphically quite distinct species which are mainly differentiated morphologically by thecal overlap and spinosity of *M. parapriodon*).

In summary, it is clear that different species of one genus with very similar thecal structure, can clearly be differentiated using “Graptolite Profile” plotting.

(9.3.1).3. DVW comparison of *M. priodon* and *M. parapriodon* .

Measurements were made of DVW of *M. priodon* and *M. parapriodon* specimens. Separate measurements of protheca width and overall total DVW including metatheca were recorded at recognised thecal levels (th.1, th.5, th.10 etc.). A comparison of the readings for both species was made in order to find out if the same proportion of the total DVW is occupied by the free section of the metatheca of both species.

The results are plotted in figure 9.3.6. It can be seen that the spacing between the two points measured at each thecal level (ie metatheca length) is remarkably similar for both species at the same thecal level, for example, the metatheca of both *M. priodon and M. parapriodon* at th. 25 occupies about 0.5 mm of the total DVW. However, at th. 25 of *M. priodon* , 0.5 mm of metatheca occupies 33% of the total DVW, but for *M. parapriodon* at th. 25, the metatheca occupies 40% of total DVW.

The percentage of total DVW of *M. parapriodon* occupied by the metatheca increases far more distally than for *M. priodon.* Consistently all along the stipe, the metathecae of *M. parapriodon* occupies a much greater percentage of the total DVW than it does for *M. priodon* .

Genus *MONOCLIMACIS* Frech, 1897.

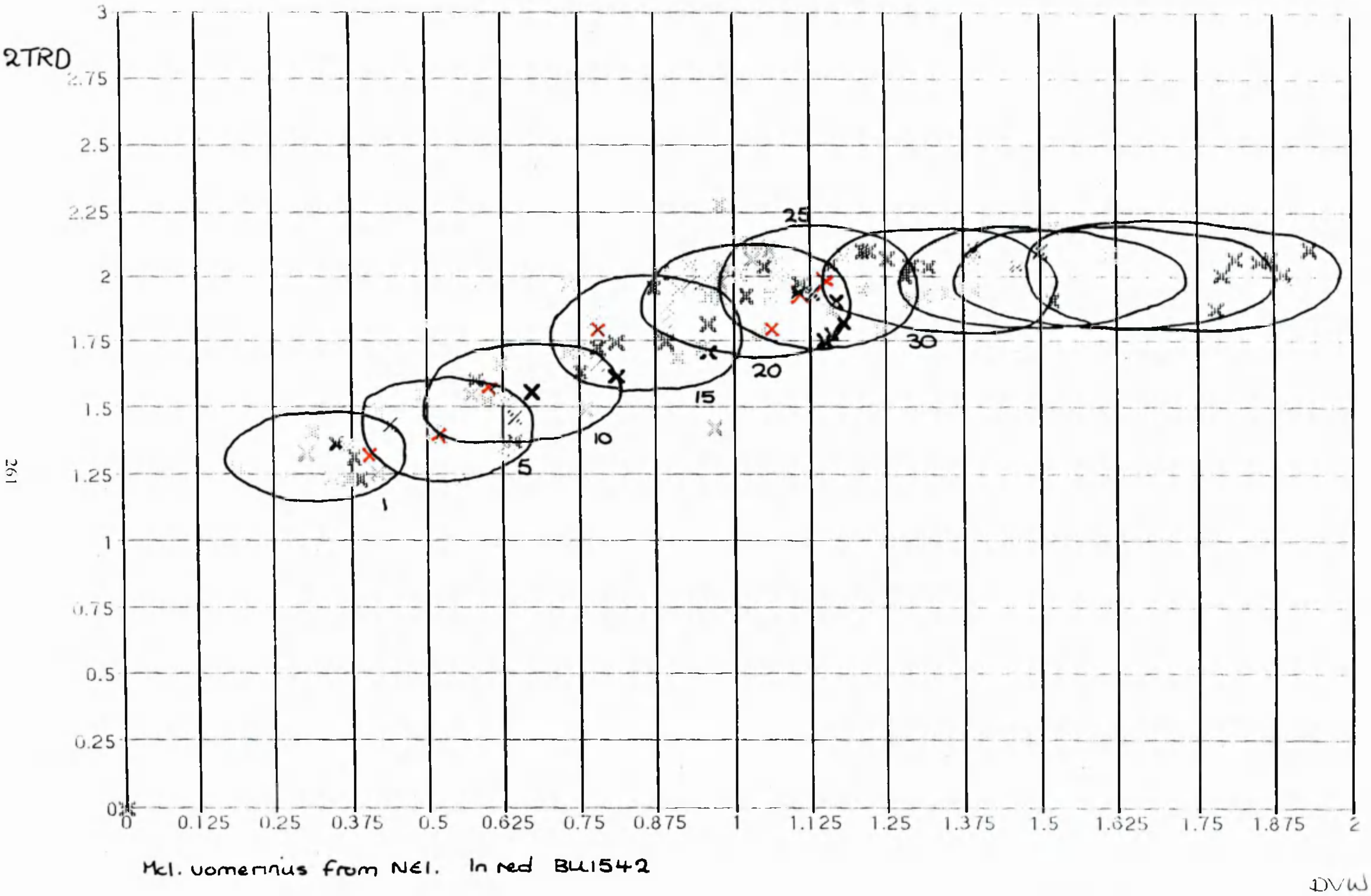
Type species. Original designation; *Graptolithus vomerina* Nicholson, 1868, from the Llandovery Coniston Flags of Northern England.

Diagnosis (After Hutt, 1975:56) Thecae geniculate, with straight supragenicular wall approximately parallel to axis of rhabdosome; apertural margin somewhat everted; aperture often hooded by an outgrowth of microfusellar tissue from the geniculum of the succeeding theca.

Monoclimacis vomerina (Nicholson 1872)
Figs. 9.3.5;9.3.7 A-G;9.3.12.C

1850 *Graptolithus colonus* Barrande, Pl. 2:4.
1872 *Graptolites vomerinus,* Nicholson, p. 53, fig. 21.
1876 *Monograptus vomerinus* (Nicholson): Lapworth, p.353-354, Pl. 12: 6a-e.
1910 *Monograptus vomerinus,* (Nicholson): Elles and Wood, p. 409-411, Figs 275a-f, Pl. 41:1a-e.
1923 *Monograptus vomerinus* Nicholson sp.:Gortani, p.49-50, Pl.8:28-32, Pl.12:5, Pl. 13:2E.
1940b *Monoclimacis vomerina vomerina,* Nicholson: Pribyl, p 2-3, Pl. 1:1-4.
1940 *Monograptus vomerinus,* Nicholson, Laursen, 23, figs 10 a-c, Pl. 1:4-6.
1945 *Monograptus (Monoclimacis) vomerina vomerina,* (Nicholson): Waterlot, p.76, table 31:322. Pl. 28:10-11.
1947 *Monograptus vomerinus,* (Nicholson):Ruedemann,p.490, Pl.85:23-24,?25
1952 *Monoclimacis crenulata* : Lamont p.27
1968 *Monograptus vomerinus vomerinus* (Nicholson): Kowalski, p.117, fig.1.
1971 *Monograptus (Monoclim.) vomerina vomerina,* (Nicholson): Schauer p.67, Pl. 28:10-11, Pl. 29: 7-8.
1974 *Monoclimacis crenulata (sensu* Elles and Wood 1910): Tipper
1975 *Monograptus vomerinus vomerinus,* (Nicholson): Bjerreskov, p. 55-56, fig.17E, Pl. 8:E-G. Table 5.
?1978*Monoclimacis vomerina vomerina* (Nicholson): Krstic, p.11-12, Pl.2:2b
1981 *Monoclimacis vomerina* s.l. (Nicholson): Bjerreskov p.26 not figured.
1982 *Monoclimacis vomerina vomerina* (Nicholson): Howe, Pl. 2:d not described
?non 1988 *Monoclimacis vomerinus vomerinus* (Nicholson): Lenz, p. 1965 figs. 4:J,L,Z &AA.
1988 *Monoclimacis vomerina* (sensu lato) : Robertson p.138.

Type Lectotype designated by Pribyl (1940:2) as Nicholson (1872:53, Fig. 21). The specimen in this figure has not been identified and a neotype from Lapworth's material, BU 1542, figured in Elles and Wood (1910, Pl. 41:1a), was selected by Strachan (1971:65); from the Riccarton Beds, South of Scotland. 32 specimens from the Nicholson collection are available in the BM(NH) all registered as "P2047", two representative specimens are illustrated here (fig 9.3.5).



Mcl. vomerinus from NE1. In red BW1542

FIG. 9.3.3

Material, location and stratigraphy. Common throughout the marine Silurian of the Pentland Hills, rocks yield a constant number of specimens but this species becomes proportionally more prevalent as other species dwindle up section. More than 50 specimens are known, with numerous distal fragments.

Specimens described in this study derive from the *Oktavites spiralis* graptolite biozone and range up to the Llandovery-Wenlock boundary (possibly ranging through *grandis* and *insectus* biozones). This species is recorded as characteristic of Uppermost Llandovery and Wenlock graptolite faunas, worldwide.

Lapworth (1876) cited the "Lower Pentlands at Habbies Howe" as one of the localities from which this species is common. If the synonymy of Lapworth's (1876) material of *Monoclimacis vomerina* is accepted (which it is here) then this, the typical form of monoclimacid from this locality, must be *Monoclimacis vomerina*. Habbies Howe is in fact a locality further down the North Esk river in Carlops village itself, south of the Pentlands Fault, where only rocks of Carboniferous rocks are exposed. It is suggested that the locality referred to by Lapworth was the within the lower part of the Silurian succession, from the Reservoir Formation, possibly from either the Gutterford Burn, the Monks Burn or from the Bavelaw Castle Inlier, all Reservoir Formation sediments (Robertson 1985), in which this species is the common robust monoclimacid.

Description. Thecae of typical *Monoclimacis* type. Rhabdosome straight with very slight dorsal curvature proximally. The sicula may be displaced back from the straight line of the dorsal margin of the rhabdosome. Rhabdosome over 60 mm long with specimens with more than 60 thecae preserved. 8-10 thecae in 10 mm distally, 11-13 in 10 mm proximally. Thecal overlap half of thecal length and sometimes more distally. Apertural excavation one quarter of stipe width.

Thecal spacing (2TRD) increasing gradually until theca 20, and constant after this level. Width increasing rapidly proximally (up to theca 5) and increasing gradually all along the stipe, without reaching a maximum. Sicula unornamented, 1.1-1.3 mm long, 0.26 mm wide at aperture, reaching to the aperture of th. 1 and slightly above. Interthecal angle constant at up to 45°.

Specimens from the Pentland Hills agree very well in rhabdosome width, straightness of stipe and thecal structure with those in previous descriptions. They differ in the smaller length of sicula (1.1 vs. 1.5 mm). However, measurement of the lectotype BU 1542 records a sicula length of 1.14 mm. Average stipe sizes as below (see figs. 9.3.5 and 9.3.7).

Thec.	2TRD	DVW
1	1.2-1.4	0.2-0.4
5	1.3-1.6	0.4-0.7
10	1.4-1.7	0.5-0.8
15	1.6-2.0	0.7-1.0
20	1.7-2.1	0.8-1.2
25	1.8-2.2	0.9-1.3
30	1.8-2.2	1.2-1.5
35	1.8-2.2	1.3-1.7
40	1.8-2.2	1.4-1.8
45	1.8-2.2	1.5-2.0

Discussion The *vomerina* group is quite important. Elles and Wood (1910) described together in their *Monograptus* group III, a number of species now known as species of the genus *Monoclimacis*. Within that group four varieties of the species "*Monograptus vomerinus*," namely the "typical form" *M. vomerinus* itself, Var. *basilicus*, Var. *gracilis*, and Var. *crenulatus*. These have all now been recognised as separate species, but some authors still refer to these species as sub-species of *Monoclimacis vomerinus* (e.g. Lenz 1988:1965).

The whole group needs a thorough review. Different authors seem to have different ideas as no agreement has yet clearly emerged as to standard taxonomic descriptions for the similar *Monoclimacis* species such as *vomerina*, *crenulata*, *geinitzi*, *gracilis*, *basilica*, etc. and new species are appearing regularly such as *Monoclimacis quanyinqiaoensis* (Ye, 1978). Each author appears to have his or her own idea as to what each species looks like, and their own interpretation of the "original description", fuelled by the inaccuracy of the said original description and illustration. Similarly *Mcl. vomerina* is such a common species, it is often referred to (and only sometimes illustrated, eg. Howe, 1982 Pl.2:d),

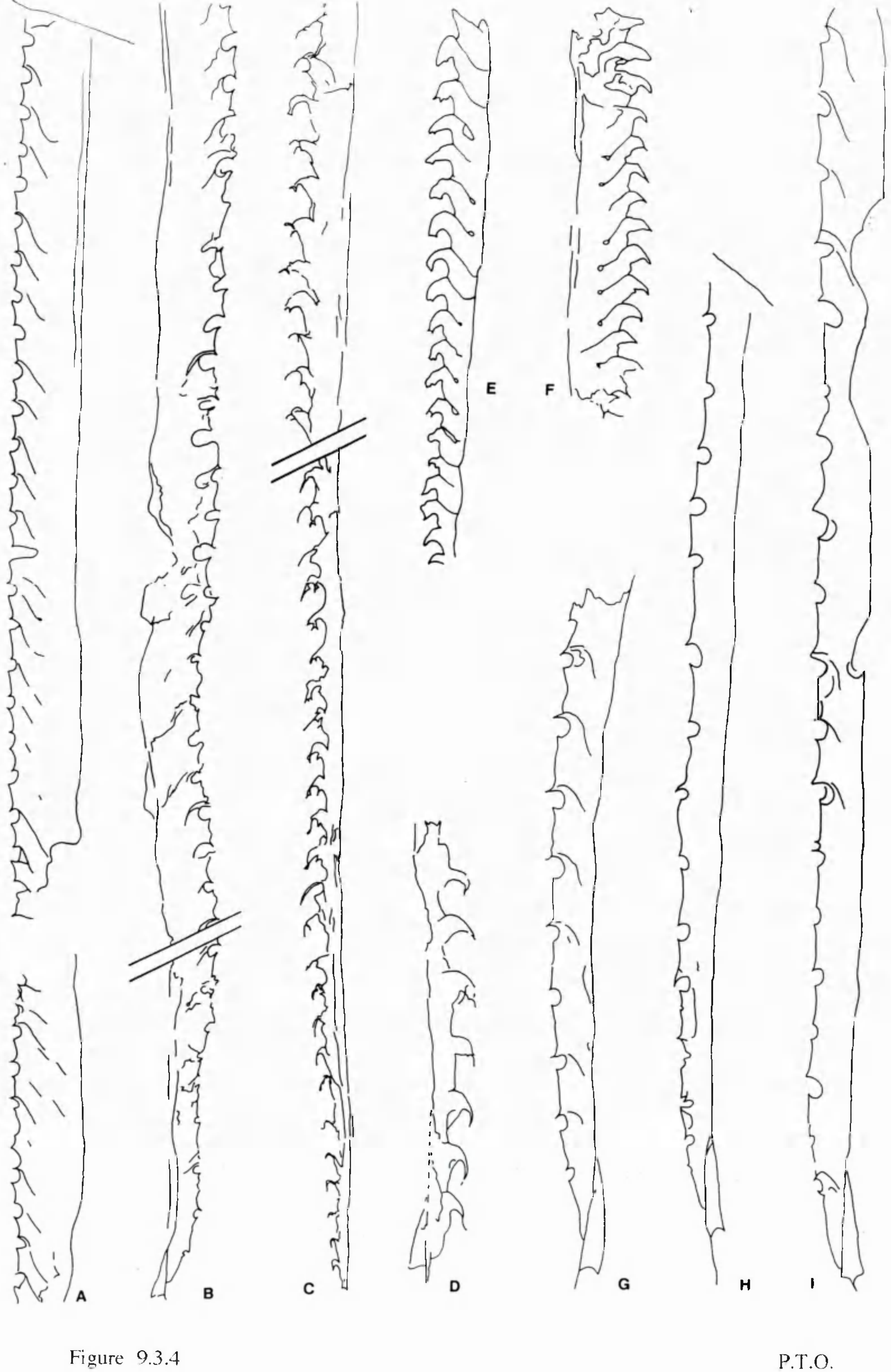


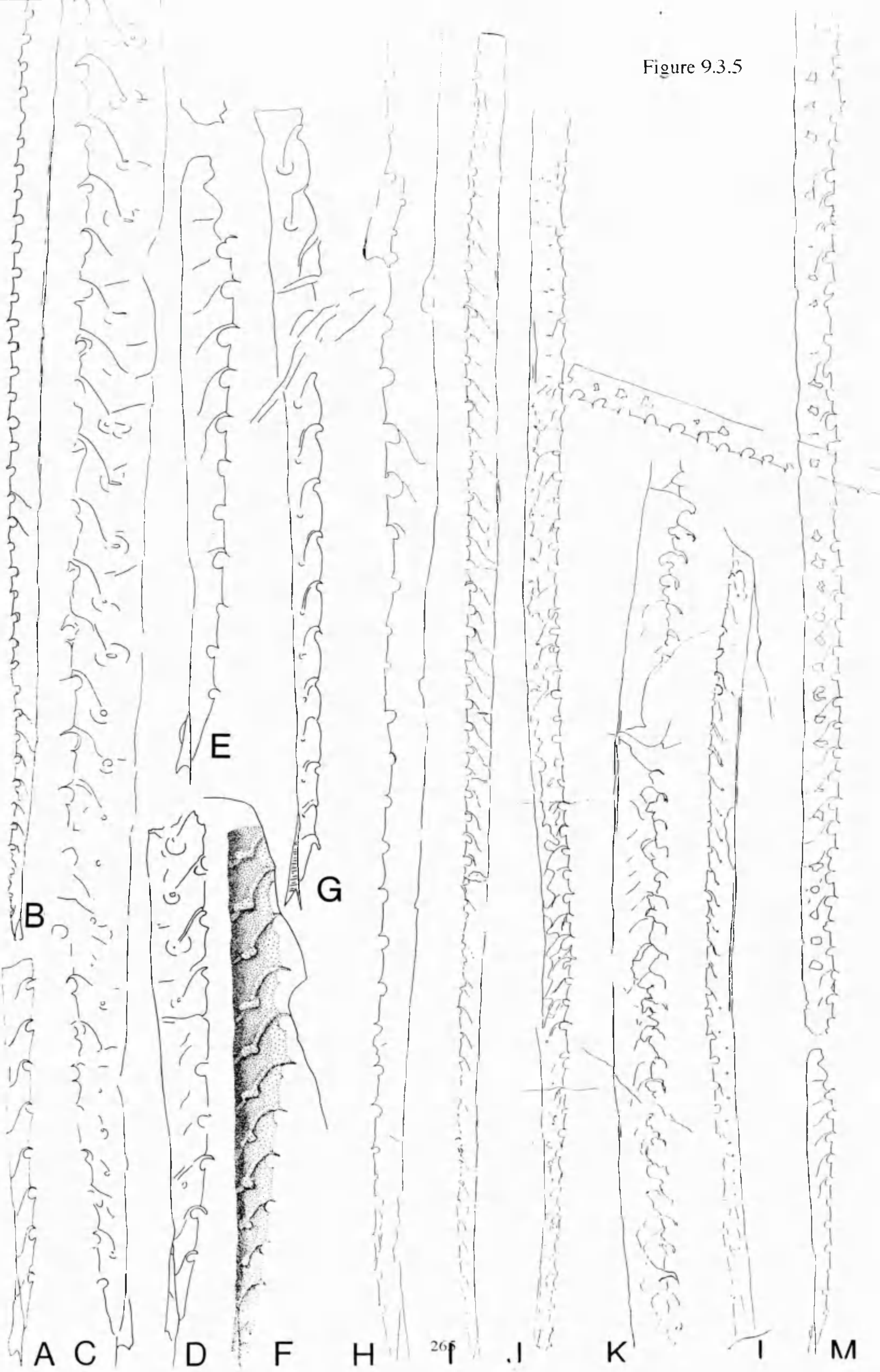
Figure 9.3.4

P.T.O.

Figure 9.3.4 (fig 4 Bull and Loydell 1995) A, B, C, E and F X5, D, G, H and I X10. A-B *Monoclimacis vomerina* , A: GI 47567, distal portion, well developed interthecal septae. B: EEB 79a, distal and proximal portions of long specimen, middle 47 thecae (46 mm) omitted. C-D *Monograptus parapriodon*, C: EEB 223, distal and proximal portions of long specimen, middle 10 thecae (12 mm) omitted D: GI 47560, proximal portion with well preserved sicula. E-F *Monograptus priodon* E: EEB 207, F: GI 47565; G-I *Monoclimacis geinitzi* Very slender specimens showing genicular hoods, sicula to top of th. 1, sicula with prominent virgella. G:RSM GY 1985 30 5, H: EEB 205, I: RSM 191. (Identification based on comparison with type material, as original drawing (Boucek 1953) is inaccurate).

Figure 9.3.5 A-B, *Monoclimacis gracilis* (Elles and Wood 1911); C-F, I-J and L-M, *Monoclimacis vomerina* ; G, *Monoclimacis crenulata* (Elles and Wood 1910); H, *Monoclimacis geinitzi* ; K *Monograptus priodon* (Bronn, 1835).
A: A 51065 X10; B: A 22148 X5; C: P2047 (Nicholson material) X 10; D: P2048 (Nicholson material) X 10; E: BU 1542 (neotype) X 10; F: A 22094 X 10; G: BU 1555 (lectotype) X 10; H : RSM.GY.1897.32.375, X 10; I : GI20226, X5; J: GI 22218 distal section. X5; K: GI22214 , X5; L: GI47569 distal section X 5; M: BU 1542 (neotype) X 5.

Figure 9.3.5



without full taxonomic description, so it is unclear if the author has made a correct identification. Many specimens identified as *Monoclimacis crenulata* or *Monograptus vomerinus crenulatus* (Törnquist 1881) (e.g. Willefert 1963:84), will prove to be attributable to *Monoclimacis vomerina*, just as many of the specimens attributed to *Monoclimacis crenulata* may prove to be *Monoclimacis gracilis* (Elles and Wood, 1910), if a full taxonomic review of the whole group, including a full survey of the actual material all published descriptions, were undertaken.

Mcl. vomerina is a species that existed throughout a long time span and had a range of typical sizes, but it should be considered as a distinct separate species, and not a portmanteau species. Often, material that due to lack of proximal end would otherwise be unidentifiable, except for a distal DVW of around 2 mm and *monoclimacid* type thecae, is assigned to *Mcl. vomerina (sensu lato)* (Robertson 1985:45). To avoid further confusion, and to clarify identification of *Mcl. vomerina* itself, these should be referred to *Monoclimacis* sp. just as *Mcl. basilica, Mcl. geinitzi* , etc are recognised as separate species and not subspecies.

Some authors refused initially to recognise *Monoclimacis* as a valid genus, and some continue to refer to many species as subspecies of *Monoclimacis vomerina* (e.g. Lenz 1988:1965). This has lead to a plethora of names in existence referring to the same species.

Authors who do not recognise *Monoclimacis* as valid refer to:-
Monograptus vomerinus, basilicus, crenulatus, geinitzi, and *crenularis*
Authors recognising *Monoclimacis* as valid refer to
Monoclimacis vomerina, basilica, crenulata, geinitzi, and *crenularis*

Distinguishing from other species.
Mcl. vomerina has a much smaller DVW distally than Mcl. basilica. The latter species has similar dimensions to *Mcl. vomerina* for the first two thecae, but increases in width much more rapidly proximally.

Monoclimacis crenularis is much longer (often more than 10 cm) and thinner than Mcl. vomerina , with a maximum DVW distally of only 1 mm with 10-12 thecae in 10 mm, also the rhabdosome of *Monoclimacis crenularis* is flexed dorsally proximally. Also *Monoclimacis crenularis* is characteristic of middle to Upper Wenlock. It is most unfortunate that *Mcl. crenulata* and *Mcl. crenularis* have such similar names, but as both are well known species, little would be gained by attempting to change either name now.

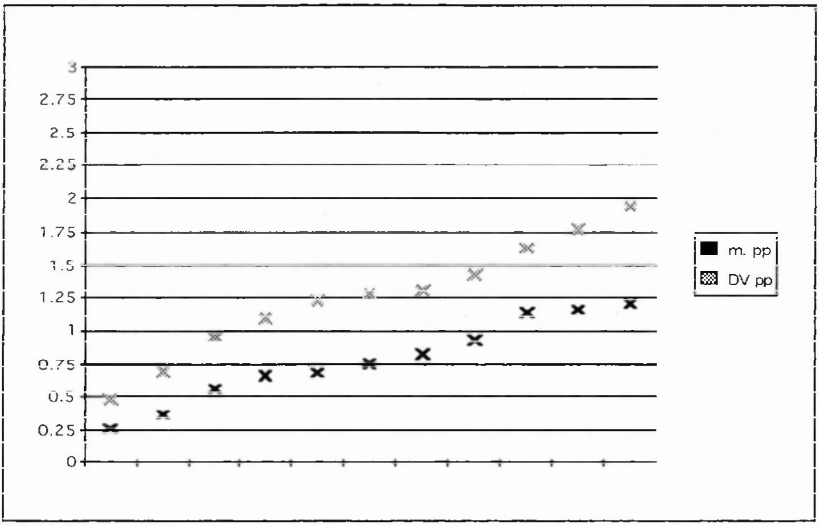
Mcl. vomerina has a greater DVW and by smaller 2TRD relative to DVW than *Mcl. geinitzi* and *Mcl. geinitzi* has a distinctive spine ornament to the sicula.

Mcl. gracilis is a slender monoclimacid requiring taxonomic revision. According to the original description (Elles and Wood 1911:411) its most distinguishing features are the slender dimensions and the gentle proximal recurving of the stipe, a feature not apparent in the illustration or the material when borrowed and studied. Some specimens of *Mcl. crenulata* and *Mcl. gracilis* as figured by Elles and Wood are conspecific. In particular a number of specimens supposedly *gracilis*, lack the characteristic proximal curvature. See below (taxonomic description of *Mcl. geinitzi)* for further comment.

Distinguished from *Monoclimacis crenulata* by *Mcl. vomerina* 's greater width and 2TRD proximally, and in particular th.1 of *Mcl. crenulata* is very short and hooked, hence the sicula of *Mcl. crenulata* (which is a similar size to that of *Mcl. vomerina)* reaches to the aperture of th.2. *Mcl. vomerina* also has a greater thecal excavation distally.

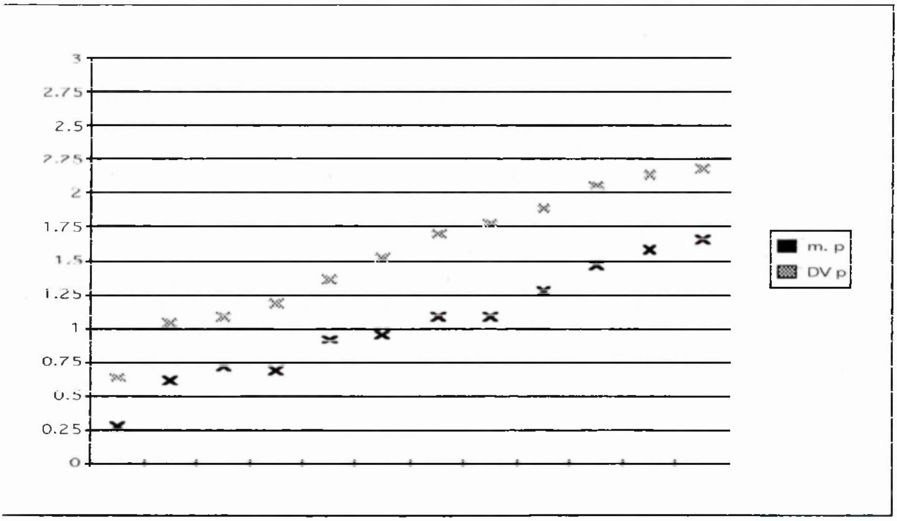
A submission has been made to ICZN concerning this group, (Loydell, Bull and Storch, 1992), and resulted in the formalising of authorship of *Mcl. crenulata* as Elles and Wood (1911), and the selection of BU 1555 as lectotype. This submission also confirmed the recognition of the Elles and Wood (1911) specimen (BU 1542, selected by Strachan 1971) as neotype for *Mcl. vomerina* (Nicholson 1872) and the conspecificity of specimens described as *Mcl. crenulata* (Törnquist 1881) with Mcl. vomerina (Nicholson 1872) therefore producing a formal basis for future taxonomic work. This is the most important step towards sorting out the taxonomic difficulties of this group. It is further hoped the the process of creating graptolite "profile plots" as described above, will help this formalising process, as the unique range of sizes of each species can be accurately plotted and compared. Specimens BU1555, BU1542 and Nicholson material are illustrated in figure 9.3.5.

It is often stated that *Monoclimacis crenulata* (Elles and Wood, 1911) is differentiated from other *monoclimacids* of similar age by the hooked nature of the proximal thecae (White *et al.* 1992). This stems from the obvious hooking of th.1 of the lectotype (fig. 9.3.5.G). Clearly th.1 of *Monoclimacis crenulata* is quite considerably hooked, but as can be seen in fig. 9.3.5, *Monoclimacis vomerina* also has some slight hooking of the first



9.3.6.1 *M. parapriodon* m. pp = prothecae width
DV pp= overall dorsal/ventral width including metathecae

9.3.6.2 *M. priodon.* m. p = prothecae width.
DV p = overall dorsal/ventral width including metathecae



theca. Similarly other species have been described, such as *Monoclimacis vomerina* n. subsp. (Bjerreskov 1975:58), with two or three proximal thecae hooked. Added to this is the difficulty of identifying hooking of thecae in less than perfectly preserved material, if the stipe has undergone any degree of torsion during deposition, or if the angle of rock fracture is not completely in the plane of the aperture, then slight eversion of the thecae can easily be missed or destroyed during preparation.

Both species have straight rhabdosomes with little or no curvature, similar widths, and both exhibit the same development of an elongated, small, spine-like genicular hood.

A further distinguishing feature of *Mcl. crenulata* and *vomerina* is the angle of the interthecal septa. In crenulata the interthecal septa lie sub-parallel with the rhabdosome axis. In Mcl. vomerina they are inclined at up to 45° to the rhabdosome axis, both species often exhibiting a bulging in the side of the preserved graptolite at the site of increased interthecal tissue at the base of the inclined section of the septum. The angle of the interthecal septum can only realistically be used as taxonomically important, in areas where the specimens have not been greatly affected by tectonic activity, as tectonisation would alter the apparent interthecal angle.

The type and figured material of the vomerinus group (Elles and Wood 1910) has been studied in detail. All specimens form this group illustrated by Elles and Wood were borrowed and measured. Some were drawn and are illustrated in fig. 9.3.5.

Lenz (1988:1965) distinguished *Mcl. vomerinus vomerinus* (referred to as a subspecies) from ?*Monograptus crenulatus* (by which it is probable that he means *Monoclimacis crenulata*) by suggesting that *Mcl. vomerinus* has gentle proximal curvature and widens much more gradually than *Mcl. crenulata.* This is however not evident from the specimens illustrated in Lenz's paper, and this description is therefore considered a incorrect identification of *Mcl. vomerinus* . The specimens illustrated in Lenz (1988) do however appear to be correctly identified.

Monoclimacis geinitzi (Boucek, 1932)
Fig 9.3.5.H; fig. 9.3.7 H-J

1932 *Monograptus geinitzi*, n. sp.: Boucek, p.5, fig 2:c,d.
1940 *Monoclimacis geinitzi* (Boucek 1932): Pribyl. p. 5-6, Pl. 2:9,10 &11.
1962 *Monograptus vomerinus* aff. var. *gracillis* : Mykura and Smith, p.14.
1974 *Monoclimacis* sp. : Tipper

Original diagnosis. "Polyparium upright, quite straight, not very long, only ca. 4-5 cm) extending symmetrically to 1.3-1.4 mm. The hydrothecae are of *vomerinus* type and are ca.. 11 to 10 mm. M. Chuchle; *Monogr. subconicus* zone. Occurs together with *M. subconicus, M. largus, M. praecedens, wimani, Cyrtogr. lapworthi, c. pulchellus, Retiolites geinitzianus* var. *angustidens* etc."

Type Lectotype selected by Pribyl (1940b): specimen figured by Boucek (1932) as fig. 2c,d. (orig. 118), from Vyskocilka (M. Chuchle), Prague Basin. It is believed that Boucek's material is still available in the Geological Institute of the Charles University, Prague. Also the type collection of Pribyl is still available. One of the specimens of *Mcl. geinitzi* illustrated by Pribyl (1940b Pl. 2:11) from Vyskocilka (*spiralis* biozone), could also be selected as paratype, and has been included in an atlas of type material being prepared by Dr. J. Zalasiewicz and BIGG. The collections of the Sedgwick Museum in Cambridge and the National Museum of Wales have a number of specimens identified and donated to the Museums by Boucek himself in the mid 1960's. Some of this material has been studied by the author, dimensions of these specimens are given below.

Figure 9.3.7 All specimens from the Reservoir Formation, Gutterford Burn, North Esk Inlier, A-G *Monoclimacis vomerina* (Lapworth 1867), H-J, *Monoclimacis geinitzi* (Boucek 1932). E-J, growth stages. A. RSM.GY.1885.26.76.0, distal section showing apertural excavation x 14; B EEB 208, proximal section showing interthecal angle x12; C, EEB 219a.1, proximal section with sicula and th. 1 strongly hooked, thecal bodded prsent x14; D, EEB 217 (3), proximal section with sicula, th. 1 hooked, rhabdosome damaged distally x 27; E, EEB201 b 1, proximal section inc. sicula x 27; F, EEB 204 a 2, proximal section inc. sicula x 27; G, EEB 204 a 1, proximal section inc. top of sicula x 28; H, EEB 202 a 8, very well preserved with details of virgella, prosicula, interthecal angle and apertural hoods of proximal thecae x 27; I, EEB 202 b 26, proximal portion with virgella x 27; J, EEB 204 c1, proximal portion with virgella , slight curvature. x 27.


A
B
C
D
E
F
G
H
I
J

Material, location and stratigraphy. Common throughout the Reservoir Formation of the North Esk Group, most commonly found in the better preserved of the more calcareous horizons from the "Gutterford Burn Limestone Beds" locality. More than 50 specimens known, with numerous proximal fragments, some just the sicula and th. 1. The very small size of this species makes it quite difficult to find in the field as most proximal or fragmentary specimens are invisible to the naked eye. Commonly found on specimens collected for their well preserved sheets of *Dictyocaris*.

Specimens described in this study are restricted to the *Oktavites spiralis* graptolite biozone and have not been found from any later horizons.

The *Monograptus geinitzi* biozone was recognised as a subzone of the "*Spirograptus*" *spiralis* biozone by Boucek (1953:57&61). This species and the subzone (representing the middle of the *Oktavites spiralis* biozone) of which it is characteristic has also been recognised by Fu and Song (1986) from China, and found recently from Wales (Loydell and Cave 1994). Graptolite biostratigraphy is discussed in more detail in chapter 3, and correlation charts for the upper Llandovery graptolite zones worldwide are given.

Description. Thecae of typical *Monoclimacis* type. Rhabdosome straight with very slight dorsal curvature proximally. Rhabdosome very slender 0.2 mm wide proximally, 1 mm wide distally and only rarely reaching more than 2 cm long. 8-10 thecae in 10 mm distally, 12-14 in 10 mm proximally. Apertural hood prominent, projecting out from stipe slightly, beneath geniculum of succeeding theca. Apertural excavation one third of stipe width. Supragenicular wall slightly concave, but generally parallel with stipe axis. Thecal spacing (2TRD) and stipe width (DVW) increase gradually all along stipe,without reaching a maximum. The increase in stipe width is most marked over the first few thecae, as the first few thecae are quite short. Distally 2TRD is large relative to DVW, as thecal overlap is about one third. Sicula 1.2-1.4 mm long, 0.25 mm wide at aperture, reaching to the aperture of th. 1 and slightly above, ornamented with a long spine (virgula) up to 0.7 mm long. Interthecal angle constant at 30°-45°. Average sizes as below (see also figs. 9.1.6 and 9.1.7).

Range of sizes of *Mcl. geinitzi* from NEI material.

Theca	2TRD	DVW
1	0.8-1.4	0.2-0.4
5	1.2-1.7	0.3-0.6
10	1.5-2.0	0.3-0.6
15	1.7-2.3	0.4-0.8
20	1.9-2.4	0.6-0.9
25	2.0-2.5	0.7-1.1

Measurements taken from other specimens
(See fig 9.3.8 and fig 9.3.5)

A) Specimen from Sedgwick Museum (A 75581) as presented (and identified) by Boucek in 1967.
B) Specimen drawn by P. Storch from material figured by Pribyl 1940 pl. 2:11.
C) Specimen (RCV1907) illustrated by Loydell and Cave 1993, Fig 7a.

A

Theca	2TRD	DVW
1	0.9	0.37
5	1.3	0.50
10	1.6	0.62
15	1.9	0.75
20	2.1	0.92
25	2.4	1.01
30	2.6	1.05

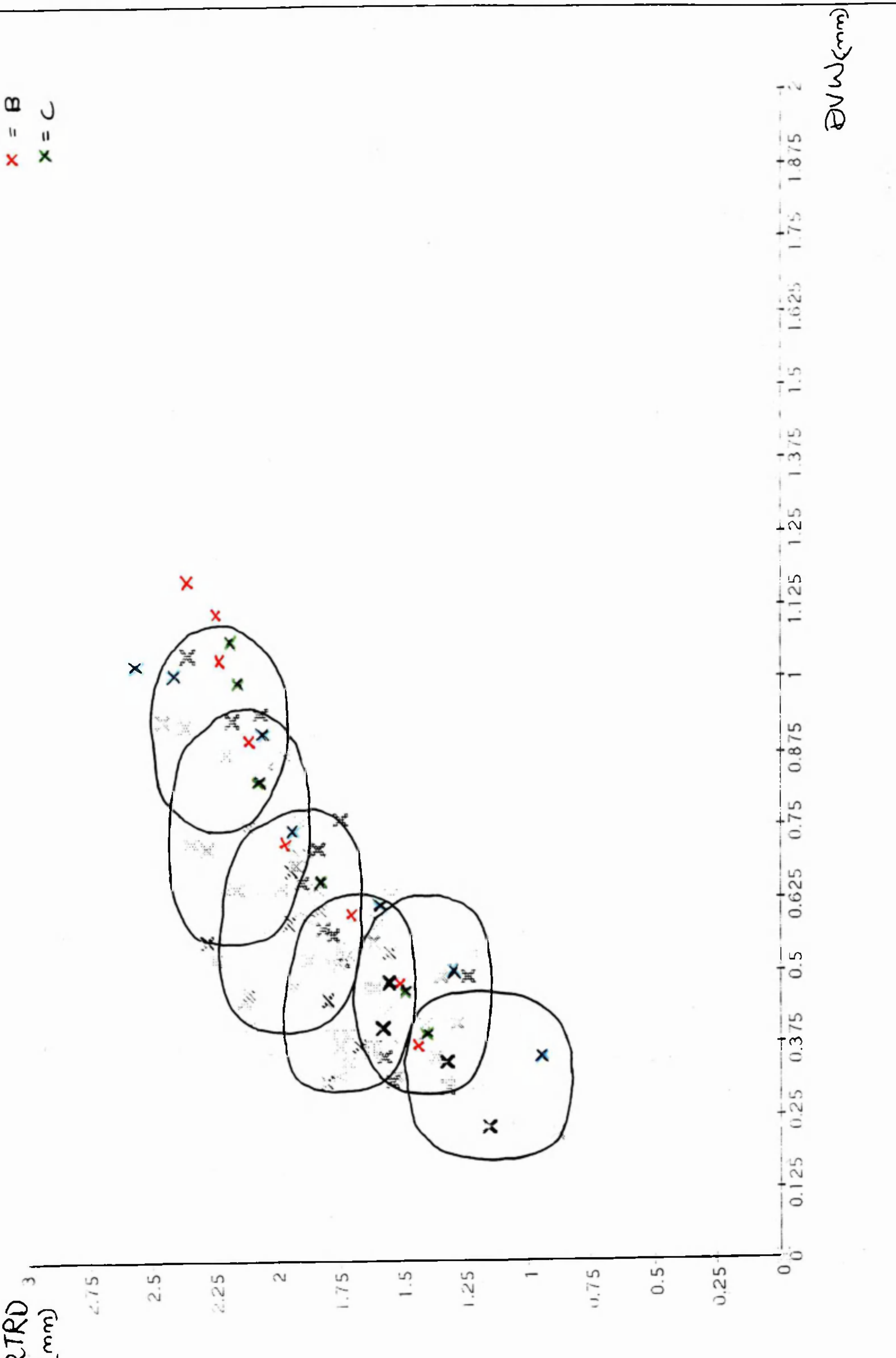
B

Theca	2TRD	DVW
1	1.44	0.40
5	1.53	0.49
10	1.72	0.61
15	1.98	0.71
20	2.01	0.86
25	2.13	0.89
30	2.24	1.11
35	2.25	1.13
40	2.34	1.16

C

Theca	2TRD	DVW
1	1.43	0.42
5	1.51	0.48
10	1.84	0.64
15	2.04	0.81
20	2.16	0.98
25	2.23	1.06

Figure 9.3.8. "Profile plot" of Mcl. geinitzi specimens A, B, and C as detailed above. Circles are range of measurements at each thecal level for PH material. Measurements for specimens A, B, and C all fall within the same range at each thecal level, as the PH material.


× = B
× = C
2TRD (mm)
3
2.75
2.5
2.25
2
1.75
1.5
1.25
1
0.75
0.5
0.25
0
DVW (mm)
0
0.125
0.25
0.375
0.5
0.625
0.75
0.875
1
1.125
1.25
1.375
1.5
1.625
1.75
1.875
2

Discussion This species is distinguished from *Mcl. vomerina* in that *Mcl. geinitzi* has closer thecal spacing for first few thecae, and a slightly larger sicula. Distally *Mcl. geinitzi* is much narrower with much larger 2TRD relative to DVW, and is overall much smaller, and shorter. *Mcl. geinitzi* continues to increase in all dimensions distally, whereas the 2TRD of Mcl. vomerina is constant after th.20.

This species is differentiated from other species such as *Mcl. vomerina, crenulata, flumendosae* and *basilicus* by its small size. *Mcl. crenularis*, and *griestoniensis* are both as thin as *Mcl. geinitzi* but both have thecae that are even longer with an even greater 2TRD relative to DVW than *Mcl. geinitzi* and both species have very long rhabdosomes. *Mcl. gracilis* and *adunca* have similar dimensions to *Mcl. geinitzi*, but both have distinctive curvature proximally or distally.

Specimens from the Pentland Hills agree with rhabdosome width, straightness of stipe and thecal structure of previous descriptions. Specimens described by Pribyl reached 4-5 cm long and 1.3-1.4 mm wide distally, and had a slightly smaller sicula. Only two published taxonomic description of the species are known by the author, and a full review and critical re-examination with stratigraphic control, of all *monoclimacid* species, is really required (Strachan 1971:64)

It is possible that material identified and figured by Cocks and Toghill (1973) from another of the Midland Valley inliers at Girvan, as *Monoclimacis crenulata*, is in fact *Mcl. geinitzi*, which if confirmed would have a great bearing on Midland Valley history.

9.3.3.

Genus *OKTAVITES* Levina, 1928

Type species. Subsequently designated by Obut 1964:328; *Graptolithus spiralis* Geinitz, 1842, from the Llandovery of Germany.

Diagnosis. Spirally coiled rhabdosome bearing triangular metathecae, sometimes almost rastritiform proximally, with little or no overlap. Thecal apertures are laterally expanded, sometimes asymmetrically with, in one case, the development of rostral processes. Torsion, affecting the whole of the metatheca, is developed in distal thecae. Extension of the dorsal wall of the metatheca over the central portion of the thecal aperture causes this to face dorsally, whilst the laterally expanded portions of the aperture face dorso-laterally. The metatheca narrows appreciably before expanding laterally.

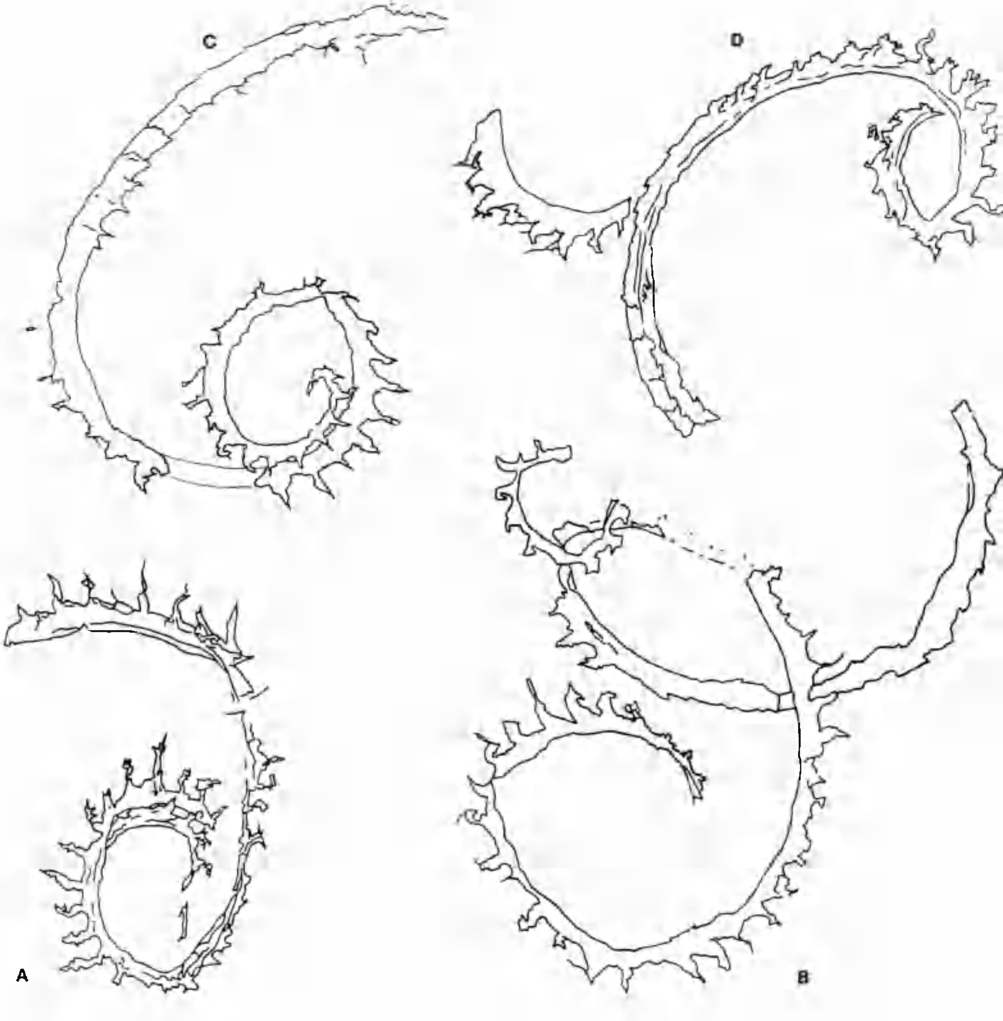
Assignation to genus *Oktavites* depends on identification of thecal morphology, and has been recognised as valid by Rickards et al. (1977:73), discussed by Koren and Enokyan (1970), and by Loydell (1992:24; 1993:123).

Oktavites excentricus (Bjerreskov 1975).
figs. 9.3.9 - 9.3.12.

1940 *Monograptus spiralis* Geinitz. : Laursen, p. 28, pl. 2:5
1952 *Spirograptus* aff. *falx* (Suess) : Lamont p. 27.
1974 *Monograptus spiralis* : Tipper
1975 *Monograptus spiralis excentricus*. Bjerreskov, p. 73, fig. 20 G-H.
1989 *Monograptus spiralis* : Robertson p.138.

Holotype. Specimen number MMH 13476, Figured Bjerreskov 1975, Fig. 20:G, the middle part of the *spiralis* Biozone, loc. 26, Øleå, Bornholm.

Figure 9.3.9 All specimens X6. A-D *Oktavites excentricus* (Bjerreskov, 1975). A: RSM GY 1985 28.3, second whorl superimposed on first, thecal apertural spines well preserved. B: RSM GY 1985 28.6, loosely coiled specimen, sicula preserved, some torsion of stipe axis. C: RSM GY 1985 28.1, regularly coiled, showing complete torsion of stipe axis. D: EEB 201, torsion of stipe axis, superimposed on another specimen, (if apparent branch were a cladium, thecae would face the other way). E: 1985.28.1.1 ; F: 1985 28.1.2 proximal portion showing sicula.


C
D
A
B

Material and horizon. Fairly common species, some bedding planes with many scattered fragments, mostly flattened. 11 good specimens with numerous fragments both proximal and distal. Specimens (rare) have been found throughout the Reservoir Formation, but the species is not known to extend into the overlying Deerhope Formation.
This species is characteristic of the middle of the *spiralis* graptolite Biozone on Bornholm (Bjerreskov 1975:73), and the NEI is the only other locality where it has yet been recorded worldwide. The associated fauna in the NEI, (particularly *Mcl. geinitzi* and *M. parapriodon* and conodont Biozonation) is also consistent with a middle *spiralis* Biozone age (see chapter 3). It is possible that some of the material figured by Lin (1988) as *Oktavites tullbergi spiraloides* (Pribyl), may also be *O. excentricus* (particularly Pl. 2: 4) but the diagrams and text are too imprecise to warrant synonymy without inspection of the original material.

Original Diagnosis. "The rhabdosome is excentrically coiled with a maximum of two whorls. The extreme distal portion is slightly ventrally curved. The width increases from 0.65 mm proximally to about 2 mm distally. The thecae are of spiralis type, numbering 9-10 per 10 mm."

Description. Rhabdosome small, coiled in a low conical spiral, up to a maximum of three revolutions. Sense of curvature maintained throughout, no reflexion. Diameter of inner whorl 4-6 mm, gradually opening out distally, diameter up to 14 mm. Overall rhabdosome length up to 58 mm. Sicula 0.9 mm long, 0.2 mm wide, reaching to the top of the protheca of th.1, with th.1 starting 0.1mm above sicula aperture. Stipe quite thin throughout, 0.7 mm wide proximally, increasing to 1.7 mm distally. Metatheca occupying up to 70% of the width proximally, down to 50% distally. Thecae generally on dorsal (convex) stipe margin. Some thecal rotation by stipe torsion.

Thecae closely spaced (prothecae short), resulting in 13-15 thecae in 10 mm proximally, decreasing to 10-11 thecae in 10mm distally. Thecae of typical *Oktavites* type, triangulate and partially isolated, overlapping very little proximally and only up to 30% distally. Protheca triangular, skewed away from the sicula. Metathecae tubular with the distal portion strongly hooked, so that the aperture is turned away from the sicula, then further ornamented with long apertural processes (the "rostral processes" of Lenz and Melchin 1989:342) that project back towards the sicula giving the thecae the apparent sinuous curvature. A distal increase in length of the tubular portion of the metathecae is observed.

Discussion Specimens of *Oktavites excentricus* (Bjerreskov 1975) from the NEI, agree with the type material with regard to thecal morphology, shape of rhabdosome and stipe width, but up to three whorls have been observed on the NEI, whereas the maximum overall length so far recorded is 58 mm. compared with a recorded maximum of 150 mm. in the type material. The thecae number per 10 mm is greater for the NEI material than the stated number for the type material, but measurements made from the original illustration (Bjerreskov 1975 fig 20:6), record 14 thecae per 10 mm proximally, with which the NEI material agrees. The type material has slight ventral curvature in the distal portion, which has not been observed for any specimen so far collected from the NEI, although the distal portion is noticeably less tightly curved than the proximal portion.

The curvature of *Oktavites excentricus* (Bjerreskov 1975) from the NEI gradually decreases so that the inner whorls are tighter than the outer whorls, the rhabdosome straightens slightly, so that for fragmentary specimens, the degree of curvature (along with the stipe width) suggests if the piece is from the proximal or distal portion of the specimen. Apparent unevenness of coiling, where one whorl is superimposed on another due to post-mortem compression of conical form into planispiral form, is common, conforming to the eccentric ("excentric") nature of the coiling of this species, after which it is named.

The thecae are almost always on the dorsal margin of the stipe unless involved in stipe torsion, where thecae from dorsal margin may be twisted far enough to lie on the ventral margin. The thecal torsion is the result of the translation of the tension and elasticity inherent in a structure maintaining a 3-dimensional conical shape in life, into lateral rotation on compression into two-dimensions on deposition. It is further noted that at points of maximum torsion, the regularity of the coiling is interrupted. This is thought to be post-mortem breakage on deposition.

The width of the common canal increases gradually (Bjerreskov 1975:73 recorded an increase from 0.2 mm to 0.7 mm wide distally). It is thought from the NEI material, that even distally, the common canal only occupies a negligible proportion of the stipe width, being obscured by the overlapping of the metathecae.

emphasis on the "known" age of the rocks from which the specimens have been found dictating the identification, rather than pure taxonomic detail (Strachan 1971:60). This lead to Pribyl (1944) suggesting that specimens figured by Elles and Wood (1913, pl 48, figs.7a,c and text-fig.331a) as *M. spiralis spiralis*, should be assigned to *M. spiralis contortus*. I agree with Hutt (1975:107) that this assignation is invalid. Rickards *et al.* (1977:72) suggested that the genus *Spirograptus* Gürich is valueless, however it has recently been resurrected to include only the tightly coiled species of *turriculatus* type (Loydell 1993:82).

Torquigraptus tullbergi (Boucek 1931b) (see taxonomic notes), resembles *Oktavites excentricus* closely in rhabdosome dimensions, width, total length, and irregularity of coiling. The thecae however are very different, as *T. tullbergi* does not have the aperture ornamented with any spines, simply hooked at the aperture (Bjerreskov 1975:66). All of the sub-species of *T. tullbergi* are very narrow in the proximal portions, more so than *O. excentricus* .

T. tullbergi spiraloides exhibits the same degree of curvature distally as *O. excentricus* and both are coiled less tightly (almost straight) in proximal regions, *T. tullbergi spiraloides* however, exhibits a much greater degree of reduced coiling proximally than *O. excentricus* .

A comparison can be made with *Torquigraptus? involutus* (Lapworth, 1876) (sensu Lenz 1982:82). This species has similar dimensions to *Oktavites excentricus* (Bjerreskov 1975) and the presence of spines is similar, however the prothecae of *Oktavites excentricus* (Bjerreskov 1975) are of a larger and more triangulate nature, also the metathecae are further recurved rather than the simple hook, and rhabdosome coiling is slightly more eccentric. Thecal spacing of *Oktavites excentricus* (Bjerreskov 1975) is much closer than in *T. involutus* Lapworth 1876, which according to Lenz (1982:85) would lead to a comparison with *M. calamistriatus* Churkin and Carter (1970:37). This species is very similar to *Oktavites excentricus* (Bjerreskov 1975), but is restricted to the *M. gregarius* Biozone of Alaska (? equivalent to the *triangulatus* biozone?) and would merit further comparison of type material, before being placed in synonymy. Loydell (1993:115) described *Torquigraptus involutus* and suggested that the material figured by Lenz (1992:82) as *Monograptus involutus*, would not be assigned to this species, *Torquigraptus involutus sensu* Loydell (1993:115) is much less tightly coiled than *Oktavites excentricus*.

In the absence of good thecal preservation, *Oktavites excentricus* (Bjerreskov 1975) is distinguished from other curved forms (Pribyl 1944) by the following criteria:-

-Forms that are not as tightly curved or coiled as *Oktavites excentricus* (Bjerreskov 1975), these include *M. falx* (Suess, 1851), *M. curvus* (Manck 1923), *Torquigraptus arcuatus* (Boucek 1931b), *Monograptus convolutus* var. *communis* Lapworth 1876, *Torquigraptus planus* (Barrande 1850), and *M. formosus* Boucek, 1931b. *Torquigraptus proteus* (Barrande 1850) is curved much less sharply proximally, as is *M. grobsdorfensis* (Hemmann, 1931), which also has characteristic rounded thecal terminations.

-Forms that have thecae ventrally rather than dorsally (concave rather than convex side of stipe) include *T. curvus* (Manck 1923) and *Streptograptus plumosus* (Baily 1871). "*M.*" *gemmatus* (Barrande 1850), *T? conspectus* (Pribyl 1944) and *M. mirus* Perner 1897, have thecae rotating around the stipe to both dorsal and ventral positions regularly (Pribyl 1944:199).

-Forms that are too tightly curved or coiled, including *Spirograptus turriculatus* (Barrande 1850).

-Forms that have proximal portions that are straight or weakly ventrally curved (Lenz 1982:112), including *Oktavites contortus* (Perner, 1897), and *Torquigraptus tullbergi spiraloides* (Pribyl, 1944).

-Forms that are too regularly curved include "*M*". *chanygangensis* Sun, 1933, (which in the original description (Sun 1933:43) the thecae described are much narrower and slender than those of *Oktavites excentricus* (Bjerreskov 1975) (length about 5 times width) and according to Loydell (1993:116) include the specimens referred to above as *Torquidograptus involutus* (Lapworth, 1876) (sensu Lenz 1982:82). Also "*M*". *convolutus* (Hisinger 1837) which has thecae which are also more isolated, being almost rastritid-like proximally and without separation into triangular metathecae and tubular protheca.

Figure 9.3.11 Photograph of apparently sinuously curved thecae of *Oktavites* showing thecal spines. *Oktavites excentricus* (Bjerreskov 1975). All photographs of the same specimen taken under different conditions. A-C part, D-F counterpart. A, C and D, specimen with a layer of alcohol poured over the surface of the rock, B and E, specimen completely immersed in alcohol, E with much stronger lighting. F, no immersion in alcohol, specimen dry. All x 10.

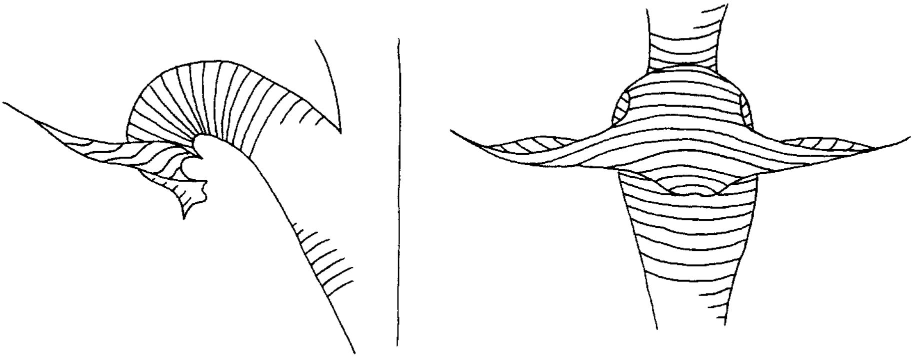


Figure 9.3.10 Characteristic thecal shape of Oktavites (idealised) with thin ornamentation (apertural processes) at the distal end of the protheca (after Rickards 1975:400, Rickards et al. 1977: 72 and Lenz and Melchin 1989). "Growth rings" purely for illustrative purposes.

Thecae are of typical *Oktavites* type, which means that the thecae are apparently sinuously curved (see figs. 9.3.10 and 9.3.11), with a triangulate metatheca, partially overlapping with its neighbours, a tubular protheca, with the dorsal wall of the protheca hooked over at the end and stretched out to form two spine like projections (see fig 9.3.10 and illustrations in Lenz and Melchin 1989). Most specimens seem to have the characteristic thin ornamentation at the distal end of their apertural processes preserved. In some specimens it appears that the hooked portion is fairly flexible and that the whole of the terminal portion is often flipped up, turning up on contact with the sediment surface rather than being buried in it. This results in some apparent variation in thecal terminations. The narrowness of the stipes and close thecal spacing (associated with limited overlap), are also very distinctive features of this species.

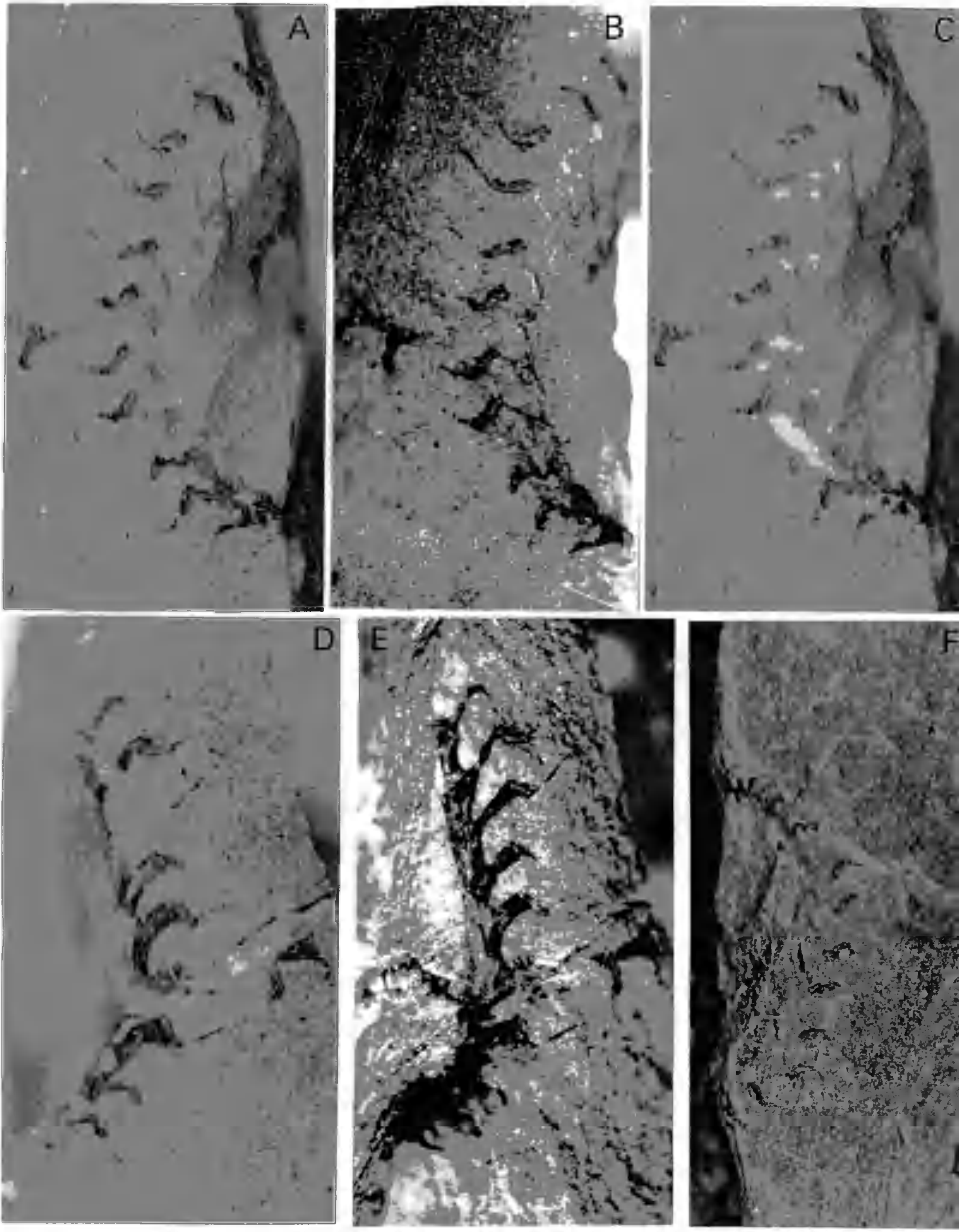
Measurements of 2TRD are as follows. Further statistical data pertaining to this species can be found in appendices.

Comparisons with other described species. *Oktavites excentricus* (Bjerreskov 1975) is very similar in general rhabdosome morphology (including eccentric coiling) and thecal shape to other specimens illustrated as "*Monograptus*" *spiralis*" by Elles and Wood (fig. 331a, pl. 48, figs.7a-d.) and by Toghill and Strachan 1970:518, as *M. spiralis* (Geinitz) sensu Elles and Wood). *Oktavites excentricus* (Bjerreskov 1975) is distinguished by its much smaller stipe width and closer thecal spacing, associated with limited thecal overlap and overall shorter rhabdosome length.

There is some debate (Bjerreskov 1975:72) about the sicular length of *Oktavites spiralis* (Geinitz, 1842), the recorded range being 1.1 mm (Bjerreskov 1975) to 1.5 mm (Lenz and Melchin 1989:342). The sicula length of *O. excentricus* in the type material is stated as 1.4 mm, whereas in the NEI the average sicula length is 0.9 mm, with a maximum recorded length of 1.1 mm. The eccentric coiling of O. spiralis s.s. is detailed by Hutt (1975:106), who describes the characteristic mixture of spiral and cone, prominent in most of the species of *Oktavites* (or sub-species of M. *spiralis sensu* Hutt 1975).

Oktavites excentricus is distinguished from other *Oktavites* species by thecal spacing. *Oktavites contortus* (Perner 1897) has slightly wider spaced thecae, and more regular coiling, although distal dimensions are very similar (Loydell 1993:123).

If the thecal structure of *Oktavites excentricus* is not well preserved, then it is difficult, particularly on rhabdosome shape alone, to identify this species. The distinctive spiral form however, restricts an initial identification to a limited number of species. Indeed, Pribyl (1944) felt that the spiral form (and triangulate thecae) were so important that he suggested a subdivision of *Monograptus* and referred these forms to the genus *Spirograptus* Gürich. Pribyl's paper is a very useful collation, but the work is greatly biased by his


A
B
C
D
E
F

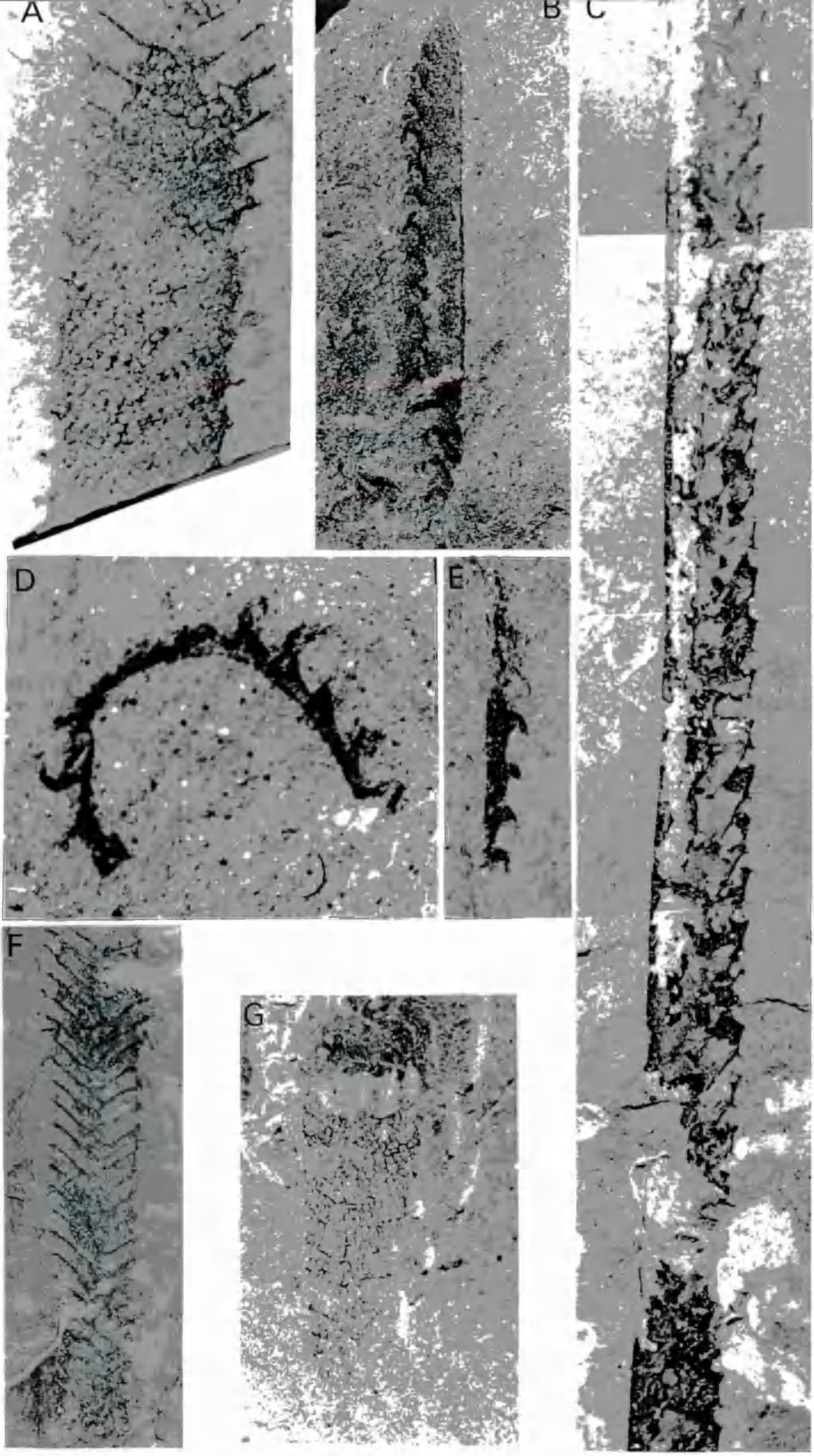
Forms that have very similar curvature to *Oktavites excentricus* (Bjerreskov 1975) include:-

Spirograptus andrewsi (Sherwin 1974) (see Loydell et al. 1993), which also has a similar thecal profile, with associated spinose thecal ornament. There is however no thecal overlap, and the thecal aperture of *S. andrewsi* (Sherwin 1974), is a simple opening at the end of the tube without further hooking, hooding or curvature.

Oktavites contortus (Perner 1897) is very similar to *Oktavites excentricus* (Bjerreskov 1975) in Pl. 2, figs 2-5 of Pribyl (1944), however, reference to the original illustration (Perner 1897, pl. 12, fig 24) shows that the distal portion of this species is straight or dorsally curved (see also Hutt 1975:107). (Note: Perner 1897:14 only refers to *Monograptus planus* Barrande 1850 in the text and the name *M. spiralis* var. *contorta mihi* only occurs in the plate explanation).

Also*Oktavites spiralis* (Geinitz, 1842) *(M. spiralis spiralis), T. tullbergi* , as discussed above and below.

Figure 9.3.12 All specimens from the North Esk inlier. Photographed completely immeresd in alcohol, except for F which was only partially immersed. A: Retiolites distal section x 10; B: Monograptus priodon distal section in full relief, first 3 thecae mould only x 4; C: Monoclimacis vomerina distal section x 10; D: Oktavites excentricus proximal portion including sicula x 10; E: Monograptus parapriodon proximal portion x10; F: Retiolites distal section x 5; G: Retiolites proximal portion x 10.


A
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Oktavites spiralis

Oktavites spiralis (Geinitz) is one of the most ubiquitous of species, recorded as common from most localities with graptolites preserved, ranging from *sedgwickii* Biozone to end Llandovery, end *spiralis* or *grandis* and equivalent biozones.

The *Oktavites spiralis* (or *M. spiralis* s.s.) specimens figured by Elles and Wood (1913, pl 48, figs.7a-d and text-fig.331a-c), are decidedly less robust than those of Lenz (1982:111) and Bjerreskov (1975:72). In the original description, two specimens were figured by Geinitz (1842), figures 27 and 26. One (fig 26) was selected as lectotype (Strachan 1971:60) by Pribyl (1944) and is the more robust of the two illustrated, (figure 27 being more slender). Elles and Wood did admit that a range of sizes existed, and suggested that "smaller individuals are usually found in lower beds".

There does seem to be a range of sizes that different authors consider to be O. spiralis, and two separate species may emerge possibly equivalent to the two different drawings of Geinitz:-

-A slender version (referred to as *sensu* Elles and Wood 1913), which possibly covers those illustrated by Lenz (1988); Hutt (1975:106); and Toghill and Strachan (1970). This may include some specimens referred to *M. spiralis contortus* Perner 1897 by Lenz (1982:112), with continuity of curving (slight ventral curvature very proximally is normally characteristic of contortus) (see also Hutt (1975:107) and Wilson (1954:78)).

-A robust morph, (Lenz (1982:111); Bjerreskov (1975:72); and Sudbury 1958).

Clearly a full taxonomic review of "*Oktavites*" species generally, and particularly *Oktavites spiralis* species is required, including physical comparison of the various authors figured specimens. As detailed by Rickards et al. (1977:72), a great deal of further work will still be required, studying the intricate details of the thecal structure, before clear evolutionary patterns can be established.

"M". tullbergi.

This species has been referred to the genus *Torquigraptus* by Loydell (1993:114, see also p. 119) Further research involving consultation with type material is necessary, but three sub-species seem to occur in the literature:-

1) *T. tullbergi tullbergi* (Boucek 1931b) which appears to be the same as Pribyl (1944: 202) which is fairly straight, semi-circularly curved only. Stipe width increasing from 0.2 mm (very thin proximally) to a maximum of 1.6 mm, 9-10 thecae in 10mm. Conforms with illustration (fig 9f, Boucek 1931b) selected as lectotype by Pribyl (1944:202). Also conforms with description of Zalasiewicz (1994:11). Specimens identified by Boucek as *Spirograptus tullbergi tullbergi* and now in the national Museum of Wales were inspected and conform to this morph (NMW.91.53G.17-20).
2) *T. tullbergi aff. tullbergi* (Boucek 1931b) sensu Bjerreskov 1975:66, which is coiled two or three times but retaining the same dimensions as in (1) above.
3) *T. tullbergi spiraloides* (Pribyl, 1944:203) fairly irregularly coiled two or three times in a flat conical form with a large degree of stipe torsion. The proximal portion of this sub species (first 8-10 thecae) according to Lenz (1982:117), is either straight or slightly dorsally curved. Stipe width increasing from 0.5 mm to a maximum of 2 mm, thecae in 10mm, 10-11 proximally, 8-9 distally, *T. tullbergi spiraloides* expands more rapidly proximally than *T. tullbergi tullbergi.*

Specimens of *Retiolites geinitzianus angustidens* were judged not well enough preserved to warrant further taxonomic description, but could with some degree of confidence be identified as this species, recorded generally as restricted to the *crenulata* Biozone. Specimens are illustrated in figure 9.3.5.

9.4 Terminology

2TRD	Two Thecae Repeat Distance, usually used for graptoloids and not yet applied to dendroids. Measured at thecae 2, th.5, th.10, th.15 etc (Howe1983). Measure of thecal spacing, useful for numerically comparing species. See section 7.8.1
adnate	joined up, stuck together, as in thecae which are in constant contact with their neighbours throughout their length.
anastomosis (anastomose)	approach and joining of two dendroid stipes or branches, to form a single stipe. Any subsequent separation is a separate bifurcation, or lateral branching episode. Beware superposition of stipes where individual characters of original stipes are retained, without even partially anastomosis.
anchoring fibres	part of a dendroid =>holdfast structure, long, nema like fibres secreted by benthic dendroids to secure them in the soft sediment surface. Sometimes wrapped around objects such as shells. Term replaces "root" to avoid confusion with plants (see sectionX)
aperture	entrance, mouth, terminal end of theca. Usually open, but dendroid bithecae can open into the stipe wall. Aperture often ornamented with apertural spines (projections originating from margin of the thecal aperture), lappets, or other distinctive modifications
apical disc	holdfast structure of some benthonic dendroids. Disc like structure developed from the sicula, spreading out over the sediment at the apex of dendroid cone, used to attach dendroids to the sea floor.
aseptate	without septae, often biserial rhabdosomes lacking median septum.
assemblage	biozonal term, used to describe the fossil group that are representative of a particular biozone. The group of fossils (e.g. graptolites) that are found at any one time.
astogeny (astogenetic)	growth history of a colonial animal.
automobile	ability to move about under its own power, postulated ability of graptolite rhabdosomes to move through the water column by coordinated movement of zooid tentacles or other zooidal action.
autotheca	Large type of regularly developed graptolite (dendroids) theca. Usually paired with a bitheca and characteristic of dendroids. Autothecae possibly thought to house female zooids. Referred to as hydrothecae by Bulman (1928)
bandages	ribbon shaped components of the periderm, laid down over the fuselli, usually on the outside of the thecae.
basal disc	dendroid hold fast structure, secreted to secure or anchor a benthonic form and support the remainder of the colony. Basal discs may have spread out across solid surfaces, with "anchoring thread" modifications to secure the colony on soft substrates.
benthonic (benthic)benthos (noun)	animals living at or near sediment -water interface, mostly sedentary or fixed forms, or mobile forms that are bottom dwelling or semi-infaunal.
bentonite	assemblage of clay minerals, usually formed from weathering of pyroclastic rocks, particularly volcanic ash falls
bifurcate	to split into two approximately equal divisions of the original.
BIGG	British and Irish Graptolite Group. An organisation set up by Dr R. B. Rickards, which meets twice annually to discuss recent work on graptolites, to initiate projects and share information. Authors of Palmer and Rickards 1991. A very successful, useful and productive forum for promotion of graptolite research work.
biostratigraphy	study of sedimentary strata by means of the fossils contained within them. Fundamental subdivision recognised is the biozone. Identifying and matching fossil assemblages to correlate between rocks from different areas.
biota	living organisms, usually pertaining to all life present at one place, at any one time.

bioturbation	disturbance of sediment by organisms. May be during burrowing, feeding, locomotion or even resting, and traces of these activities can be preserved in sediment to be studies as ichnofossils, intense activity an obliterate individual traces and disturb all of the sediment (complete bioturbation).
biozone	subdivision of biostratigraphy based on the stratigraphic ranges of certain species, and ideally of overlapping ranges of an assemblage of fossils. Zonal schemes recognised for graptolites, conodonts, brachiopods, ammonites, ostracodes, etc.
biserial	scandent graptolite rhabdosome with two series of thecae enclosing nema (or virgula).
bitheca	smaller type of regularly developed (dendroid) graptolite thecae, possibly housing zooids of one sex only (possibly male).
branching	formation of new dendroid stipes by the splitting up of an existing stipe, by either dichotomous branching (bifurcation) or lateral branching. See: monopodial branching; twigs.
branchlets	small side branches of stipe (bundle of thecae) characteristic of the Acanthograptidae.
Camera-lucida	type of modified binocular microscope used for drawing fossils, formed by the addition of a mirror system allowing the image of a piece of paper and pencil (and hence a drawing) to be superimposed on the image of the fossil, resulting in accurate drawings.
cauda	narrow proximal part of the prosicula.
chronostratigraphy	correlation of rocks based on their time relationships against a standard scale and divided into time equivalent units, system, series, stage and chronozone. Presently few chronozones recognised, biozones give only relative ages, biozone/chronozone equivalence would be the pinnacle of biostratigraphical accuracy.
cladium / cladia (plural)	stipe developed from a thecal or sicular aperture
clathria	skeletal framework of rods composing the rhabdosome (retiolitids), sometimes supporting attenuated periderm.
coenoecium	tubular exoskeleton of colonies of pterobranchs.
collagen	a protein, now found in cartilage and bone, of which graptolite fibrils were constructed.
colony / colonial	population of genetically similar organisms living in close proximity and interacting to some extent. Graptolite rhabdosome secreted and populated by zooids. Colonial animal, one that liver in a colony, not found individually except at early growth stages.
common canal	Continuous tubular cavity collectively formed by prothecae of graptoloid: rarely involving some portion of the metatheca.
cone	conical habit. Common shape of dendroid rhabdosome, expanding regularly from a point to a circle.
conodont	extinct elongate eel-shaped protochordates, possessing distinctive natural assemblages of tiny, bilaterally symmetrical elements. Conodont biozonal schemes now accurately recorded and being correlated with graptolite biozonal schemes.
conspecific	of the same species.
cortical	cortical fabric cortical layer exterior layer of graptolite periderm component of cortical tissue composed of linear bundles of collagen fibrils outer layer of graptolite periderm, composed of bandages.
curate/curator	to be in charge of, generally to organise by identifying, classifying, labelling and recording of specimens in some recognisable system in a museum.
cyrtograptids	graptolites possessing cladia.
dendroid	habit of growth, particularly a bushy colony formed by irregular branching of stipes.

dendroids	colloquial or informal diminutive term for Order Dendroidea. Most rhabdosomes with a number of branches are commonly referred to as dendroids.
denticulate	term used to describe overall appearance of stipe due to outward projection of sharply pointed thecal apertures. Serrated, (saw tooth) edge to stipe, or looking like rows of teeth.
dichotomous branching	branching pattern of dendroids where a stipe bifurcates (splits) to form two stipes. These are two new main stipes that are continuous and go on to bifurcate again, or two thinner branches that usually terminate rapidly (see also zones of bifurcation, lateral branching) (Bull, 1986, p. 121).
diminutisation	becoming smaller or becoming less.
dimorphograptids	graptolite rhabdosomes formed by two modes of secretion of thecae, usually commencing with a uniserial habit, and then becoming biserial after a specific number of thecae have formed.
dissepiments	strand of cortical periderm serving to connect adjacent branches in denroid rhabdosome (especially in *Dictyonema*). Formation is discussed in section 7.4.3. Forms one margin of dendroid meshwork (=>fenestellae). (See also =>anastomosis).
Dorso-Ventral Width DVW	total width of a graptolite at the widest point, excluding any spines. See section 7.8.1
ecdysis	Moulting. Process whereby the rigid exoskeleton of certain animals is shed at regular intervals and a new larger exoskeleton is formed, allowing the animal to grow.
ecophenotypic variation	Change in animals shape caused by change in physical conditions. Environmental influence on the appearance of an animal, typically leading to the same species appearing different when developing in different conditions
endemic	Animals restricted to a certain province, not found outside of that particular area or set of conditions.
epi-planktonic	Animals living as part of the plankton.
epibenthos	Animals living as part of the benthos
epithelium	fleshy layer involved in the secretion of new tissue
everted / eversion	Plane of aperture facing outward
extrathecal	Outside of the thecae, particularly cloaking or surrounding graptolite hard parts in soft tissue.
fenestellae	holes in the regular meshwork of dendroid stipes formed by either anastomosis, dissepiments or branching pattern. Size and shape of fenestellae often characteristic to each species. Previously described as "meshes" or "fenstrulae".
fibrils	Fibrillar material. Particularly used to describe the fibres of the cortical layer, or collagen fibrils of the fusellar layer of graptolite periderm.
flabellate	In the form of an open fan
furcate	to split or to branch, as in bifurcate. Old term, and often found in translations from other languages into English.
fuselli (fusellus) fusellar fabric	single growth element of graptolite periderm, forming a half ring. peridermal layer of criss-cross fibrils, often inner layer of periderm, several fabric types.
geniculum	angular bend in direction of growth of graptolid theca.
herontic	old aged, study of processes occuring in old age.
global standard	biostratigraphical term, a chart with which stratigraphy can be corellated worldwide. Chronostraigraphy, and the selection of standard sections with which others can be corellated

graptolite	colloquial term for the Graptolithina, colonial marine organisims which secreted sclerotised skeleton with growth bands, thecae housed individual zooids and connected by internal stolon system.
graptolithologist	a person who studies graptolites
graptoloid	planktonic, single or multistiped planktonic graptolite, often used to refer to the Monograptacea
half-ring	building brick of graptolite construction, the shape of fibrils.
ICZN	International Committee on Zoological Nomenclature.
inlier	a limited area of rocks completely surrounded by younger rocks, a window through to older rocks beneath created by erosion, faulting or folding or all three.
interthecal	between thecae, such as interthecal septum.
introverted	plane of aperture facing inwards
isolation	separation of distal portion of theca (metatheca) from the stipe.
lacina	delicate skeletal network external to rhabdosome proper.
laminae	thin discrete layers of rock, usually sedimentary
lappet	broad round lateral apertural process of theca or sicula
lateral branching	new stipes by formed by branching to the side, which can be same thickness or thinner than original. 'Division of the stipe in which branches diverge at an angle to parent stipe, which continues its original direction of growth" (Bulman 1970) (=> dichotomous branching, =>bifurcation, =>twigs)
lithostratigraphy	corellation of rocks based on rock type, used in mapping.
lophophore	tentacled and cilliated arms, paired or in groups, found adjacent to the mouth and used for feeding and respiration.
median septum	partition in biserial graptolites separatingtwo series of thecae.
metasicula	distal portion of the sicula, composed of normal fusellar growth bands, the second formed part.
metatheca	distal, later formed part of graptoloid theca terminating in the aperture, secreted as an extension of the protheca and often ornamented, hooked or bearing apertural processes
monoclimacis	graptolite genus with square shaped thecae, prominent geniculum lying above the aperture of the previous theca
monograptid	colloquial term for single stiped , single sided graptolite. Member of the family Monograptidae
monopodial branching	suppressed term describing formation of lateral branches from only one side of a dendroid stipe.
morph / morphosis / morphogenetic	shape or form, particularly animals with a characteristic shape. Mode of morphological development origin and development of a particular shape, form or organ.
multiramous	many branched
nema / nemata	Thread like extension of the apex of the prosicula (plural)
palaeopathology	pathology (disease) of extinct or fossil animals
pendent	parallel branched graptolite with stipes hanging below the sicula See Clarkson 1986:283.

periderm	graptolite skeleton, or material forming it, inner fusellar layer, outer cortical layer
planispiral	a spiral form that is two dimensional, all lying in one plane
prosicula	proximal initially formed part of the sicula
protheca	proximal portion of graptoloid theca
prothecal fold	curvature of part of the protheca, often at curves in the stipe, causing a ridge or bulge in the dorsal margin of the stipe
pterobranch	extant dendroid-like hemichordates related to the graptolites. "Living fossils"
reclined	graptolite rhabdosome with stipes growing up from the sicula, and stipes lying with dorsal margins facing one another at an angle of less than 180°
reflexed	stipes approximately horizontal, stipes at close to 180° to one another.
regrowth / rejuvenation	recommencement of growth of a colony return to juvenile form on recommencement of growth
retroverted	hooking, or strong curvature of thecae (metatheca) causing aperture to face proximally
rhabdosome	entire graptolite skeleton
root / rootlet	terms used to describe attachment structures of benthic graptolites such as dendroids. use of this term is discouraged as it is too closely associated with plants which grow by completely different methods.
scalariform	preservational view with ventral (thecal) margin of the stipe presented to view. Often in laterally compressed specimens
scandent	graptolite with stipes growing erect, enclosing nema, effectively back to back.
sensu lata / sensu stricto	laterally or broadly interpreted, not strictly defined in the wide sense / strictly interpreted, in the strict sense, or understanding
septa (septum)	partition separating two thecae
sessile	attached directly, without stem
sicula / siculate	skeleton of initial zooid of colony
spinose	bearing spines, spiny
SSSI	Site of Special Scientific Interest. Established and maintained list of sites that demonstrate some important scientific feature such as an important fossil locality. Administered by Scottish Natural Heritage in Scotland.
stem	bundle of stipes often secondarily thickened, forming the base of a benthic graptolites between the attachment disc and the full cone or fan etc. of the rhabdosome
stipe	one branch of a branched rhabdosome or entire colony of unbranched rhabdosome
stolon	thin sclerotised sheath presumably surrounding thread of soft tissue, from which dendroid thecae appear to originate.
sub-apertural	beneath the aperture
suprageniculаr	above the geniculum
synrhabdosome	association of several attached graptolites
teratology	the study of antenatal growth malformations, or growth defects occuring in juvenile forms

twigs	Acanthograptids forming a side branch or branchlet. Usually associated with lateral branching.
ultrastructure	fine details of the construction, of structure of graptolite periderm
uniserial	one sided, graptolite with thecae only on one side of the stipe
vesicles	sub-spherical bodies thought to contain gas, or fat, associated with membranes and possibly origiated as flotation devices.
virgella	spine developed during growth of the metasicula, part of the sicula wall projecting freely from its apertural margin
virgula	nema of scandent graptolites
zone	stratigraphic term used to describe a subdivision, such as a biozone.
zooecial	pertaining to graptolite zooid
zooid	soft bodied tentacled animal inhabiting all graptolite thecae. Thought to be interconnected colonial animals, involved in feeding and secretion of hard parts (=>rhabdosome) of graptoloids and dendroids. Possibly hermaphroditic in graptoloids and separate male/female in dendroids.

Chapter 10

Taxonomic notes and illustrations

Ichnofossils

Planolites is commonly associated with chondrites burrows in the sediments of the Reservoir Formation (fig 4.6). Different species of *Planolites* are identified as follows (After Bruce 1992:134), all are filled with darker sediment thought to have formed by the animal ingesting sediment, and depositing it behind them to fill the burrow.

Small burrows, curved or tortuous......*P. montanus* (2.2 mm wide)
Large straight to gently curved...*P. beverleyensis* (13.7 mm wide)
Transversely anulated *P. annularis*.

Ichnogenus A.

Horizontal burrow which may be linear or curved and cross cutting (following execution of a turning circle 6-8 cm in diameter) formed on the surface of the sediment (see fig 4.7). One trace superimposed on another by the second passage of the animal along the same, or return path.

Trace has a rectangular cross section, with sub-vertical sides about 1mm deep, with prominent lateral ridges formed by the sediment excavated from the trace (see fig 4.7), trace 6-8 mm wide. No clear median trough. Best example found on a loose block at the north of the Gutterford burn, in the very top of the Reservoir Formation. The original position of this block can easily be traced, and further examples of this trace found elsewhere on the horizon. A latex cast was taken of the surface, and from this, the prominent lateral ridges and rectangular cross-section can be identified.

Bruce (1992:148) described this trace as 15-20 cm [mm] wide *Taphrhelminthopsis* ichnosp. because of the presence of a prominent median trough [?ridge], and that this median trough formed by a groove in either the dorsal or ventral surface of the body of the producer. She could not be more specific about whether this is a hypichnial or epichnial trace as she could not identify the way up of this loose block.

It is thought that the identification by Bruce (1992) of a median ridge and 15-20 mm width of this trace came from inspection of the part of the surface where it was traversed by the same trace-producing organism twice. Inspection clearly shows that this was not a single trace as one cuts the other, and they diverge and converge.

It is thought possible herein, that this trace was formed by a rigid structure such as the telson of a arthropod. This would imply that the animal maintained the medial line of its body straight, although slight periodic variations in the width of the trace are seen, which could correspond to the walking cycle of the animal, and one section of the trace (fig 4.7) has possible marks from walking legs either side of the main trace.

Taxonomic Notes 10.2

"Dictyocaris."

Dictyocaris is the most common fossil found in the sediments of the NEI. This did not escape the attention of the earliest author to properly describe this fossil, Salter (1860; 1861) who stated "...it is so conspicuous and common a fossil that it must receive a name".

It is an enigmatic form. As its name suggests is has so far always been described as a crustacean or "Giant Phyllopod" carapace, and is characterised by its pronounced reticulate surface ornament.

The remains of this fossil are thin carbonaceous sheets, less than half a millimetre thick, which show no internal structure in thin section. The sheets vary in size from small fragments a few millimetres across, to large sheets 30 centimetres in diameter. The sheets show no regular outline or recognisable external shape, and are generally found undulating across the sediment surface, or gently folded. No clear margin or border delineating structures have been identified, although specimens with recognisable edges are common.

Salter's diagnosis of genus *Dictyocaris* was as follows:

> "Carapace large, consisting of one continuous shield bent along a straight dorsal line. Outline in lateral view subtriangular with anterior angle about 30 degrees and post-dorsal nearly 90 degrees. Outline not known in detail. Length of carapace up to 23 cm, one fragment 33.3 cm. Body rings apparently narrow. Test with distinct ornamentation, varying from regular polygonal areas bordered by raised rims to broader ridges separating narrow depressions."

A number of different surface ornamentation structures are observed, these have been described as separate species. The most common is:-

Dictyocaris slimoni Salter 1860,

> "... Test with distinct reticulation consisting of raised narrow rims or ridges bordering level 5-6 sided polygonal areas. Diameter of meshes rather constant with an average of 0.8 mm. In certain cases the areas may be somewhat elongate."

Dictyocaris slimoni Salter, var. *tuberculata* Størmer 1935

> "Reticulation of test consisting of regular polygonal areas with a diameter of about 1mm with a central tubercle or elevation."

Dictyocaris ramsayi Salter 1860, [1]

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[1] This species was named by Salter (1860) after the great Scottish poet, Allan Ramsay who was also father of the renowned portrait painter of the same name. Allan Ramsay (Sn.) based the 1725 pastoral play, or rustic romance, "The Gentle Shepherd" written in old Scots language, in the North Esk area, a map of the area was also later published (see Kinghorn and Law 1974:200). This poem became very influential to the later Scots poetry such as that of of Robert Burns and Lewis Grassic Gibbon.

> "... Test ornamented with small circular [of] or elongate, more or less curved, depressions between broader raised ridges."

Dictyocaris salteri Størmer 1935

> "Outline of carapace is unknown. Surface of test, or counterpart of it, ornamented with narrow raised ridges bordering elongate meandering depression with an average width of 0.9 mm."

No specimens of *Dictyocaris slimoni* var. *tuberculata* have been found from the NEI, but all other types of ornamentation are present.

Two fundamental observations are thought here to preclude interpretation of *Dictyocaris* as crustacean carapace, the lack of consistent carapace outline or recognisable segments; and the apparent flexibility of remains at time of deposition. A search was made for a test that would prove if the carbonaceous remains originated as plant or animal material. It was suggested that analysis of polished thin sections on an electron microprobe might in future be able to distinguish different types of carbon, but that sufficient resolution did not exist to pursue this yet. An alternative would be attempting to isolate the carbonaceous material by dissolving away the rock. This was not attempted. Specimens were however studied on a Scanning Electron Microscope, to see if any fine microscopic structure could be observed. This proved inconclusive. Whilst scanning the specimens and observing the 3-D images, the inside of some of the polygonal structures possibly appeared to be further divided into sub-rounded structures about 0.2 mm in diameter, which could represent a cellular structure. When photographed, these structures are not readily apparent (fig10.27). They are thought worthy of further investigation, and could support *Dictyocaris* being reinterpreted as vegetable matter.

Many thousands of specimens of *Dictyocaris* are known, and although some have very distinct outlines (fig10.28) these are not consistent, with almost no two pieces having the same external outline. It is not thought possible here that an animal with an almost infinitely variable carapace outline can be envisaged. The triangular shape described in the original works can be identified in the material illustrated (which has been studied by the present author), but it would be equally possible in the field to select specimens with a circular or square outline to collect. Larger specimens of *Dictyocaris* often have multiple layers of *Dictyocaris* preserved in each hand specimen, each separated by a few millimetres of sediment. It is thought that it was these multiple layers that led Salter (1860) to suggest the carapace to be folded at one margin.

The (single) specimen described by Størmer (1935) to possess body segments has been studied, and was not found to be convincing, merely an artifact caused by the regular folding of the specimen at time of deposition. Størmer (1935:270) concluded that the presence of marginal rims was doubtful, a view supported here.

Dictyocaris is commonly (but not exclusively) found in extremely rapidly deposited sediments, and associated with exceptional-preservation horizons containing dendroids, starfish or eurypterids. As can be seen from some of the plates enclosed herein, the preservation in these horizons is extremely good and complete. It is thought that the majority of the outlines of the specimens of *Dictyocaris* preserve the shape of the specimen at time of deposition, the growing edge of the specimen (the exception to this are bioturbated specimens, which are discussed later). It must therefore be concluded that *Dictyocaris* had an irregular outline, and no recognisable external shape.

Dictyocaris specimens follow contours of the original sediment surface. Additionally where material may have been disturbed, or large specimens dragged by currents, specimens can be undulatory, or ruffled into gentle folds. No predominance of convex or concave specimens has been found. Størmer (1935:274) sought to explain the strongly crumpled test by suggesting that the test was extremely thin, and that

> "the calcareous shells remained uncovered for some time on the bottom, and the fresh or brackish water (which has a greater ability than salt water in dissolving lime) succeeded in dissolving and destroying parts of the shell, a process that was completed later in diagenesis".

Dictyocaris is only preserved as thin sheets, with reticular ornament on one surface, no further 3-D structures are seen, or internal structures that would have formed the internal muscle supports or structure of the carapace of a segmented arthropod. It is not thought to have been calcareous originally, but to have been constructed of soft, flexible, organic material, that formed on the sediment surface, and draped over it, possibly akin to an algal mat.

Individual specimens of *Dictyocaris* can be found with variations in the surface ornamentation, and can have the structures described as two separate "species" of *Dictyocaris*, on one specimen. It can be seen that the three main species form a progression from completely enclosed polygonal shapes (*D. slimoni*) to elongate ridges and furrows (*D. salteri*), with *D. ramsayi* representing the intermediate form. It is therefore recommended that the specific subdivision be abandoned. The generic name has been retained here, due to its long standing recognition in the literature, and until its proposed vegetable affinities can be irrefutably proved.

The presence of *Dictyocaris* has sometimes been used in the Oslo region to identify marker horizons indicative of Wenlockian age (Stormer 1935). This is possibly an area for further research.

The following pages contain details of measurements made of graptoloid specimens found in the North Esk inlier sediments.

page 291 : composite chart of all measurements made on specimens with *priodon* type thecae. F=flat, R=relief measurements made of the length of individual thecae and not 2TRD hence Rep len. th.n= length of theca *n* only.

Page 292 : p= *Monograptus priodon* and pp=*Monograptus parapriodon*. Measurements of DVW and 2TRD as plotted in "profile plot" diagrams.

Page 293 : *Monograptus priodon* measurements of inner (metatheca only) width and outer (total width of metatheca & protheca) width of specimens.

Page 294 : measurements of proximal portions of Monoclimacid specimens.

Page 295 : composite chart of all measurements made on specimens with Monoclimacid type thecae. TDth.n+x = 2TRD at th. n+x. BU1555 specimen of *Mcl. crenulata* from the Elles and Wood collection, Birmingham University.

Page 296 : and Page 297 : data for profile plots for *Mcl. vomerina* and *Mcl. geinitzi*. measurements taken at each thecal level, first figure given is DVW and below it the corresponding 2TRD.

Page 298 : composite chart of all measurements made on *Oktavites* specimens.

Followed by :

Illustrations of a representative selection of the fossil fauna found in the "Gutterford Burn Limestone Bed" locality. Many require taxonomic revision and further research.

All specimens in the authors collection unless otherwise stated.

Plodon spec. no	F/R	Length overall	Width th.1	Width th.5	Width th.10	width th.15	Width th.20 / Width th.25	Width th 30/35/45/55/65/75	Width dist.	n=	Rep len. th.n	Rep len. th.n+1	Rep len. th.n+2	Rep len. th.n+3	Rep len. th.n+4	Rep len. th.n+5	Rep len. th.n+6	Rep len. th.n+7	Rep len. th.n+8	Rep len. th.n+9	Rep len. th.n+10	Rep len. th.n+11	No. th. prox.	No. th. Dist	Sicula length	TTRDth.5	2TRDth.10	2TRDth.15	2TRDth.20	TTRDth.25	TTRDth.30	TTRDth.35	2TRDth.40	2TRDth.45/50/55/60/65/70	Thecae present	spec. no
GI47560	F	6.25	0.27/0.48	0.32/0.64						1	0.93	0.57	0.71	0.75	0.84	0.75	0.66						14/10		1.25	1.51									1-8	GI 47560
JCT 79/0127	F	5.19	0.22/0.44	0.28/0.72						2	?0.61	0.69	0.7	0.8	0.81	0.89							14/10			1.59									2-8	JCT 79/0127
EEB207	F	14.7	0.28/0.63	0.62/1.04	0.71/1.13	0.79/1.46	0.88/1.5			2		0.71	0.75	0.71	0.54	0.79	0.75	0.88	0.75	0.8	0.88	0.83	14/10			1.27	1.54	1.81	72.0						2-20	EEB207
EEB212	F	14.55	0.29/0.51	0.36/0.65	0.55/1.02	0.73/1.2	0.76/1.31			2		0.65	0.72	0.69	0.76	0.76	0.73	0.95	0.87	0.8	0.87	0.8	14/10			1.44	1.71	1.73	1.75						2-20	EEB212
GI1886	F	8.9			0.70/1.04	0.74/1.15																		12/10?			1.63	1.71							9-19	GI1886
GI47566	F	22.14/(32.5)				0.641.07	0.82/1.29 // 0.89/1.5	1.07/1.54	1.32/2.04															12/10					2.2	1.96	2.04	2.11			15-38	GI 47566
GI22223	R	22.22/(36.7)					0.82/1.30 // 0.96/1.44	1.15/1.63	1.30/1.78															11/10					1.74	1.98	2.07	2.15	2.07		20-41	GI 22223
GI21648	F	35.60/(50.2)					0.95/1.35 // 0.98/1.67	1.05/1.71	1.10/1.85															11/10					1.45	2.16	2.2	2.18	2.25	2.21	18-47	GI 21648
EEB211	F	13.33/(27.9)					0.89/1.41 // 0.96/1.44	1.04/1.77																10/10					2.07	2.05	2.13				20-32	EEB211
EEB214	R	11.11/(25.9)					0.93/1.38 // 1.00/1.52	1.19/1.77																10/10						2.04	2.07				23-33	EEB 214
EEB225	R	16.60/(26.8)						1.28/1.74	1.32/1.85															9/10							2.06	2.32			27-39	EEB225
R82	F	4.3/(18.85)				0.5/1.05	1.00/1.29																					1.25							14-19	R82
GI47565	R	10.74/(43.2)							1.33/1.96															13/10										1.59/1.64/1.84	43-56	GI 47565
GI22214	F	36.36/(60.9)						1.60/?04	1.56/2.22															9/10							2.04	2.18	1.93	2.18	31-60	GI 22214
EEB223	R	94.96	0.27/0.48	0.52/0.74	0.58/0.88	0.59/0.98	0.61/1.16// 0.68/1.28	069/1.31//071/1.41//084/1.76//088/064//1.2/1.96//1.12/1.98	1.36/2.04 max														11/10	9/10	0.6	1.8	1.96	2.12	2.16	2.2	2.28	2.31	2.33	212/214/215/224/231/232/250/252	1-85	EEB 223

pp D/V width	th. 1	th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35	th. 40	th. 45	th. 50	th. 55	th. 60	th. 65	th. 70	th. 75	th. 80	
EEB 223	0.48	0.74	0.88	0.98	1.16	1.28	1.31	1.41		1.64		1.76		1.96		1.98	1.98	
EEB 225												1.74		1.96				
GI 22223							1.3	1.44		1.63		1.81		1.89				
EEB 212	0.51	0.65	1.02	1.2	1.31													
JCT 79/0127	0.44	0.72																
GI 47560	0.48	0.64																
average pp	0.48	0.69	0.95	1.09	1.23	1.28	1.31	1.43		1.63		1.77		1.94		1.98	1.98	

2TRD		th. 5	th. 10	th.15	th. 20	th. 25	th. 30	th. 35	th. 40	th. 45	th. 50	th. 55	th. 60	th. 65	th. 70	th. 75	th. 80	Th. pres.
EEB 223		1.8	1.96	2.12	2.16	2.19	2.28	2.31	2.33	2.12	2.14	2.15	2.24	2.31	2.32	2.5	2.52	1-85
EEB225												2.06	2.22	2.32				27-39
GI 22223							1.74	1.98	2.07	2.15	2.07							20-41
EEB212		1.44	1.71	1.73	1.75	1.77												2-20
JCT 79/0127		1.59																2-8
GI 47560		1.51																1-8
average pp		1.58	1.83	1.93	1.96	1.98	2.01	2.14	2.21	2.14	2.11	2.11	2.23	2.31	2.32	2.5	2.52	

p. D/V width	th. 1	th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35		th. 45		th. 55		th. 65		th. 75		
GI 22214										1.89		2.07		2.14		2.17		
GI 47565												2.04		2.11		2.19		
EEB 214					1.38	1.52	1.77											
EEB 211					1.41	1.44	1.77											
GI 21648					1.35	1.67	1.71	1.76		1.79								
GI 47566				1.07	1.29	1.5	1.54	1.8		2								
GI 1886			1.04	1.15														
EEB 207	0.63	1.04	1.13	1.46	1.5													
R 82				1.05	1.29													
Average prioc	0.63	1.04	1.09	1.18	1.37	1.53	1.69	1.78		1.89		2.06		2.13		2.18		

2TRD		th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35	th. 40	th. 45	th. 50	th. 55	th. 60	th. 65	th. 70	th. 75	th. 80	
GI 22214										1.93	2.04	2.17	2.18	2.22	2.28	2.33		31-60
GI 47565										1.59	1.64	1.84						43-56
EFB 214					1.98	2.04	2.07											23-33
EEB211					2.07	2.05	2.13											20-32
GI 21648					1.45	2.16	2.2	2.18	2.25	2.21								18-47
GI 47566				1.83	1.96	2.02	2.04	2.11										15-38
GI1886			1.63	1.71														9-19
EEB207		1.27	1.54	1.81	1.95													2-20
R82				1.25														14-19
average priodon		1.27	1.59	1.65	2.01	2.07	2.11	2.14	2.25	1.91	1.84	2.01	2.18	2.22	2.28	2.33		

pp D/V width	th. 1	th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35	th. 40	th. 45	th. 50	th. 55	th. 60	th. 65	th. 70	th. 75	th. 80	
av. D/V pp	0.48	0.69	0.95	1.09	1.23	1.28	1.31	1.43		1.63		1.77		1.94		1.98	1.98	
av. 2TRD pp		1.58	1.83	1.93	1.96	1.98	2.01	2.14	2.21	2.14	2.11	2.11	2.23	2.31	2.32	2.5	2.52	
av. D/V p.	0.63	1.04	1.09	1.18	1.37	1.53	1.69	1.78		1.89		2.06		2.13		2.18		
av. 2TRD p		1.27	1.59	1.65	2.01	2.07	2.11	2.14	1.99	1.91	1.84	2.01	2.18	2.22	2.28	2.33		

priodon inner width	th. 1	th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35	th. 45	th. 55	th. 65	th. 75
EEB 223	0.27	0.52	0.58	0.59	0.61	0.68	0.69	0.71	0.84	0.88	1.2	1.12
R 82				0.53	0.98							
EEB 225								1.28	1.29			
GI 22214	0								1.49	1.56	1.72	1.78
GI 47565										1.37	1.46	1.52
EEB 214					0.93	0.98	1.19					
EEB 211					0.89	0.96	1.04					
GI 21648					0.95	0.98	1.05	1.08	1.13			
GI 22223					0.82	0.96	1.15	1.3	1.32			
GI 47566				0.64	0.82	0.89	1.07	1.08	1.22			
GI 1886			0.7	0.74								
EEB 212	0.29	0.36	0.55	0.73	0.76							
EEB 207	0.28	0.62	0.71	0.79	0.88							
JCT 79/0127	0.22	0.28										
GI 47560	0.27	0.32										
Average	0.27	0.42	0.63	0.67	0.85	0.91	1.03	1.09	1.22	1.27	1.46	1.47

priodon outer width	th. 1	th. 5	th. 10	th. 15	th. 20	th. 25	th. 30	th. 35	th. 45	th. 55	th. 65	th. 75
EEB 223	0.48	0.74	0.88	0.98	1.16	1.28	1.31	1.41	1.64	1.76	1.96	1.98
R 82				1.05	1.29							
EEB 225								1.74	1.96			
GI 22214									1.89	2.07	2.14	2.17
GI 47565										2.04	2.11	2.19
EEB 214					1.38	1.52	1.77					
EEB 211					1.41	1.44	1.77					
GI 21648					1.35	1.67	1.71	1.76	1.79			
GI 22223					1.3	1.44	1.63	1.81	1.89			
GI 47566				1.07	1.29	1.5	1.54	1.8	2			
GI 1886			1.04	1.15								
EEB 212	0.51	0.65	1.02	1.2	1.31							
EEB 207	0.63	1.04	1.13	1.46	1.5							
JCT 79/0127	0.44	0.72										
GI 47560	0.48	0.64										
Average outer widt	0.51	0.76	1.02	1.17	1.31	1.44	1.62	1.7	1.86	1.92	2.07	2.11
Average inner widt	0.27	0.42	0.63	0.67	0.85	0.91	1.03	1.09	1.23	1.27	1.46	1.47

	Proximal end measurements of Monoclimacids				
Mcl. vomerinus	sicula length	sicula widt	spine length	sic-thec	length th 1
202b 8	1.22	0.26		0.25	1.13
202a 1	1.13	0.23		0.16	1.42
204b 3	1.24	0.33		0.24	1.02
204a2	1.36	0.25	0.1	0.31	1.13
204 b1	1.21	0.29		0.33	0.96
204a1	1.01	0.29		0.2	1.02
EEB217 2	0.89	0.23		0.27	0.47
EEB 219a	1.22	0.23		0.4	0.79
GI 20226	0.86	0.29		0.15	0.61
Average vom.	1.13	0.26		0.25	0.96
Mcl. geinitzi					
EEB202a8	0.96	0.26	0.65	0.19	0.96
202b 8	1.22	0.26		0.25	1.13
202b ?	1.13	0.26	0.58	0.18	1.2
EEB204c1	0.99	0.24	0.6	0.11	0.95
202b2 5	1.05	0.29		0.2	0.85
202a 1	1.13	0.23	0.38	0.16	1.42
EEB217 3	0.89	0.24		0.24	0.57
EEB 206	1.43	0.21	0.73	0.29	1.39
EEB 205b	1.31	0.24	0.51	0.11	0.89
30.5pcG	1.35	0.28	0.28	0.4	1.04
EEB 205a	1.32	0.22		0.1	1.16
RSM 191	1.45	0.29		0.13	1.25
1897 32 375.	1.34	0.25		0.16	0.45
204b2 2r	1.15	0.24	0.1	0.2	0.95
204b2 2	1.12	0.28		0.18	1.08
202b2 6	1.22	0.25	0.35	0.22	1.02
Average gein.	1.21	0.25	0.52	0.19	1.04
			0.73 max.		
Average vom.	1.13	0.26		0.25	0.96
Average gein.	1.21	0.25	0.52 (0.73	0.19	1.04

Md. sp.a	Sicula lnth	Sicula wth	Spine lnth	Lnth sic - th1	lnth th1	Apex sic to?	th.1-th.2	th.2-th.3	2TRD th.5	2TRD th.10	2TRD th.15	2TRD th.20	2TRD th.25	2TRD th.30 +	Wth th.1	Wth th.2	Wth th.5	Wth th.10	Wth th.15	Wth th.20	Wth th.25	Wth th.30	n=?	2TRD thn	2TRD thn+5	2TRD thn+10	2TRD thn+15	TTRD thn+20	TTRD thn+25	TTRD thn+30	TTRD thn+35	Wth thn/n+5	Wth thn+10/15	Wth th. n+20/25/30	Th. prox.	Th. Dist	Known lth	Poss length	Thecae pres.
EEB202a8	0.96	0.26	0.65	0.19	0.96	mid ap. th1	0.75	0.83							0.37	0.44																					3.33		2 1/2
EEB204c1	0.99	0.24	0.6	0.11	0.95	ii	0.64	0.93							0.35	0.51	0.53																		14		4.4		~5
204a1	~1	0.29		0.2	1.02	low th 1 ap	0.57	0.69	1.36						0.39	0.46	0.63																		12		4.38		5 1/2
204 b2	1.4	0.28	0.36	0.36	1.18	mid ap th 1	1.04								0.31	0.4																					3.73		2 1/2
202b9	1.16	0.26	0.36	0.3	0.69	mid ap th 1	0.8								0.35	0.34																					2.55		2..
202b 8	1.22	0.26		0.25	1.13	ii	0.64	0.73							0.34	0.36																					2.82		2 1/2
202b2 6	1.22	0.25	0.35	0.22	1.02	ii	0.67								0.35	0.38																					2.91		2 1/2
204 b1	1.21	0.29		0.33	0.96	ii	0.67	0.56							0.35	0.44	0.64																				3.82		4 1/2
202b ?	1.13	0.26	0.58	0.18	1.2	low th 1 ap	0.77	0.76							0.31	0.33																					4.55		?4
204a2	1.36	0.25	0.1	0.31	1.13	mid Ap th 1	0.6	0.76	1.23						0.34	0.4	0.56																				4.52		5 1/2
202a 1	1.13	0.23	0.38	0.16	1.42	low th 1 ap	0.57	0.76							0.3	0.31	0.76																				3.38		4..
204b2 2r	1.15	0.24	0.1	0.2	0.95	top ap th 1	0.93								0.32	0.46																					2.64		2..
204b2 2	1.12	0.28		0.18	1.08	ii	1.1	0.84	1.83						0.38	0.56	0.6	0.75																	12		8.16		8..
202b2					0.93	mid ap th1	0.91	0.75	1.75						0.34	0.4	0.54																		13		5.64		6 1/2
EEB 205a	1.32	0.22		0.1	1.16	ii	0.84	0.88	1.88	2.16	2.35	2.37			0.32	0.45	0.52	0.64	0.72	0.92															12	10	22.64		21..
EEB 206	1.43	0.21	0.73	0.29	1.39	low ap th1	0.93	0.82	1.75	2.04					0.31	0.43	0.53	0.57																	11	10	14.11		13..
RSM30.5c	1.35	0.29	0.28	0.4	1.04	top ap th 1	0.75	0.78	1.72	1.89					0.31	0.45	0.51	0.69																	13	11	9.82		11..
RSM30.5p	1.35	0.27	0.29	0.4	1.04	ii	0.69	0.81	1.78	1.92					0.33	0.44	0.51	0.71																	13	11	9.64		10..
EEB 210							0.8	0.82	1.22	1.55						0.37	0.53	0.63																	13		6.73	8.2	10..
202 7b									?1.80	?2.29							?0.45	0.55					4	1.79	2.25							0.39 / 0.52				10	6.61	9.46	9?
203a1/203b.																							5	1.93	2.29	2.46						0.68 / 0.71	0.93 /			10	12.89	22.5	16..
215							1.04	0.72	1.79	1.89					?0.23	0.38	0.5	0.59																	12		7.68	8.2	9..
204b2 1																							10	2.11	2.21							0.41 / 0.64				10	6.07	14.29	?14
202b2 2							0.82	0.85	1.56						0.33	0.42	0.53	0.67					1												12		7.45	7.82	9..
202b2 4																							?	1.44	1.47							0.44 / 0.64					3.82	5.5	5+?
202 a7							0.9	0.82	2.14						0.31	0.37	0.45																		11		8.43	9.22	7..
202b2 3																							3	1.24	1.78							0.49 / 0.56			13		5.27	7.09	8..
202b2 5	?1.05	0.29		0.2	0.85		0.64	0.93	1.74						0.32	0.38	0.52																		11		5.09	6.18	5..
202a 4							0.79	0.84	1.61						0.32	0.41	0.47																		12		5.63	6.43	6..
204b 3	1.24	0.33			1.02		0.69	0.72	1.42						0.27	0.38	0.51																				4.29	5.09	5..
202 a6																							3	2.12	1.96							0.46 / 0.58			11		5.6	8	7..

Md. sp. b	Sicula lnth	Sicula wth	Spine lnth	Lnth sic - th1	lnth th1	Apex sic to?	th.1-th.2	th.2-th.3	TTRD th.5	TTRD th.10	TTRD th.15	TTRD th.20	TTRD th.25	TTRD th.30	Wth th.1	Wth th.2	Wth th.5	Wthth.10	Wthth.15	Wthth.20	Wthth25	Wth th.30	n=?	TDthn	TDthn+5	TDthn+10	TDthn+15	TDthn+20	TDthn+25	TDthn+30	2TRD thn+35	Wth thn/n+5	Wth thn+10/15	Wth th. n+20/25/30	Th. prox.	Th. Dist	Known lth	Poss length	Th pres.
EEB217 3	0.89	0.24		0.24	0.57	Mid th1-th2	0.59	0.57	1.33	1.56					0.19	0.28	0.34	0.48																	16	12	8.89		11..
EEB217 2	0.89	0.23		0.27	0.47	ii	0.38	0.8	1.23	1.55					0.14	0.25	0.37	0.49																	16		7.02		10..
EEB 219a	1.22	0.23		0.4	0.79	above ap th1	0.63	0.61	1.4	1.54	1.72	1.79			0.26	0.42	0.52	0.63	0.75	0.89															15	12	15.72		20..
EEB 79a	1.33	0.31	?0.22	0.37	1.03	top ap. th 1	1.17	1.22	2.37	2.4	2.48	2.54	2.58	2.56/2.35/2.41.	0.42	0.55	1.04	1.15	1.19	1.46	1.63	1.79/1.86/1.93.													10	9	48.15		42..
EEB 79b	1.11	0.29		?0.11	1.11	ii	1.14	1.25	2.36	2.57	2.25	2.18	2.07	2.16/2.08/2.29	0.36	0.51	0.77	1.02	1.01	1.45	1.54	1.82/1.88/1.95													9.5	8	47.82		42..
1897 32 37	1.34	0.25		0.16	0.45	mid th1-th2	0.83	0.71	1.82	1.9	1.84	2.07	2.19	.2.36	0.16	0.47	0.57	0.65	0.71	1.04	1.03	.1.14													13	8	28.36		29..
GI 20226	0.86	0.29		0.15	0.61	above ap th1	0.68	0.64	1.61	1.64	1.73	1.75	1.82	1.93/1.96/2.1/2.07/2/2.04/2.05	0.3	0.46	0.58	0.75	0.78	0.89	0.96	1.02/1.11/1.21/1.25 1.28/1.32/1.29.													14	10	54.71		60..
EEB 205b	1.31	0.24	0.51	0.11	0.89	mid th1-th2	0.42	0.47	1.29	1.35	1.62				0.19	0.25	0.41	0.49	0.55																16	12	13.45		17..
RSM 191	1.45	0.29		0.13	1.25	above th1	0.62	0.79	1.6	1.85	1.91	1.87			0.27	0.55	0.58	0.64	0.76	0.87															13	11	17.53		19..
1985.26.76.0.																							25	1.93	2.04	2.13						0.96 / 0.98	1.01 / 1.04			10	15.18	28	25?-39
EEB 208																							5	1.33	1.67	1.83	1.98					0.63 / 0.78	0.89 / 0.93		12		16.67	19	4?-22
EEB 203a 1																							30	1.94	2.05	2.11						1.13 / 1.46	1.39 / 1.50			10	15.79	44	30?-44
EEB 203b																							30	1.95	2.07	2.19						1.21 / 1.39	1.52 / 1.61			10	11.61	39	30?-40
EEB 87a																							5	1.82	1.97	2.02	2.05	2.08				0.5 / 0.73	0.89 / 0.93	.1.18	12	10	20.36	25	5?-25
GI 47567																							35	1.91	1.88	2.07	2.01	2.06	2.07	2.08	.2.11	1.52 / 1.78	1.81 / 1.79	1.85/1.87/1.89/1.93		10	38.63	68	35?-72
GI 22224																							15	1.92	1.95	2.01	1.78	1.93	2.06	2.09		0.98 / 1.11	1.01 / 1.04	1.06/1.07/1.09	11	10	34.37	46	12?-46
GI 20240																							10	1.56	1.62	1.71	1.76	1.78	1.83	1.93		0.67 / 0.81	0.96 / 1.15	1.16/1.18/1.17	13	11	32.89	40	8?-42
EEB 224(550LOG).																							10	1.43	1.98	2.03	2.07	2.11				0.97 / 0.98	0.99 / 1.03	.1.06	11	10	25.07	31	6?-31
GI 22218																							10	1.53	1.67	1.71	2.28	1.78	1.87	1.89	1.91/1.93/1	0.6 / 0.62	0.73 / 0.98	1.04 1.16 1.24 1.29 1.31 1.35	13	11	51.93	65	10?-66
EEB 218																							15	1.83	1.88	1.95	1.99	2.01				0.77 / 0.89	0.91 / 0.96	.1.07	12	10	21.62	24	13?-35
GI 47569																							10	1.75	1.96	2.02	2.04	1.98	2.05	2.14		0.81 / 0.87	0.88 / 1.05	1.11/1.16/1.22	11	10	33.2	40	10?-42
EEB 217 1																							10	1.49	1.55							0.42 / 0.57			13		4.3	8	10?-15
EEB 209																							40	1.69	1.73							0.91 / 0.95				10	6.04	46	40?-46
BU 1555	1.5	0.25	0.42	0.25	0.91	ap. th2	0.51	8.1	1.64	1.99	2.21				0.26	0.36	0.47	0.64	0.87																11		15.31		16..

Mcl. geinitzi														
x-DVW,y-2TRD	th1	th5	th10	th15	th20	th25	th30	th35	th40	th45	th50	th55	th60	th65
EEB202a8	0.4													
	1.58													
202b ?	0.32													
	1.53													
202b 8	0.35													
	1.37													
EEB204c1	0.43	0.53												
	1.57	1.72												
202b25	0.35	0.52												
	1.57	1.74												
202a7	0.34	0.45												
	1.72	2.14												
202a4	0.36	0.47												
	1.63	1.61												
202b 2	0.37	0.54												
	1.61	1.75												
202a1	0.3	0.76												
	1.33	1.75												
202b2 2 G	0.37	0.53	0.67											
	1.67	1.56	1.95											
206..G	0.37	0.53	0.57											
	1.75	1.75	2.04											
30.5pcG	0.38	0.51	0.7											
	1.52	1.75	1.91											
202 7bG	0.31	0.45	0.55											
	1.8	1.8	2.29											
215..G	0.32	0.51	0.59											
	1.76	1.79	1.89											
204b2 2G	0.47	0.6	0.75											
	1.94	1.83	2.12											
210..	0.37	0.53	0.63											
	1.62	1.22	1.55											
EEB217 3	0.23	0.34	0.48											
	1.16	1.33	1.56											
EEB 205b	0.22	0.41	0.49	0.55										
	0.89	1.29	1.35	1.62										
205aG	0.39	0.52	0.64	0.72	0.92									
	1.72	1.88	2.16	2.35	2.37									
RSM 191	0.41	0.58	0.64	0.76	0.87									
	1.41	1.6	1.85	1.91	1.97									
1897 32 375.	0.31	0.57	0.65	0.71	0.94	0.93	1.04							
	1.54	1.82	1.9	1.84	2.07	2.19	2.36							
203a 1G		0.68	0.71	0.93										
		1.93	2.29	2.46										
2027bG		0.39	0.52											
		1.79	2.25											
204b21G				0.41	0.64									
				2.11	2.21									
202b23G		0.49	0.56											
		1.24	1.78											
202a6G			0.46	0.58				BU 1555		0.31	0.47	0.64	0.87	
			2.12	1.96						1.32	1.64	1.99	2.21	

Mcl. vomerinus														
x-DVW,y-2TRD	th1	th5	th10	th15	th20	th25	th30	th35	th40	th45	th50	th55	th60	
202b 8	0.35													
	1.37													
202a1	0.3	0.76												
	1.33	1.5												
204b 3	0.31	0.51												
	1.41	1.42												
204a2	0.37	0.56												
	1.36	1.23												
204 b1	0.39	0.64												
	1.23	1.38												
204a1	0.42	0.63												
	1.26	1.36												
EEB217 2	0.19	0.37	0.49											
	1.28	1.23	1.55											
EEB 219a	0.34	0.52	0.63	0.75	0.89									
	1.24	1.4	1.54	1.72	1.79									
GI 20226	0.38	0.58	0.75	0.78	0.89	0.96	1.02	1.11	1.21	1.25	1.28	1.32	1.29	
	1.32	1.61	1.64	1.73	1.75	1.82	1.93	1.96	2.1	2.07	2	2.04	2.05	
202b24V		0.44	0.64											
		1.44	1.47											
1985.26.76.0.						0.96	0.98	1.01	1.04					
						1.93	2.04	2.13	2.12					
EEB 208		0.63	0.78	0.89	0.93									
		1.33	1.67	1.83	1.98									
EEB 203a 1								1.13	1.46	1.39	1.5			
								1.94	2.05	2.11	2.1			
EEB 203b									1.21	1.39	1.52	1.61		
									1.95	2.07	2.19	2.09		
GI 47567						1.52	1.78	1.81	1.79	1.85	1.87	1.89	1.93	
						1.91	1.88	2.07	2.01	2.06	2.07	2	2.11	
GI 22224						0.98	1.11	1.01	1.04	1.06	1.07	1.09		
						1.92	1.95	2.01	1.78	1.93	2.06	2		
GI 20240		0.67	0.81	0.96	1.15	1.16	1.18	1.17						
		1.56	1.62	1.71	1.76	1.78	1.83	1.9						
EEB 224(550LOG).			0.97	0.98	0.99	1.03	1.06							
			1.43	1.98	2.03	2.07	2.11							
GI 22218		0.6	0.62	0.73	0.98	1.04	1.16	1.24	1.29	1.31	1.35	1.38	1.39	
		1.53	1.67	1.71	2.28	1.78	1.87	1.8	1.91	1.93	1.94	1.96	1.95	
EEB 218				0.77	0.89	0.91	0.96	1.07						
				1.83	1.88	1.95	1.99	2.01						
GI 47569				0.81	0.87	0.88	1.05	1.11	1.16	1.22				
				1.75	1.96	2.02	2.04	1.98	2.05	2.1				
EEB 217 1		0.42	0.57											
		1.49	1.55											
EEB 209				0.91	0.95									
				1.69	1.73									
EEB 87a			0.5	0.73	0.89	0.93	1.18							
			1.82	1.97	2.02	2.05	2.08							
GI 47567							1.52	1.78	1.81	1.79	1.85	1.87	1.89	1.93
							1.91	1.88	2.07	2.01	2.06	2.07	2.02	2.11

Oktavites												
specimen number	EEBG4ab	EEB201ab	28 . 1.1	28.1.2	28.1.3	28.3.1	28.3.2	28.6.1.a	28.6.1.b	28.6.2.a	28.6.2.b	average
width inc. ap. proc., prox	0.79			0.92	0.74		0.5	0.5	0.74		0.7	0.7
width inc. ap. proc., mid	1.4	1.12	0.86	1.28	1.48	0.72	0.8	1.4		1.3	1.3	1.17
width inc. ap. proc., dist		1.68	1.63		1.65	1.98	1.75	1.5		1.6		1.68
width excl. ap. proc., prox	0.31			0.29	0.62		0.3	0.4	0.39		0.3	0.37
width excl. ap. proc., med	0.38	0.42	0.37	0.46	0.79	0.42	0.5	0.5		0.6	0.6	0.5
width excl. ap. proc., dist		0.98	0.65		0.91	0.91	1.13	1.04		0.75		0.91
sicula length				0.96	0.8			1.1	0.8			0.92
sicula width				0.38	0.2			0.2	0.2			0.24
sicula to?				top ap. th1				start th2	start th 2			start th2
number of whorls	1.5	2-3	1.5	1	2.5	2	2	2.5	1	1.5	1.5	upto3
diameter first whirl	5.5	4.6	4.9	5.25	4.96	6.4	4.2	6.3	4.5		4.9	5.15
diameter second whirl		13	8.98		7.12	13	8.75	11.7			8.3	10.12
diameter third whirl					13.3			13.9		12.5		13.2
2TRD proximal	1.3			1.13	1.36	1.61	1.3	1.56	1.65		1.4	1.41
2TRD middle	1.5	1.33	1.35	1.43	1.82	1.74	1.9	2.09		1.8	1.8	1.68
2TRD distal		1.82	2.04		1.94	2.37	2.1	2.2		2.1		2.08
Thecae in 10mm proximal	13	15	13	14	15	14	15	13	13	13	13	13.73
Thecae in 10mm distal		12	11		11	10	12	10		11	10	10.88

Figure 10.1:

A,C,E Crinoid *Macrostylocrinus silurocirrifer* Brower 1975, note cirri on columns; B, D, F, Echinoid *Aptilechinus caledonensis* Keir 1973.

A , EEB 24 X1.9, B, EEB 22a X2.2; C X 2; D, EEB 23a X 2.1 (lower part of specimen subsequently removed by Dr. N Clark); E, EEB 27 X2.3; FEEB 20b ?adoral view. X2.25

Figure 10.1

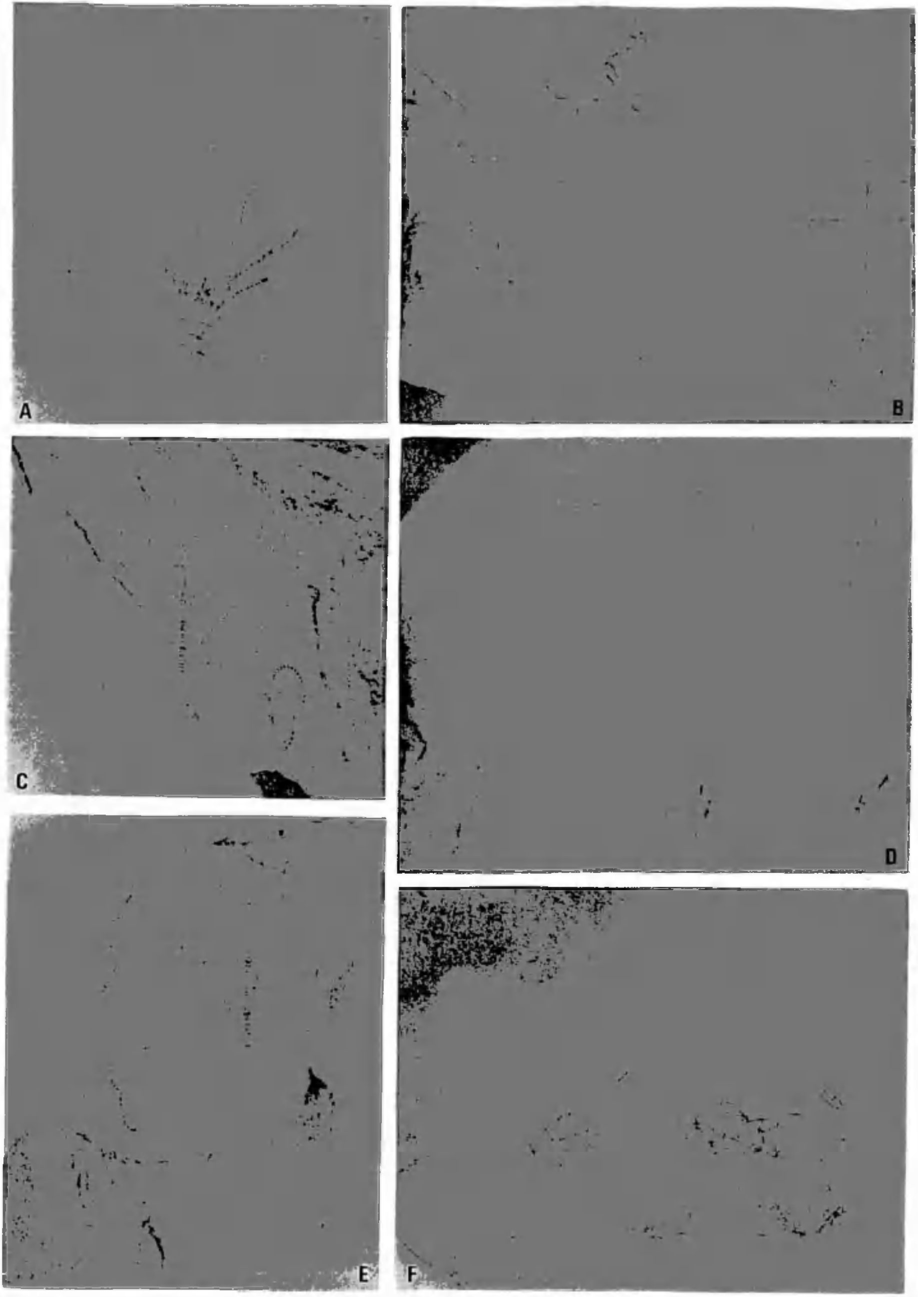


Figure 10.2:

Crinoid *Macrostylocrinus silurocirrifer* Brower 1975

A, Arms of crinoid, EEB 29 X5; B, D EEB 30 a B is latex mould of D, note nodules on calyx confirming identification. B X6.5, D X7, C EEB 30 a X6

Figure 10.

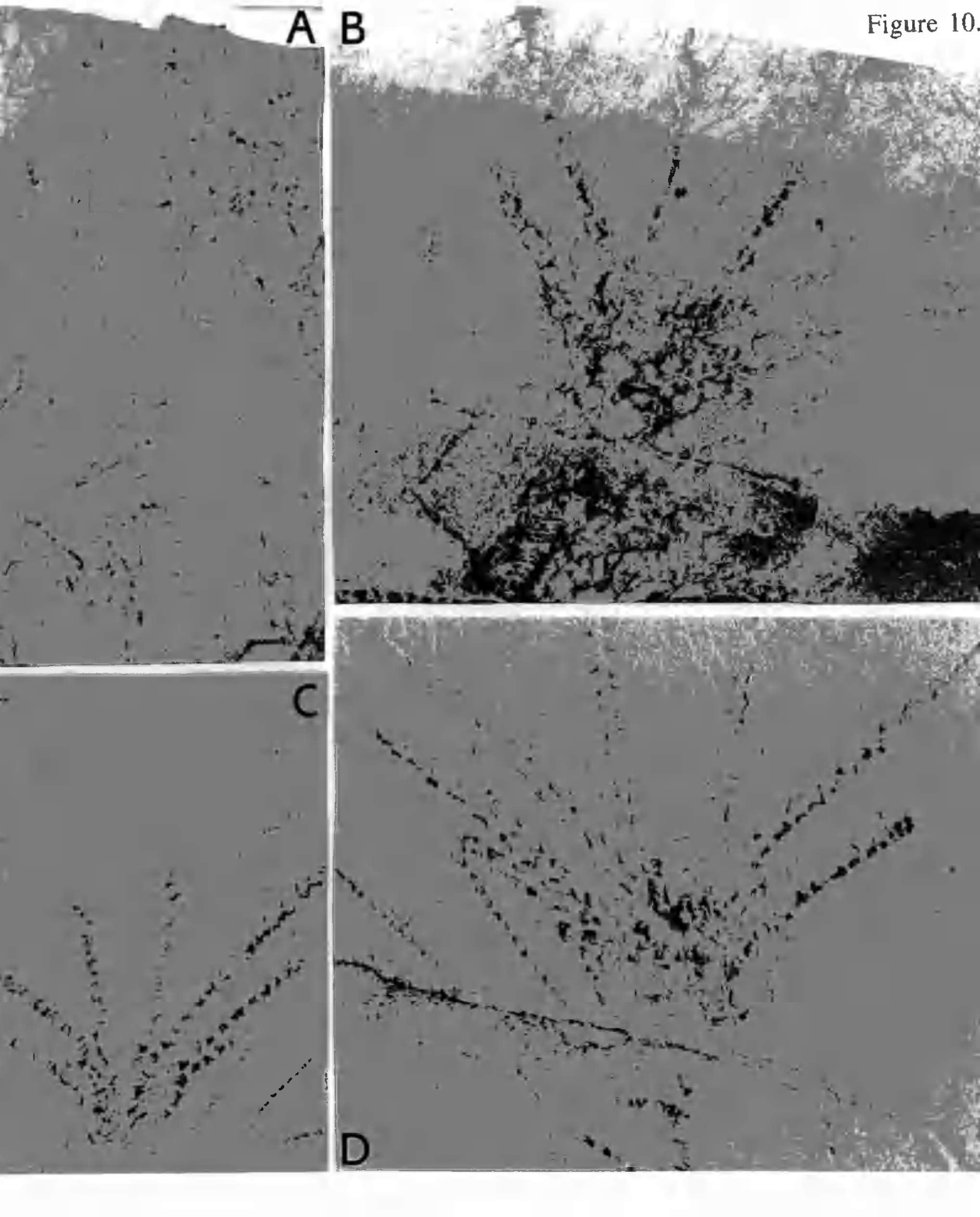


Figure 10.3:

Starfish and Crinoid.

A. EEB 61 X 1.5 *Crepidosome* sp A, B *Macrostylocrinus silurocirrifer* Brower 1975 X4; C, *Crepidosome* sp B. EEB 64 X 5.

Figure 10.3

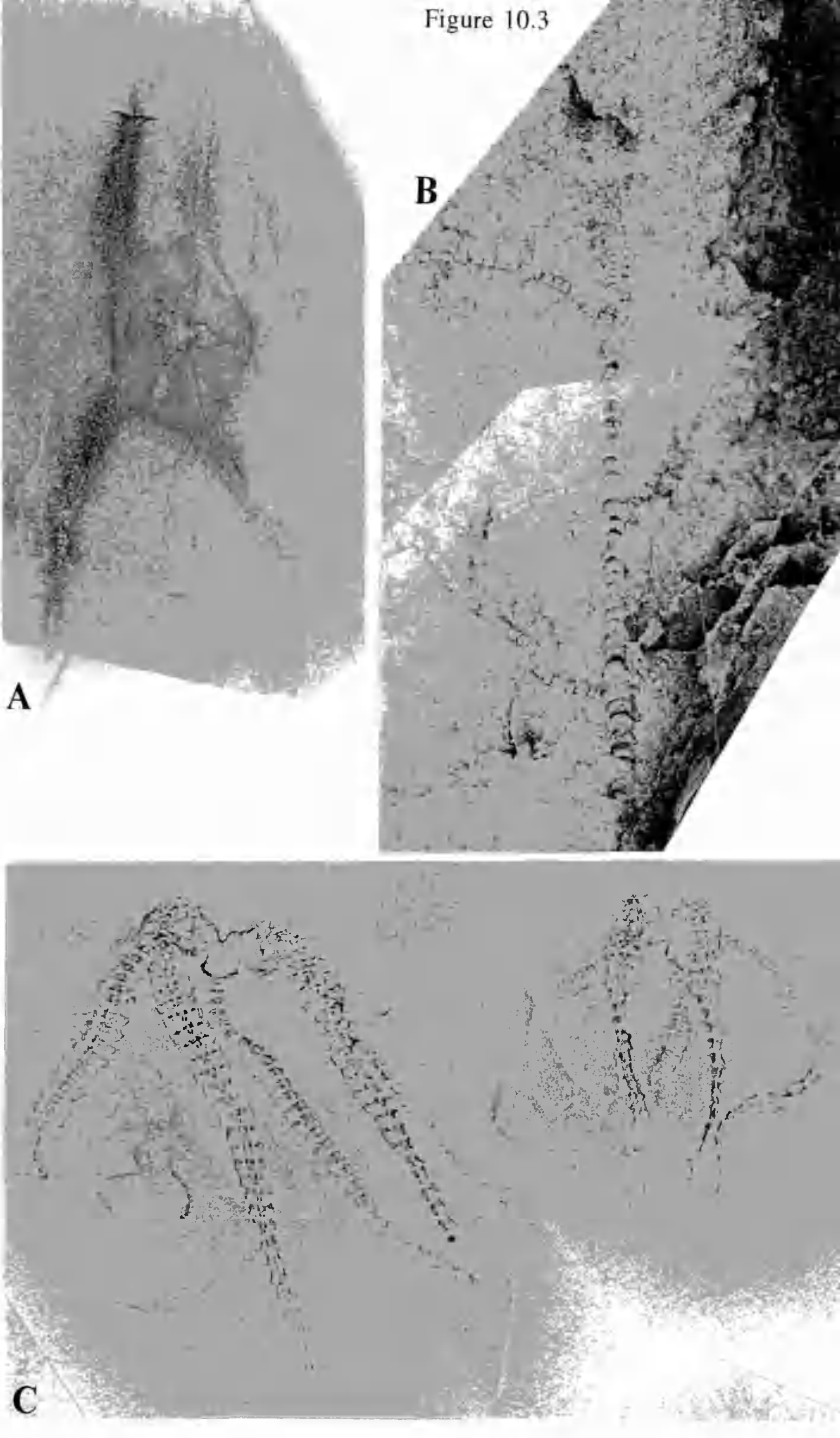


Figure 10.4:

Starfish

Crepidosome sp B; A, EEB 73a X5; B, EEB 66 X 5.8;
C, EEB 74 X 5.2; D EEB56 X 6.6; E EEB 65 X 6.7.

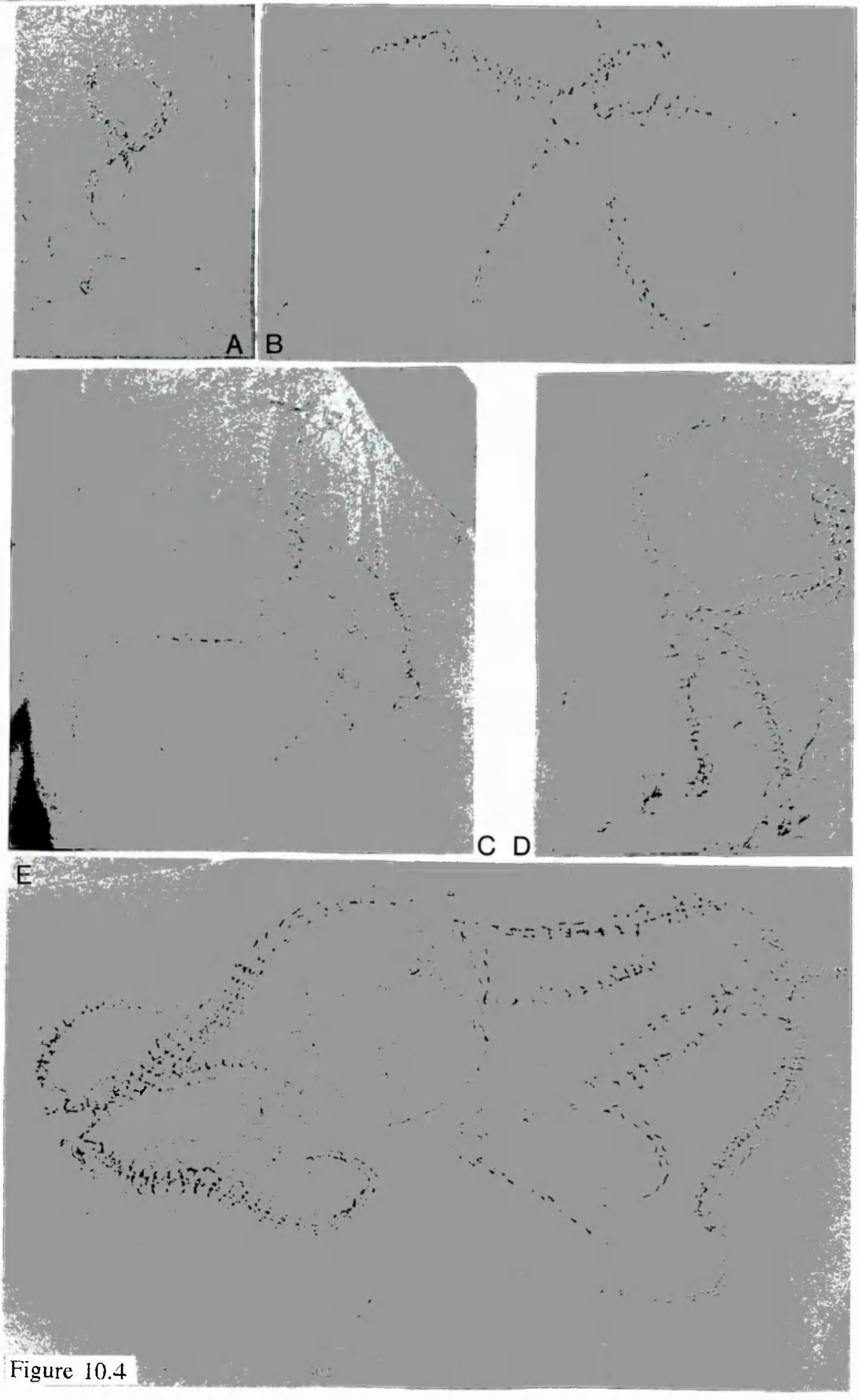


Figure 10.4

Figure 10.5:

Starfish. All from GBLB locality, *O. spiralis* biozone age.

B, D, and E *Crepidosome* sp A; A, C, *Crepidosome* sp B.

A, EEB 55a X5; BEEB 45a X3; C EEB 68 X5;

D, EEB 43b X 3.1; E, EEB 43a X3.2

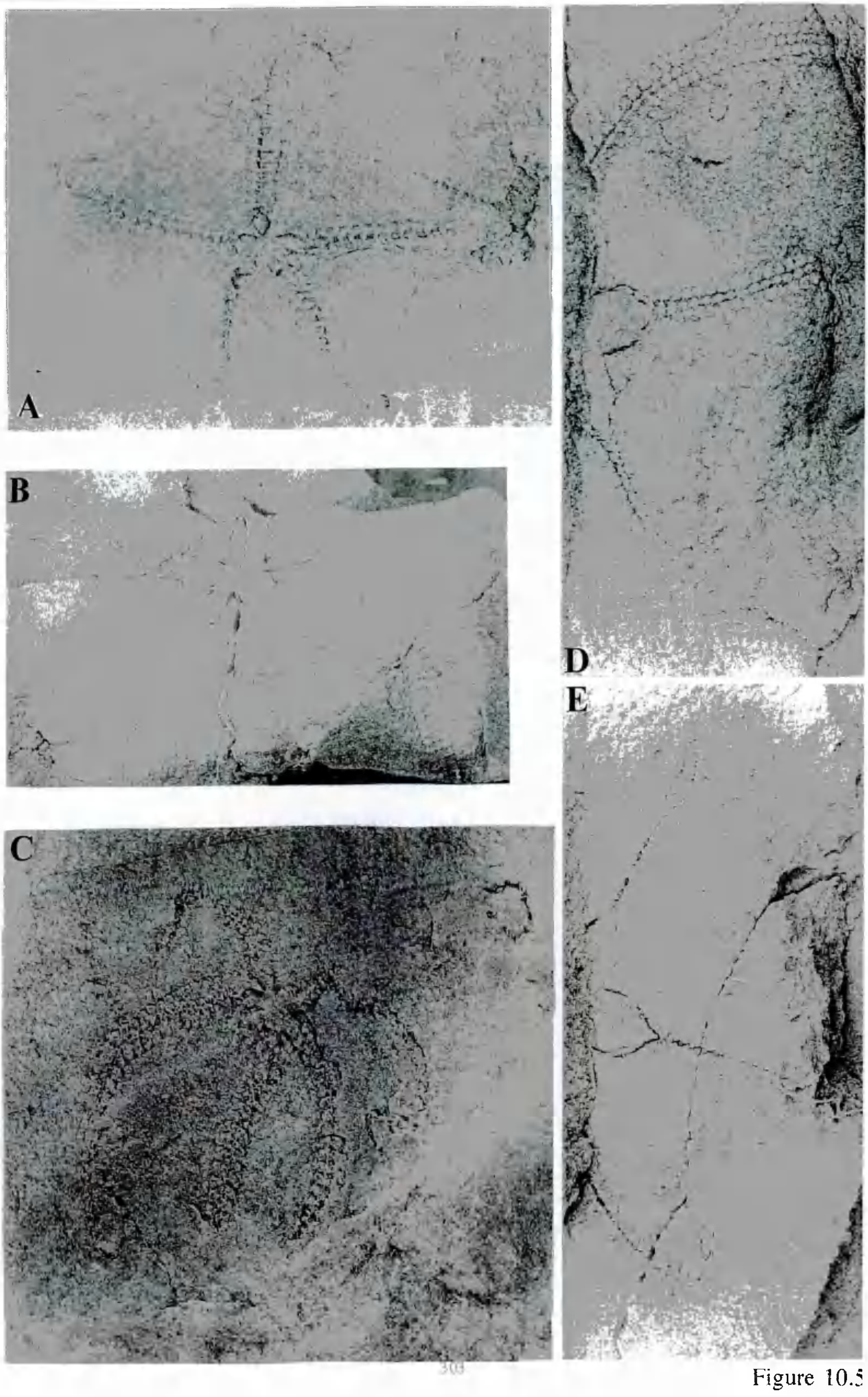


Figure 10.5

Figure 10.6:

Starfish. All from GBLB locality, *O. spiralis* biozone age.

A-C, *Crepidosome* sp B; D-G *Crepidosome* sp A.

A, EEB 67 X 5.3; B, EEB 71b X6; C, EEB 71a X5; D, EEB 47a X 5.6;

E, EEB 47b X 5.6; F, EEB 44a X 3.3; G , EEB 44b X 3.3

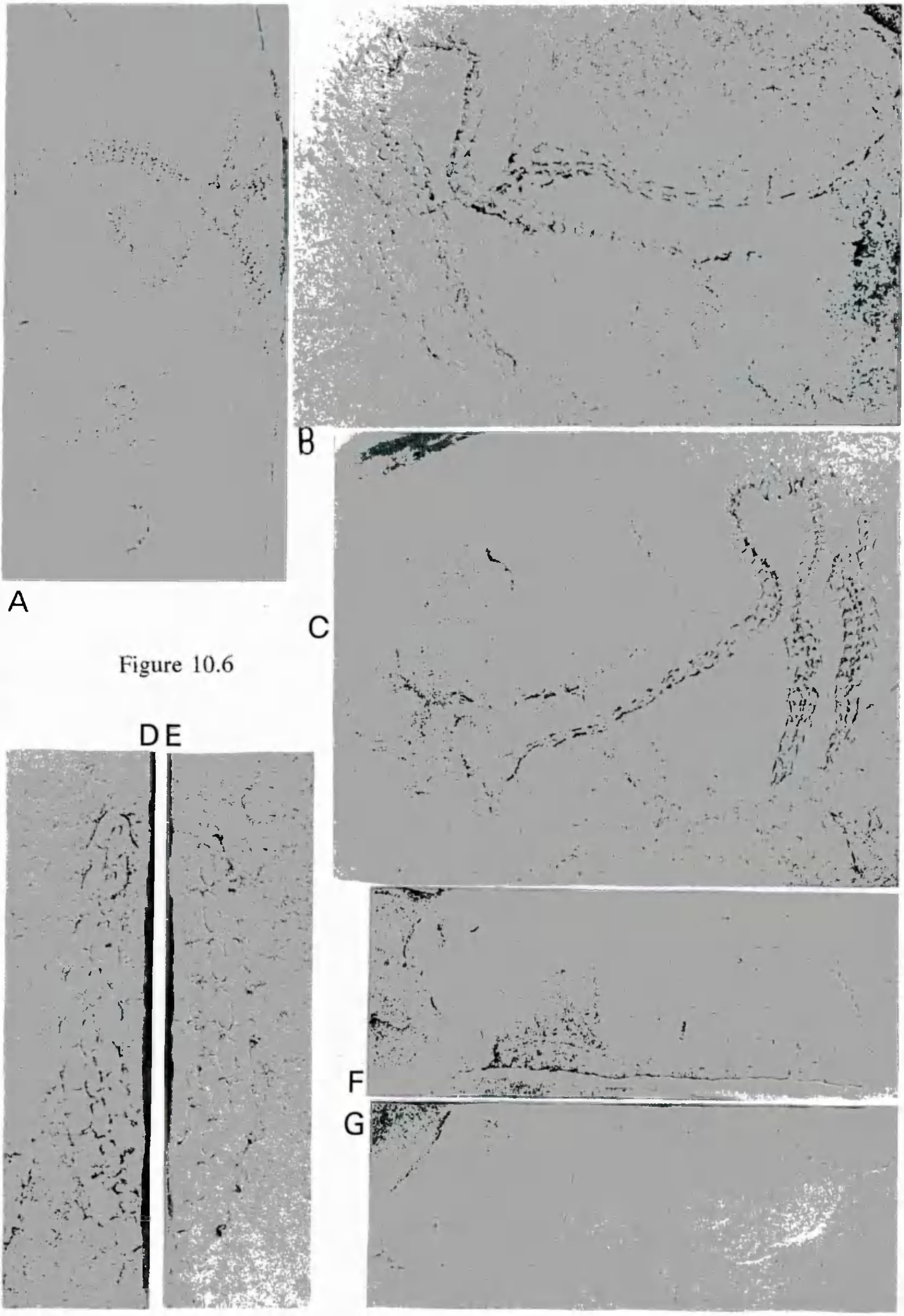


Figure 10.6

Figure 10.7:

Starfish. All from GBLB locality *O. spiralis* biozone age.
A-E, *Crepidosome* sp B. A, EEB 69 b, X 6; B, EEB 60 X 6.3;
C, EEB 69a X 5; D , EEB 57a X 7; E, EEB 73a X 5.2

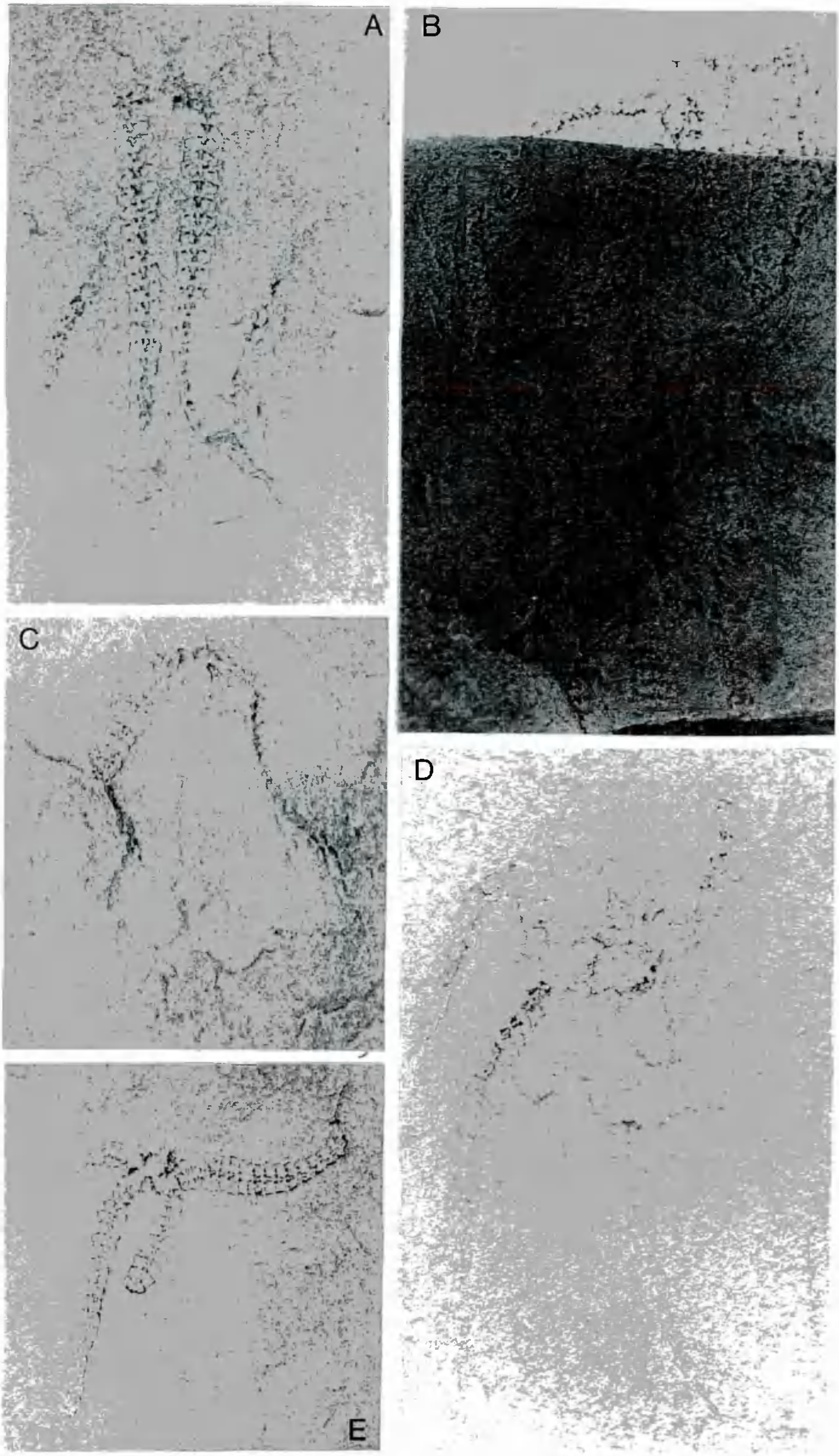


Figure 10.7

Figure 10.8:

Thin sections, all except C, X 10.

All sections taken from specimens from logged section of GBLB locality

A. pressure solution between two grains.

B.Geopetal infill of grain, redeposited

C. Punctured Brachiopod shell. X15

D. Sedimentary laminations and dewatering structures.

E. Bioturbation, loading and dewatering structures.

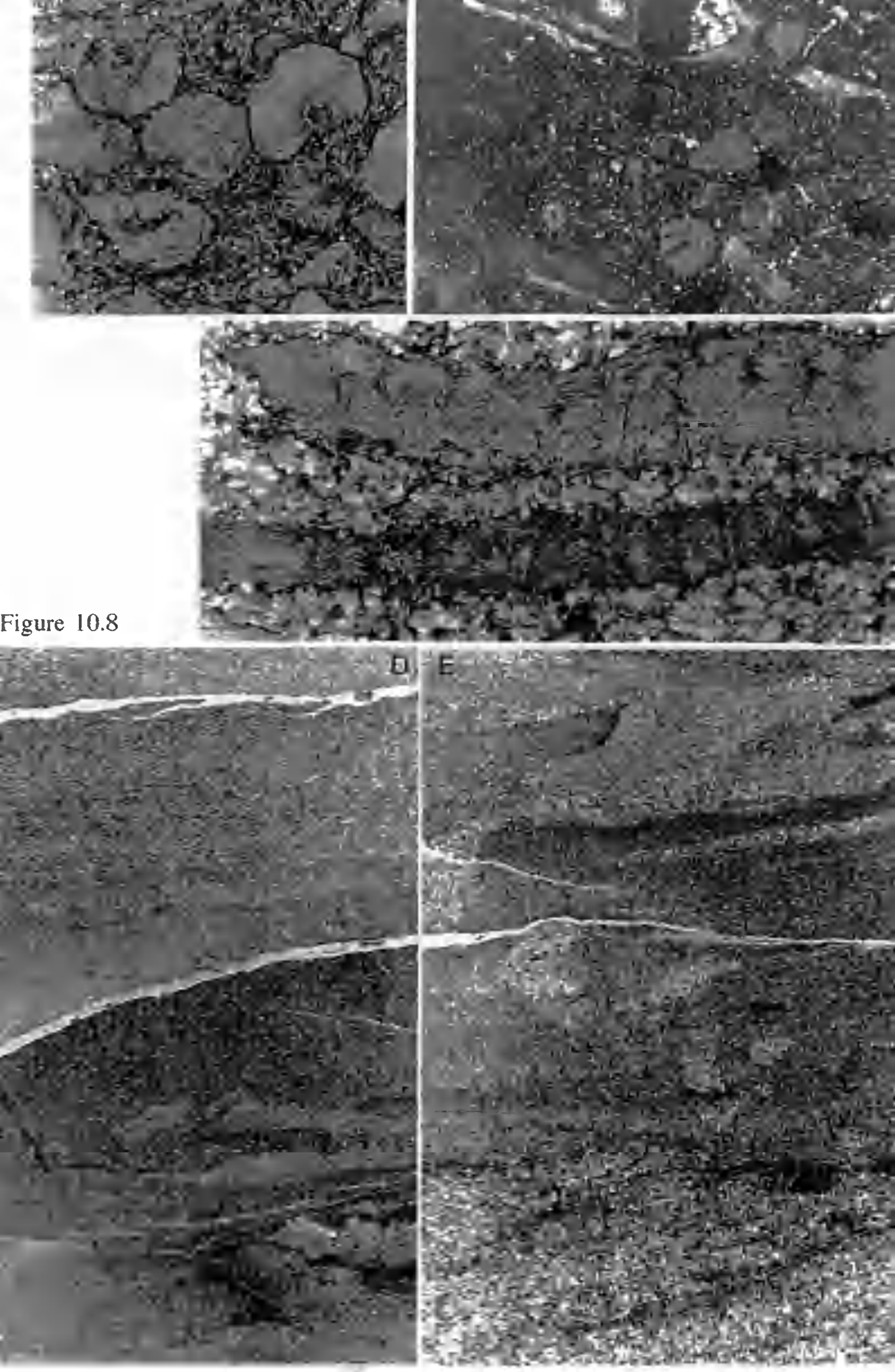


Figure 10.8

Figure 10.9:

Thin section Corals.

All sections taken from specimens from logged section of GBLB locality

A *Heliolites* sp. X12

B *Palaeocyclus* X10

Figure 10.9

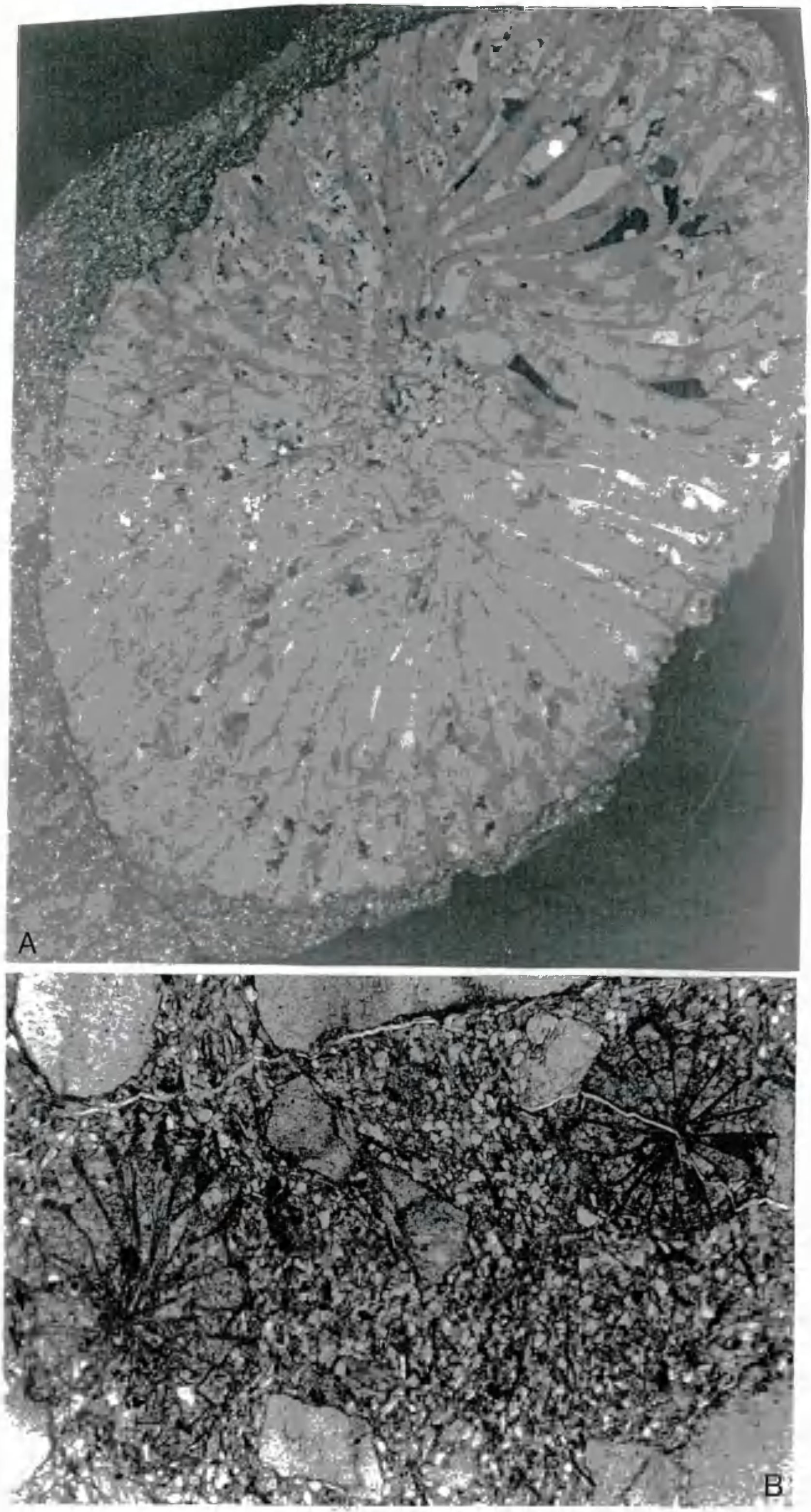


Figure 10.10:

Thin section Coral and Bryozoans.

All sections taken from specimens from logged section of GBLB locality

A. B Heliolitid coral, longditudinal sections, X 10

C, Longditudinal section of Ptilodictine bryozoan X 12.

D. *Phaulacus* sp. X20,

E, possible *Renalcis* (alga) and bryozoan cross section.

Figure 10.10

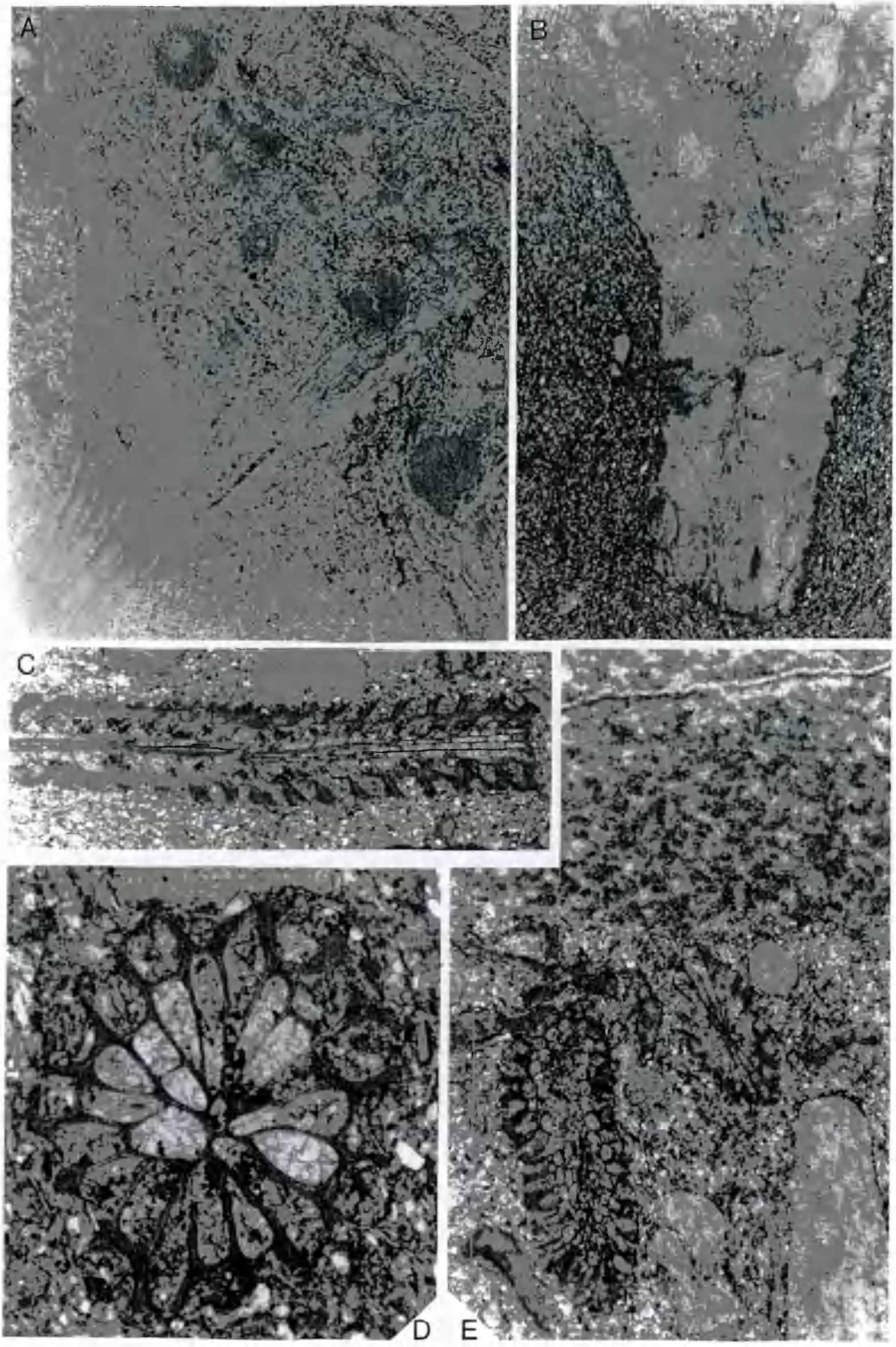


Figure 10.11:

Thin section

Coral, Crinoid and Trilobite cross section

A,Crinoid and brachiopod shell, X15

B, crinoid ossicle, X 50

C, Longditudinal section through a trilobite, *Acernaspis (Eskapsis) sufferta* Lamont X10

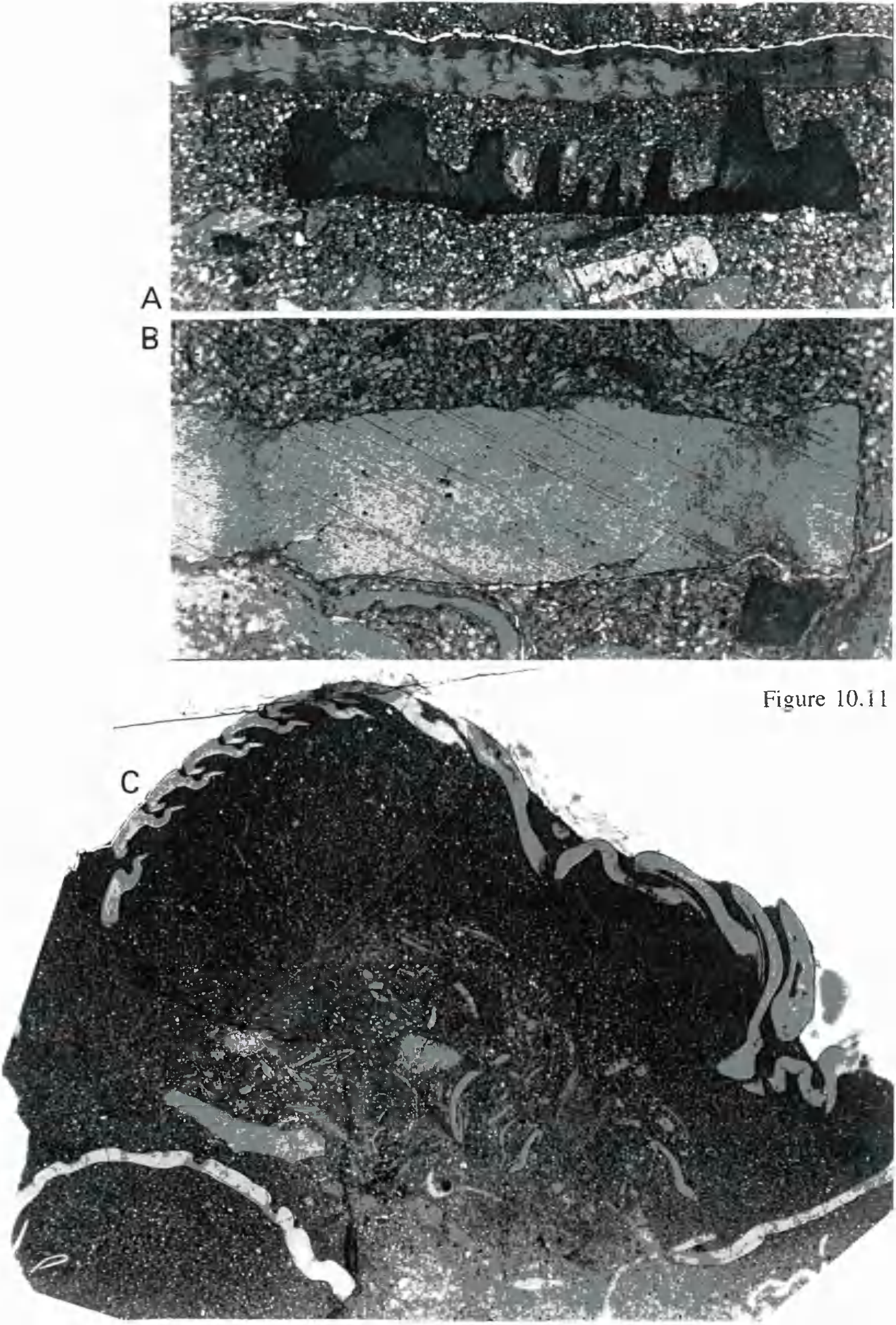
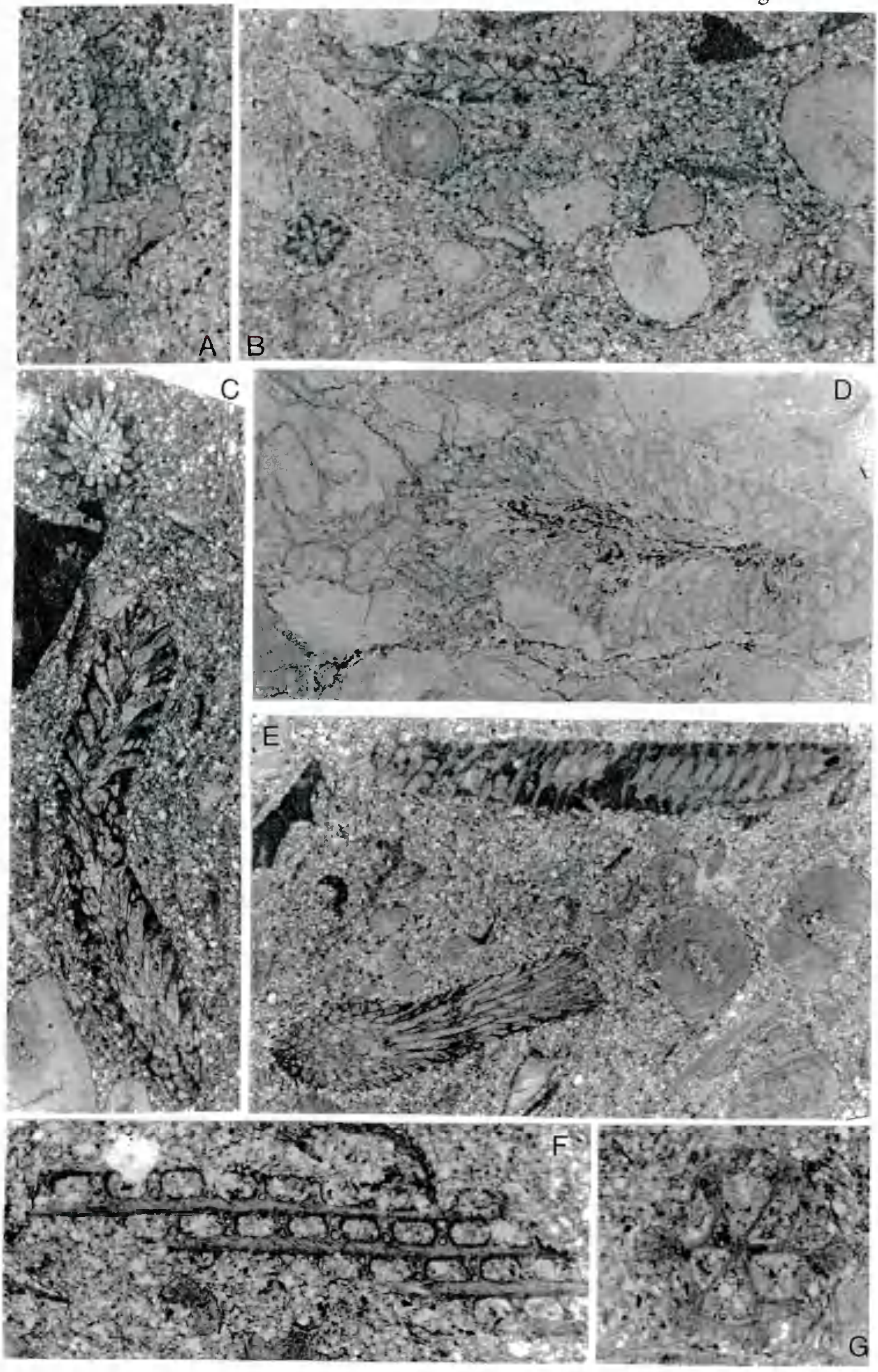


Figure 10.11

Figure 10.12:

All from GBLB locality, *O. spiralis* biozone age.

Bryozoans all X 10 except F X 20.


A
B
C
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E
F
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Figure 10.13:

Thin section. All sections taken from specimens from logged section of GBLB locality Bryozoans X 20, and E, *Dicoelosia* longditudinal section X 10.

Figure 10.13

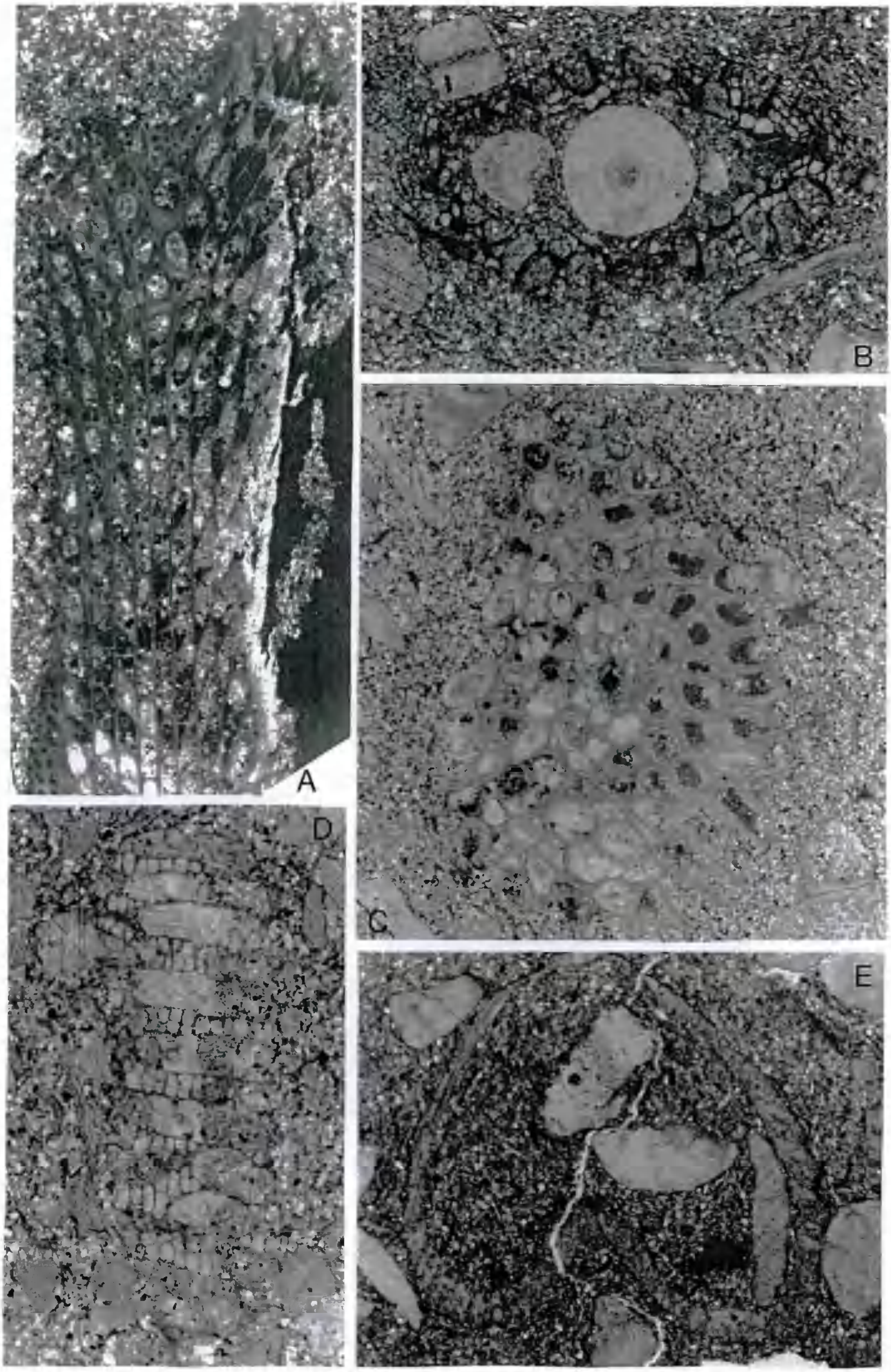


Figure 10.14

All from specimens from GBLB locality

Coral, *Angopora hissingeri*.

A, B, X7; C, X10; D, X20.

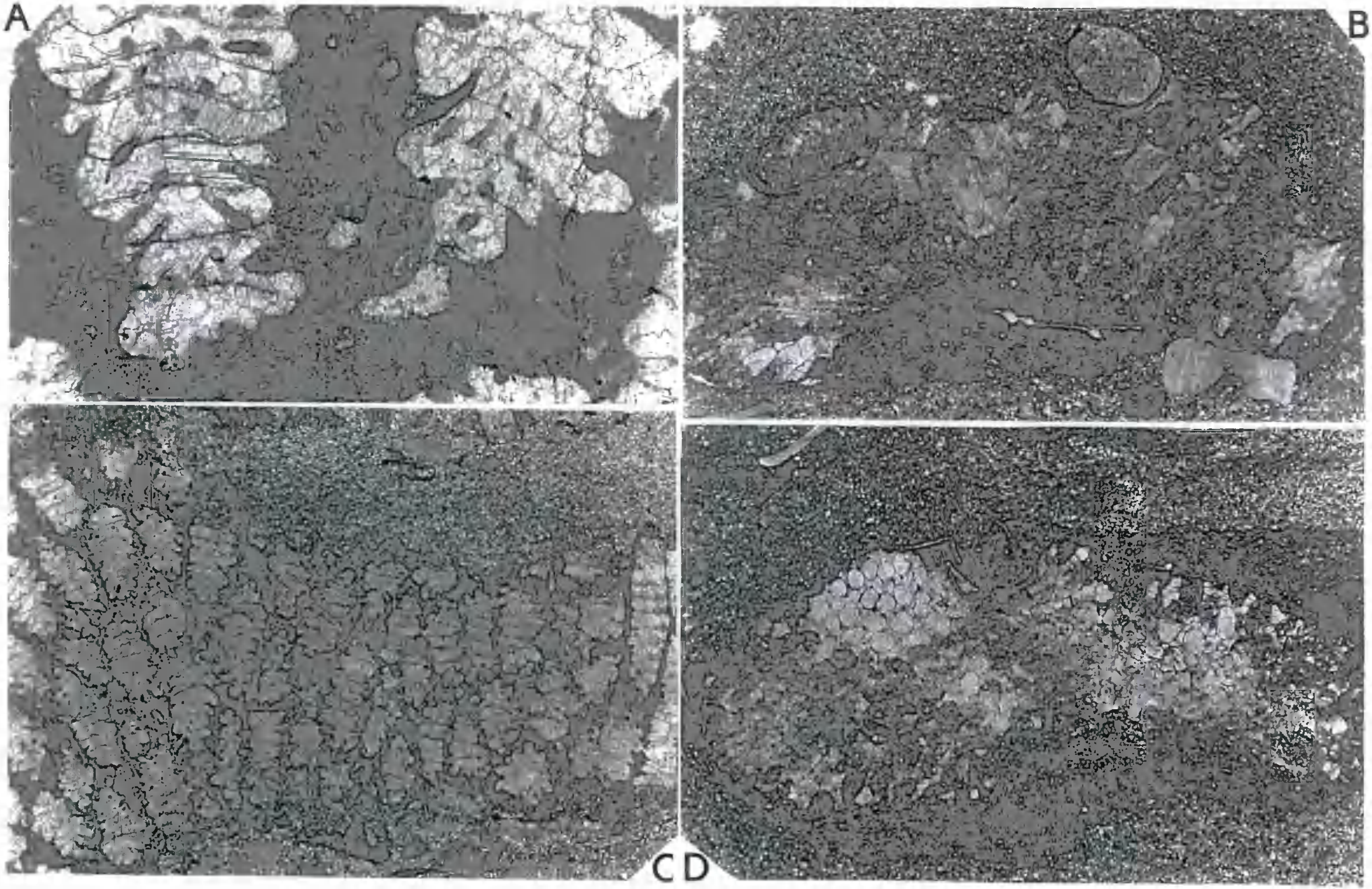


Figure 10.14

Figure 10.15

All from specimens from GBLB locality

Trilobites

A, eye of *Encrinurus sp.* X6

B, Articualted cephalon and thoracic segments of *Acernaspis (Eskaspis) sufferta* Lamont X5

C, Pygidium of *Acernaspis (Eskaspis) sufferta* Lamont X 8

D, Cephalon of *Acernaspis (Eskaspis) sufferta* Lamont, X9

E, *Encrinurus expansus* X7

F, gastropod ?*Gyronema* and *Acernaspis (Eskaspis) sufferta* cephalon X8, preserved inside a nodule.

Figure 10.15

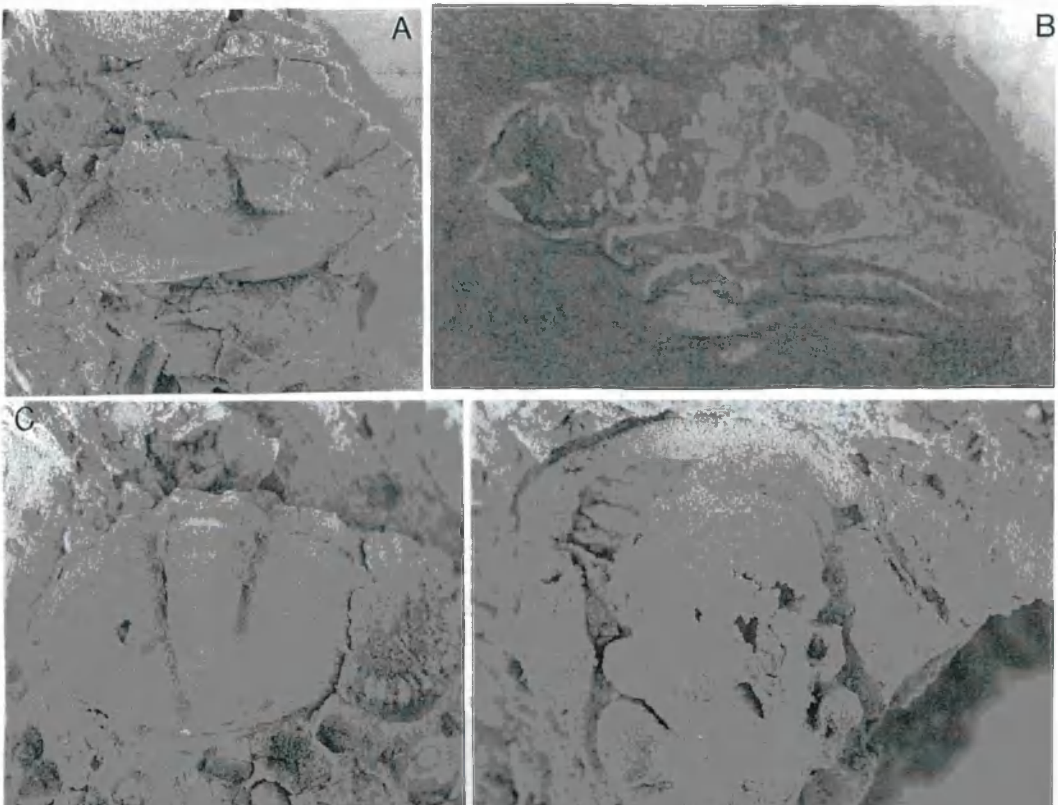


Figure 10.16

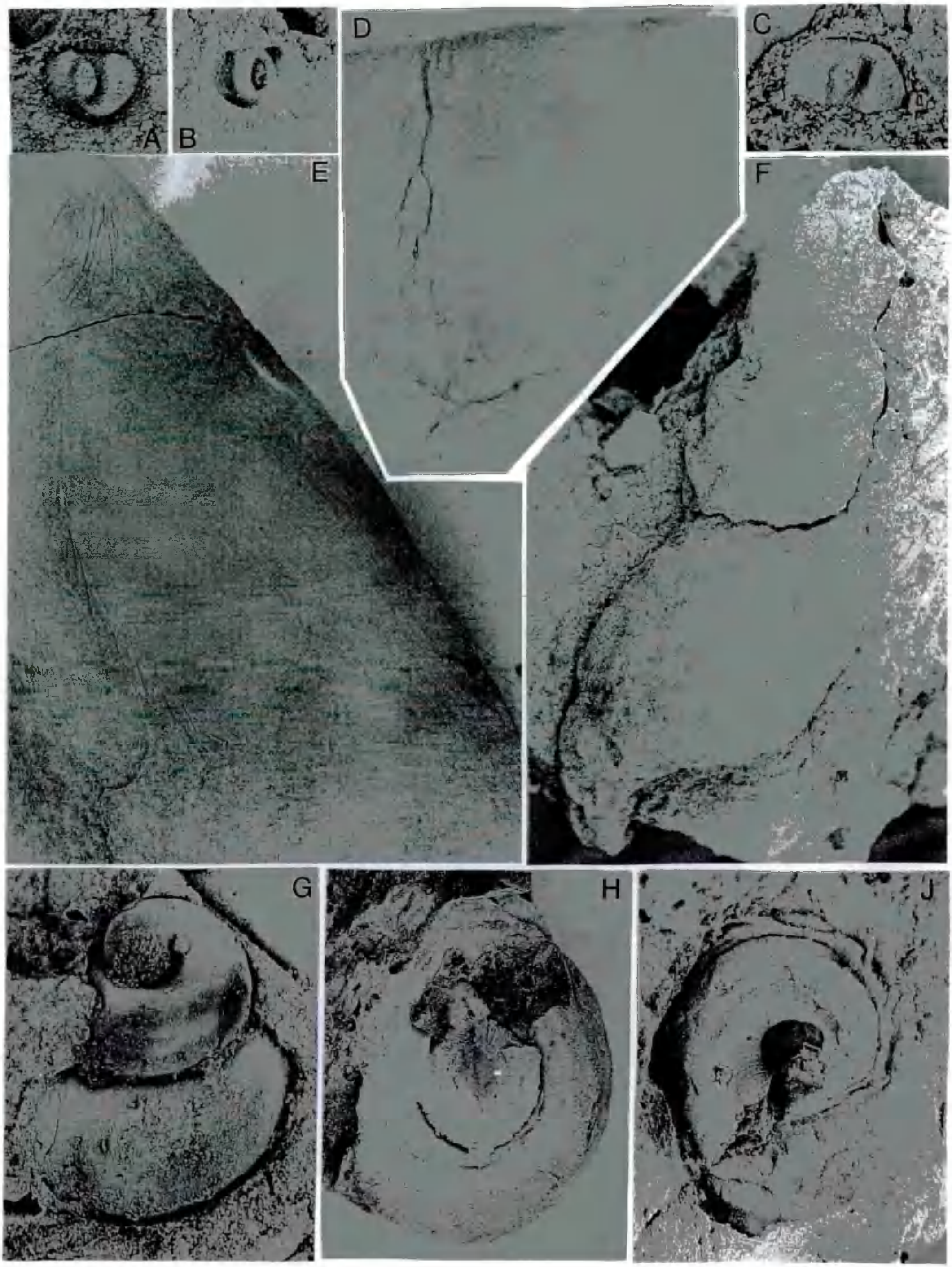
All from specimens from GBLB locality

Ostracod, gastropods and ?hairy worm.

A-C *Craspedobolbina (Mitrobeyrichia) impendends* (Haswell) X10;

D-E, possible hairy worm or other soft bodied animal. X 2.

F-J Gastropods. FX4; GX4; HX2 and JX3.


A
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J

Figure 10.17

All from specimens from GBLB locality

Corals

A X5, B, X7, part calcified *Palaeocyclus porpita*

C, ? *Planoceonites* sp. within an orthocone X 6; D-E & G, *Favosites* sp., D, X7, E, X1, G X6. H-J, *Palaeocyclus* X 4.

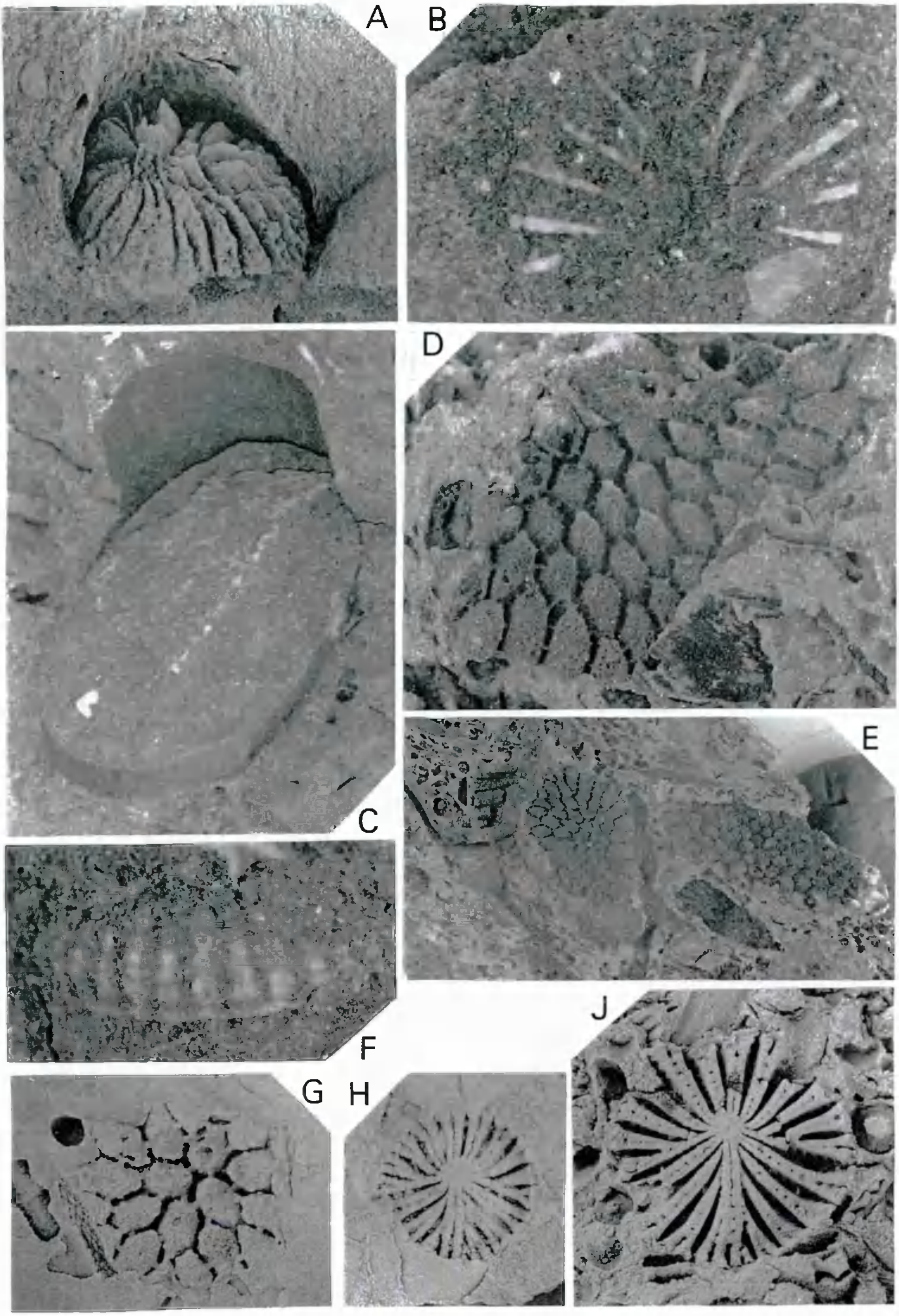

Figure 10.17

Figure 10.18

All from specimens from GBLB locality

Coral and Brachiopod

A-B Solitary coral (Heliolites?) X3.

C-F Atrypid brachiopods, X7.

Figure 10.18

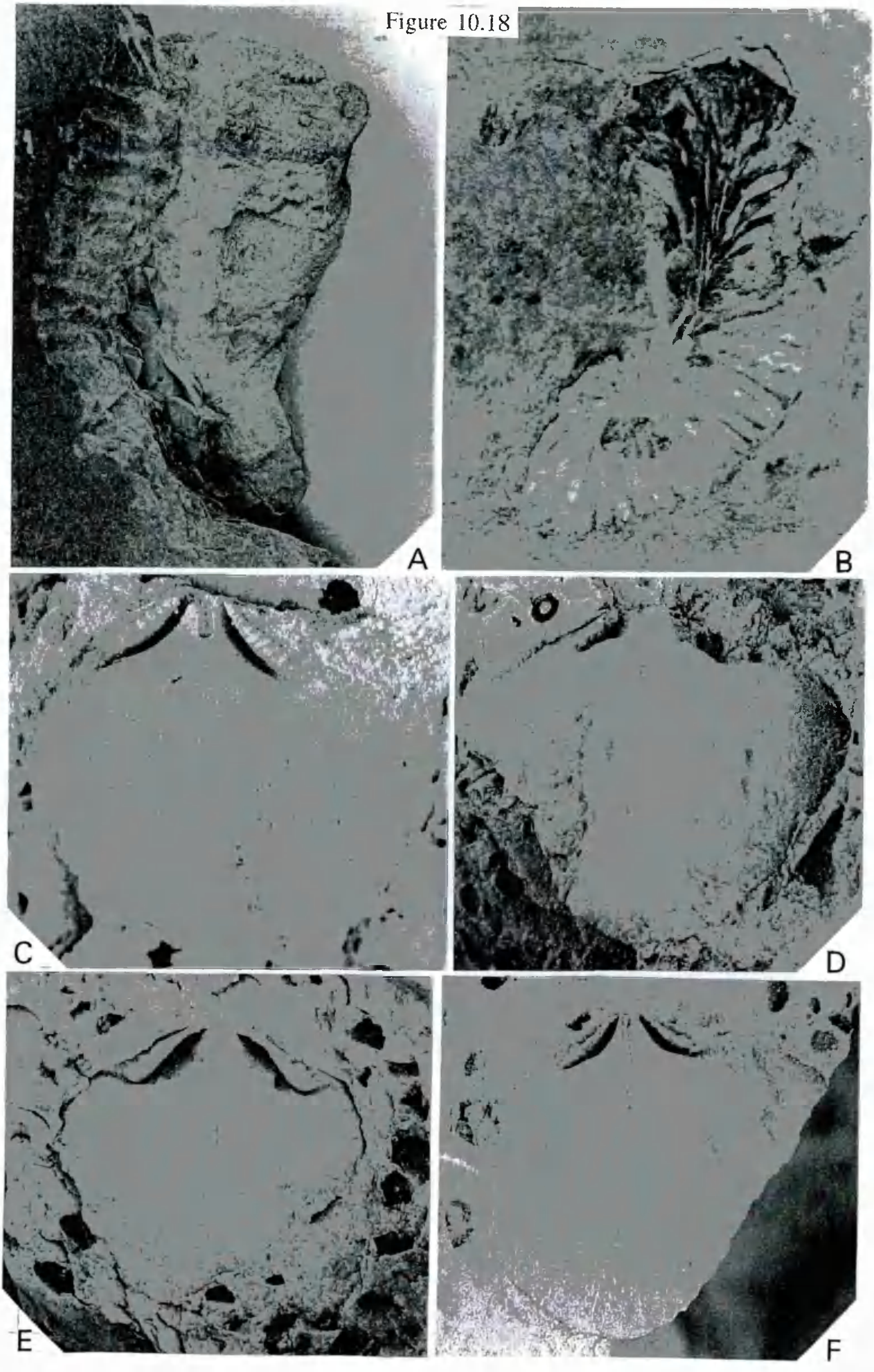

Figure 10.19

All from specimens from GBLB locality

Brachiopods

A, *Lingula* sp. X6

B, *Leptaena* sp. ?internal mould, ventral valve. X7

C, *Lingula* sp. with encrusting bryozoan, X7

D, Internal mould of ?*Dalejina* sp. X5

E, *Skenidioides lewisi* internal mould of ventral valve, X7

F, Stricklandid, ventral valve? X 5.

Figure 10.19

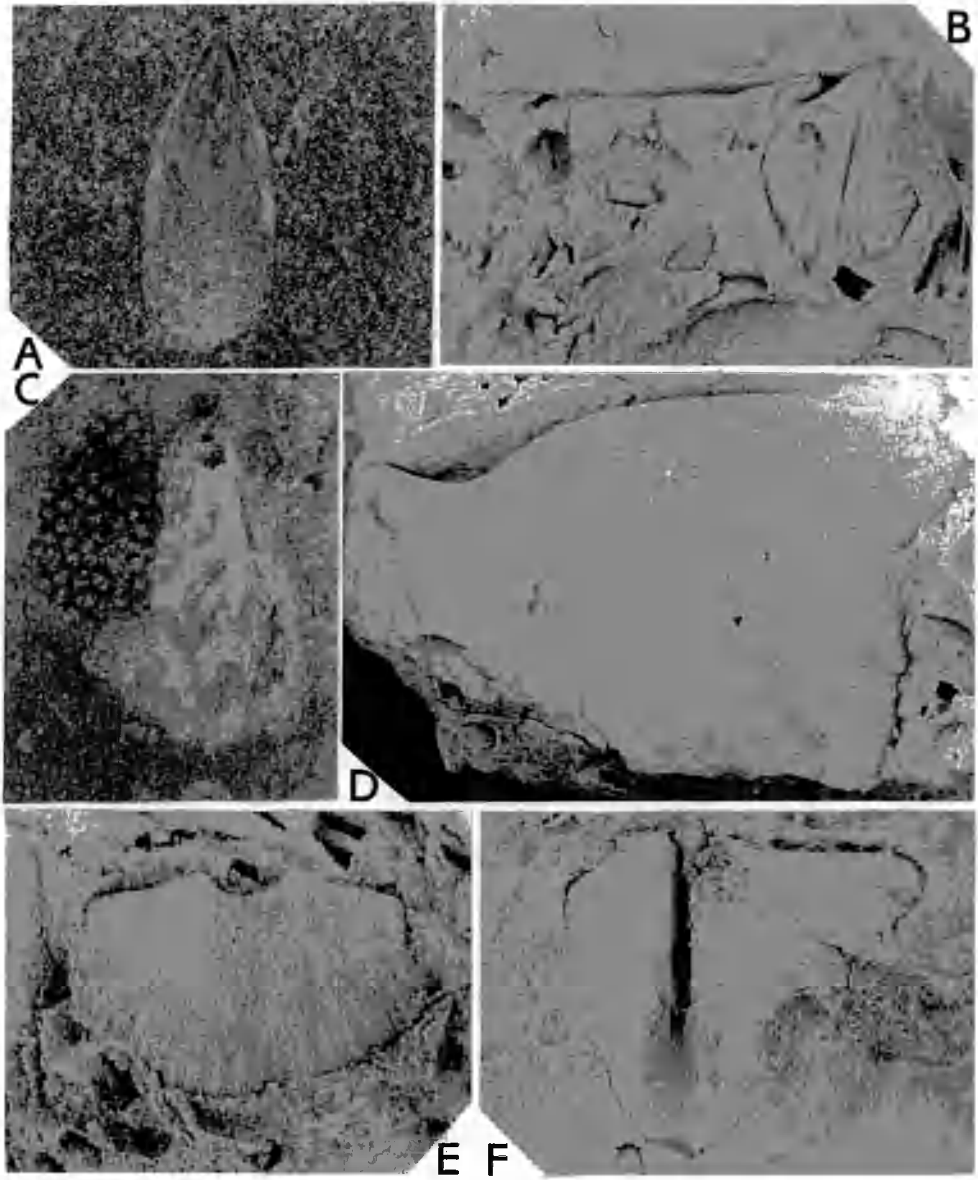

Figure 10.20

All specimens from GBLB locality *O spiralis* biozone age

Brachiopods

A, *Coolinia applanata*, (external mould) X3.

B, *Meristina* sp. internal mould brachial valve X2

C, *Skenidioides lewisi* internal mould of brachial valve, X7

D-E, *?Resserella* sp. X4

F, *?Dalejina* sp. X3

G, Atrypid, X6

H *Cyrtia exporrecta* internal mould X6

Figure 10.20

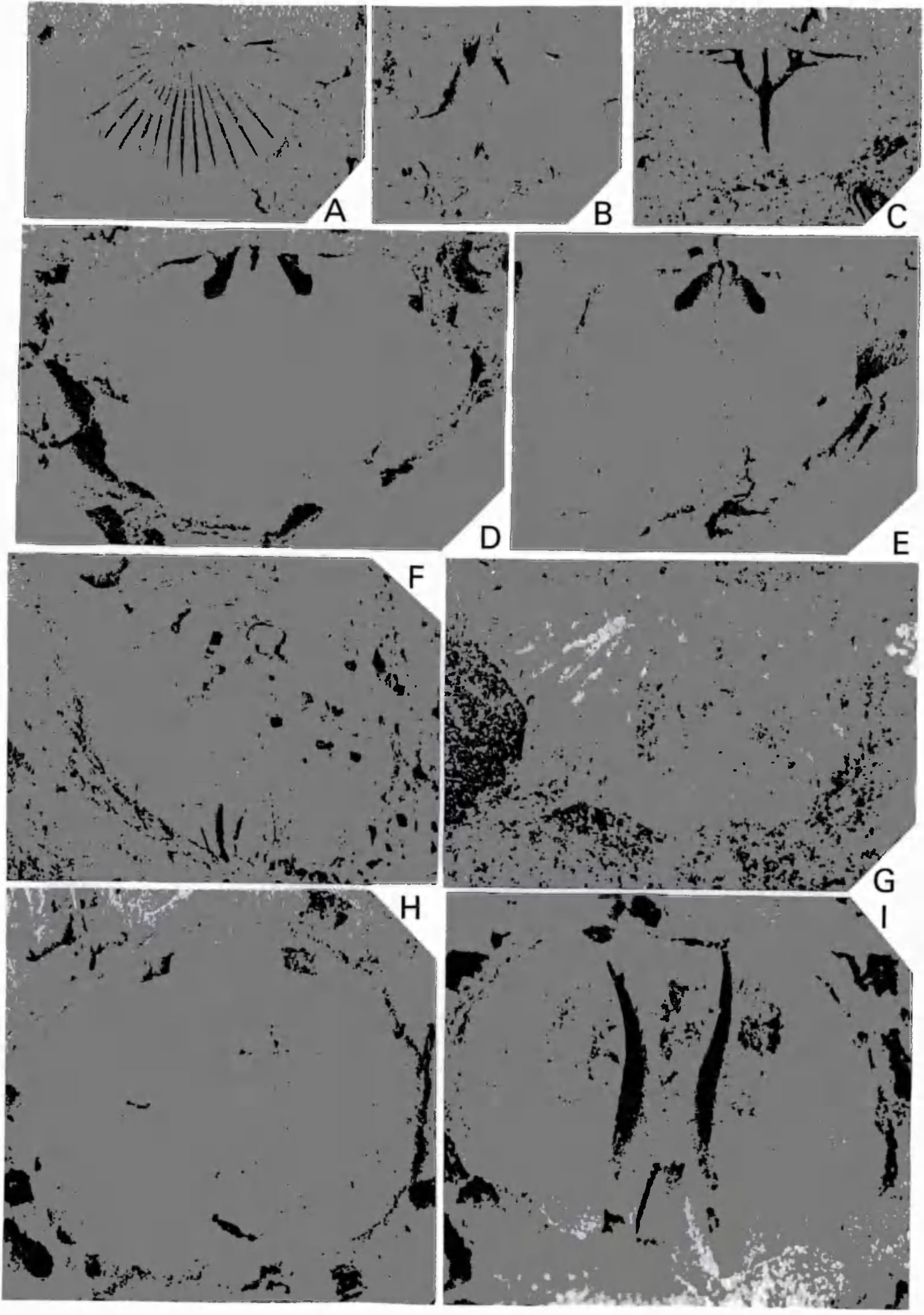

Figure 10.21

All specimens from GBLB locality *O spiralis* biozone age

Brachiopods

A-B *Pentlandella pentlandica* A, X6; B, X2

C-E, *Leptaena* sp. X2

F-L *Dicoelosia* cf. *hibernica*.. F, internal mould brachial valve X2; G internal mould X4; H, external mould X4; J external mould X5, K internal mould X6; L internal X4.

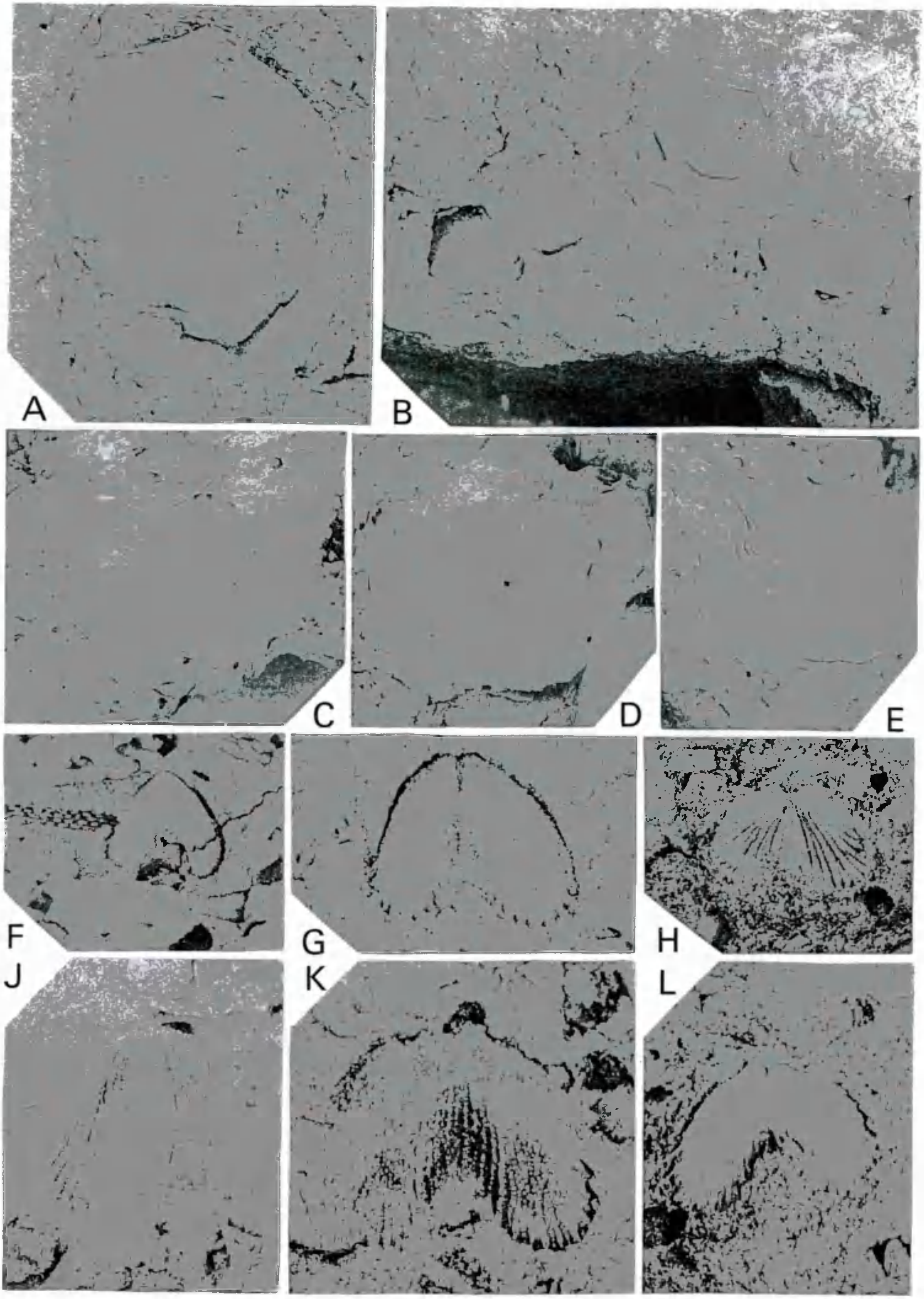
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Figure 10.22

All specimens from GBLB locality *O spiralis* biozone age

Brachiopods

A-B, internal mould pedicle valve *Visbyella visbyensis*. A, X5; B, X4

C internal mould, ventral valve, *Eoplectodonta penkillensis* X5

D, Chonetid X7.

E internal mould, dorsal valve, *Eoplectodonta penkillensis* X7

F Atrypid X7.

Figure 10.22

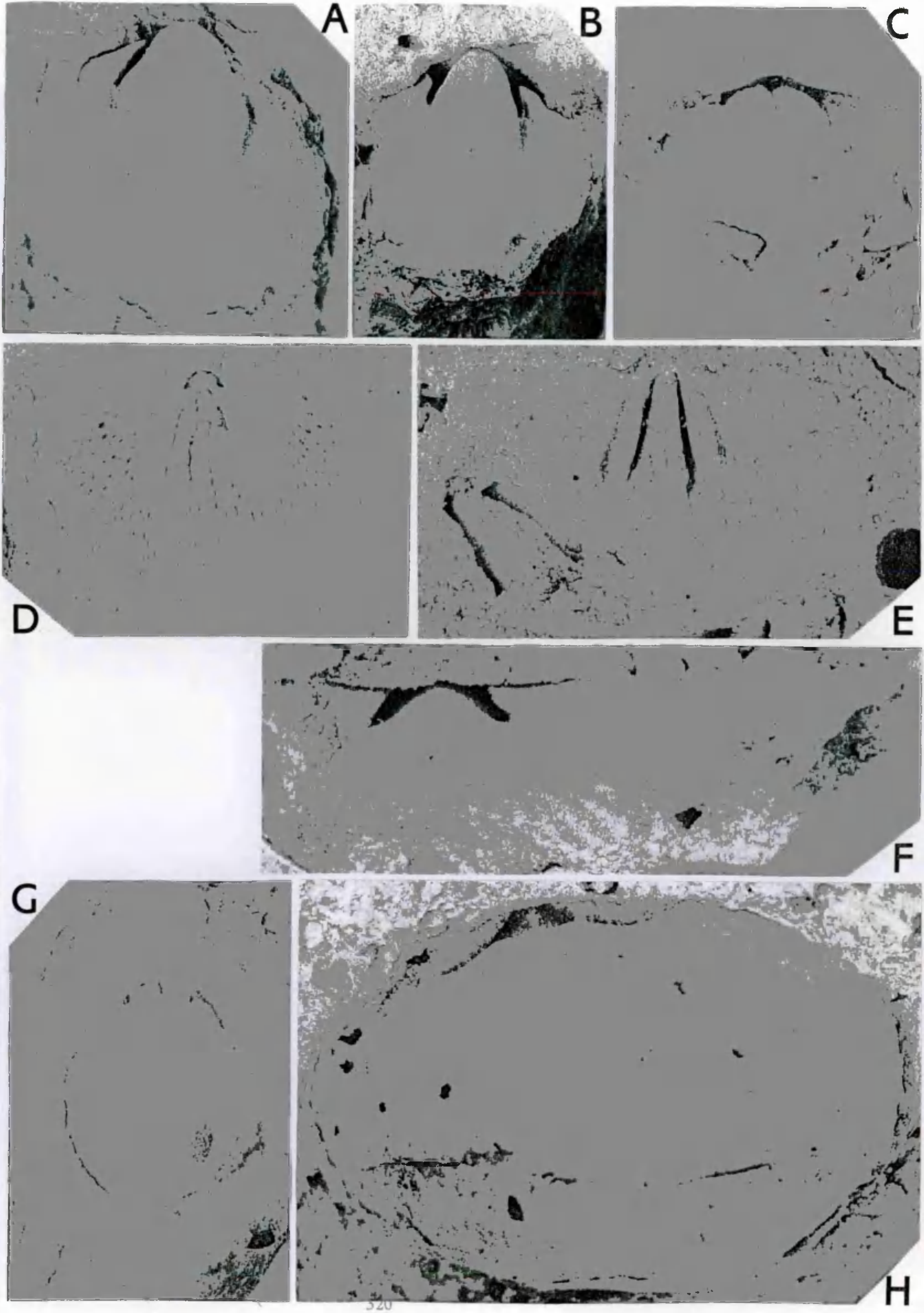


Figure 10.23

All specimens from GBLB locality *O spiralis* biozone age

Stick Bryozoans
All X3 except for E & G X4.

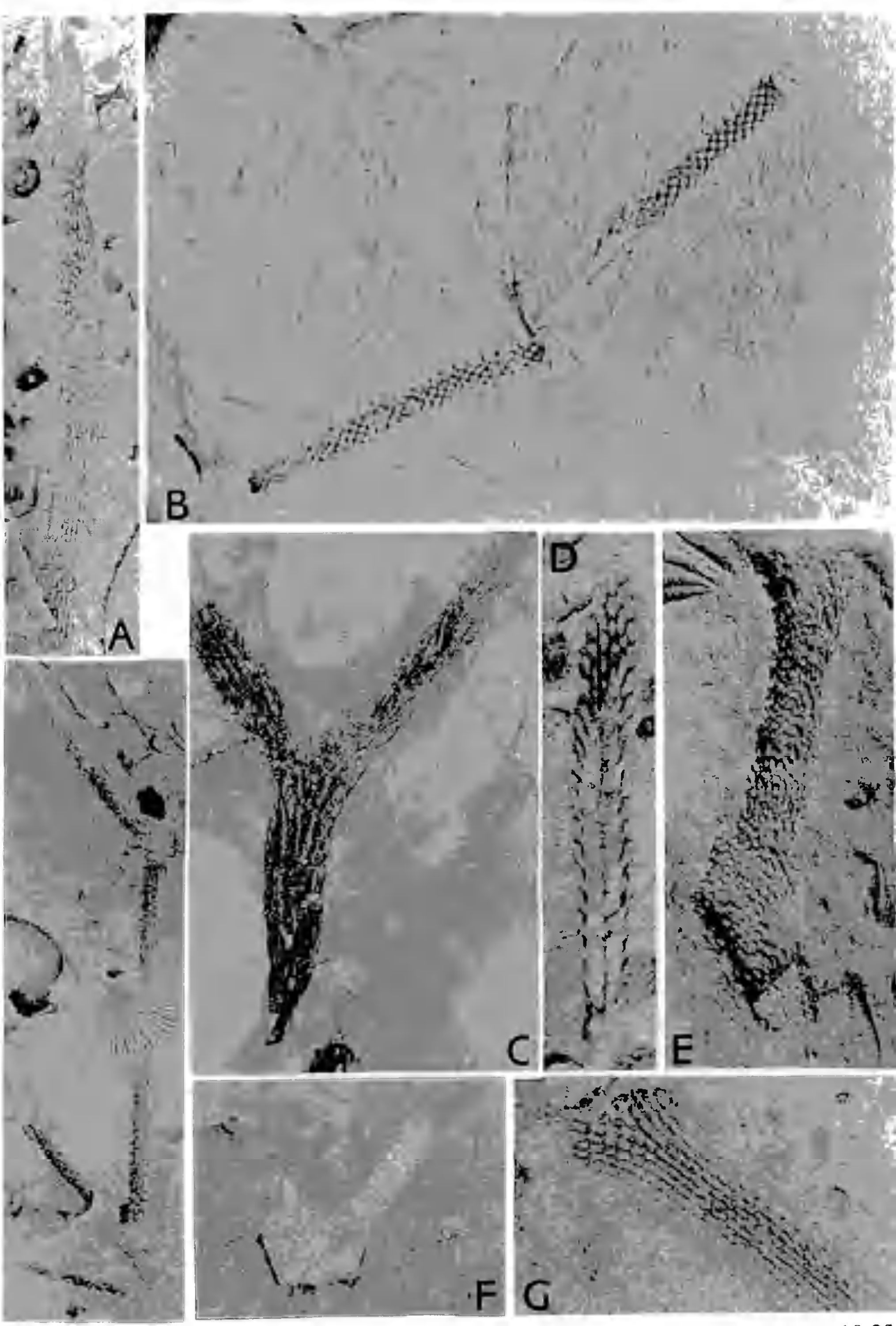


Figure 10.23

Figure 10.24

All specimens from GBLB locality *O spiralis* biozone age

Hand specimens all X 3/4

A,C,D all from 350 in logged section, B from 550. D has specimen of coral *Angopora.*

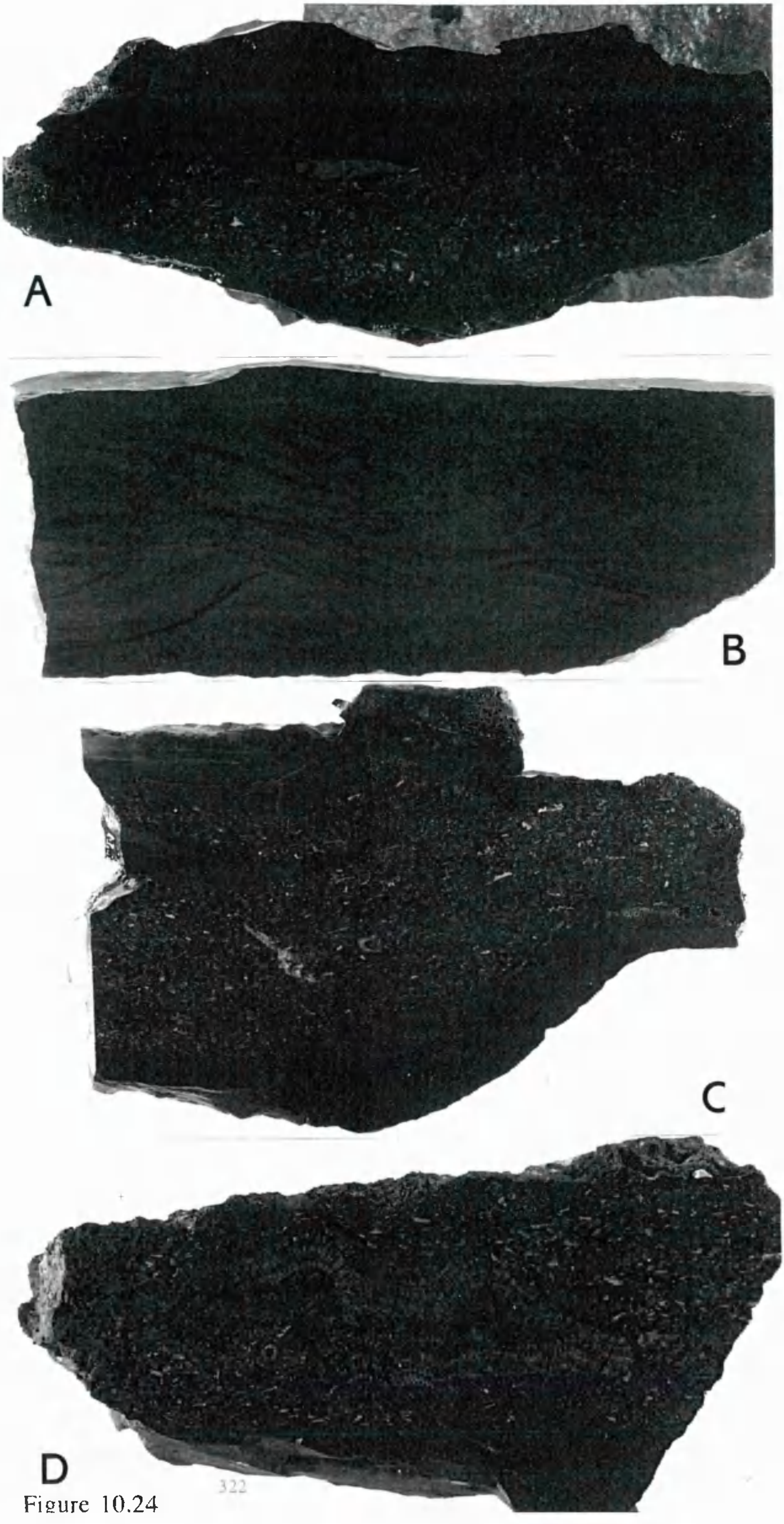


Figure 10.24

Figure 10.25

All specimens from GBLB locality *O spiralis* biozone age

Hunterian Museum dendroid specimens.

A *Thallograptus inaequalis* Hunt. Mus. 1870a X 2.5

B *Thallograptus inaequalis* Hunt. Mus. 1870c X 2.5

C *Coremagraptus* sp. nov Hunt. Mus. 1865 X 2

D ?*Thallograptus* proximal end Hunt. Mus. 1862a X 7

Figure 10.25

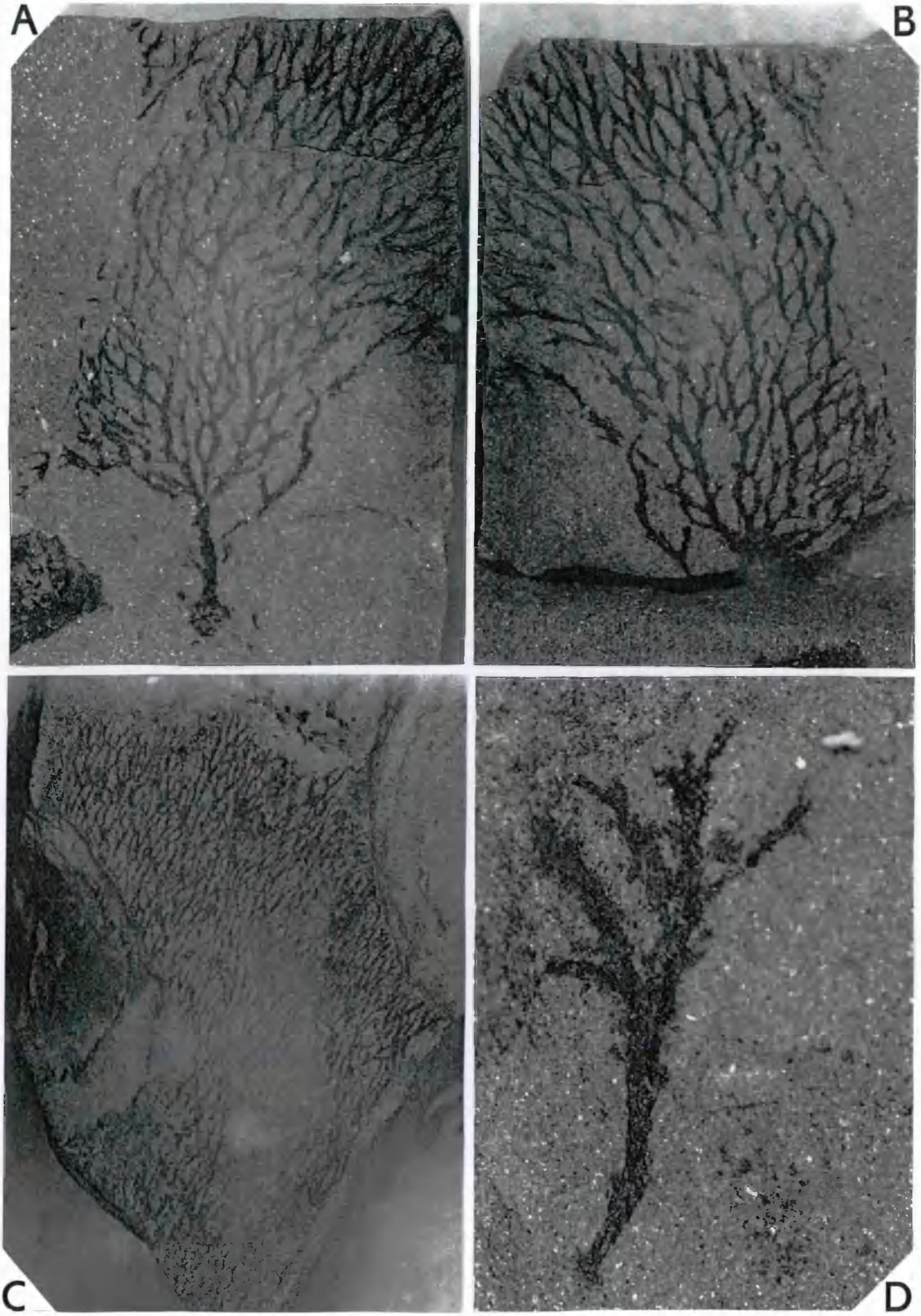


Figure 10.26

All specimens from GBLB locality *O spiralis* biozone age

Hunterian Museum dendroid specimens

A *Thallograptus arborescens* Hunt. Mus. 1860b X1.5

B *Coremagraptus imperfectus* Hunt. Mus. 1861b X 2

C *Coremagraptus* sp. nov. Hunt. Mus. 18666 X 2

D *Coremagraptus imperfectus* Hunt. Mus. 1870b X 2

Figure 10.26

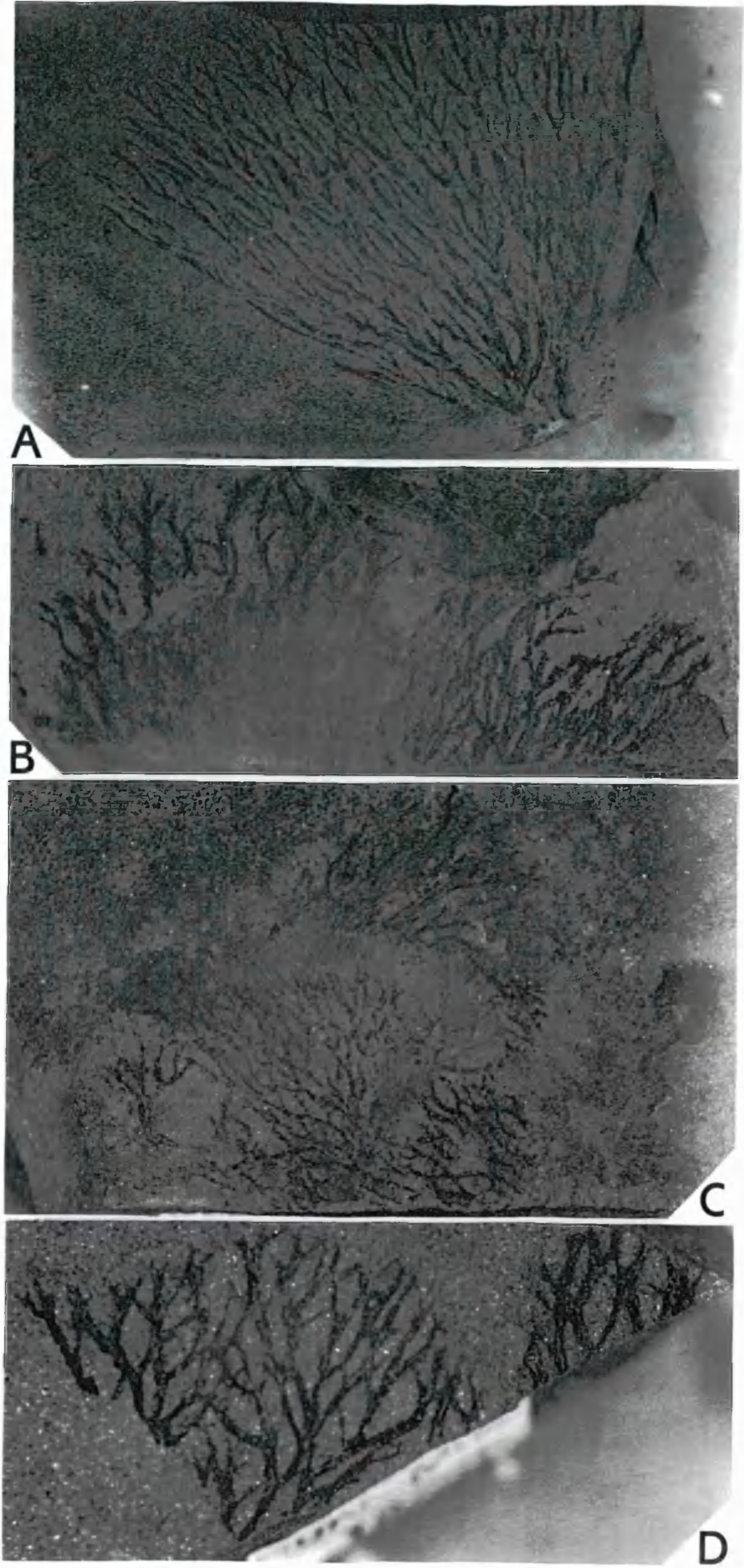


Figure 10.27

All specimens from GBLB locality *O spiralis* biozone age

Dictyocaris.slimoni

A. and C. Scanning Electrorn Microscope photographs. X 50

B, hand specimen draped and folded over sediment surface X8

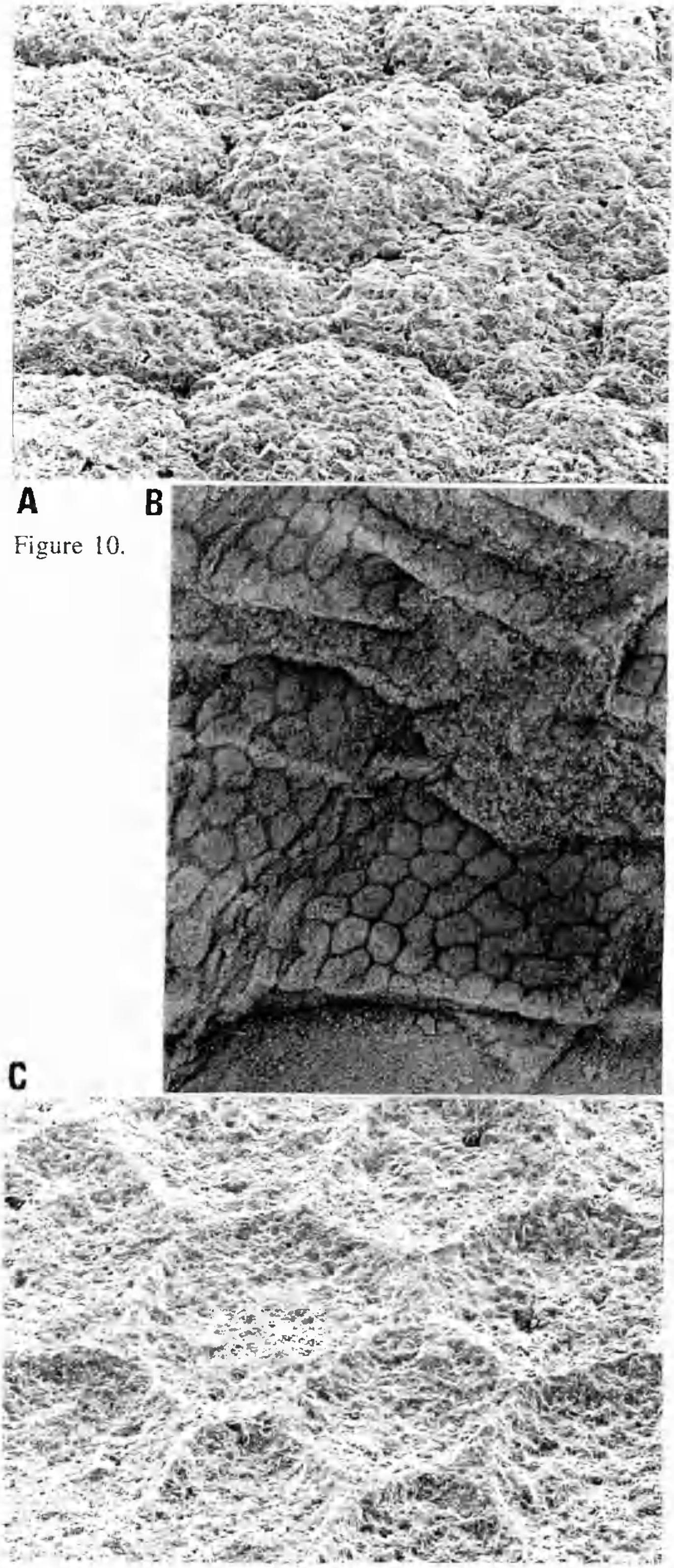


Figure 10.

Figure 10.28

All specimens from GBLB locality *O spiralis* biozone age

Dictyocaris.

A X1 *Dictyocaris ramsayi* showing typical abundance

B X4 *Dictyocaris* sp. showing holes throught the surface probably due to burrowing organisms.

C X 6 *Dictyocaris salteri* showing holes through the surface and distinctive surface ornament.

D X 8 *Dictyocaris.slimoni* showing folding of of flexible sheets.

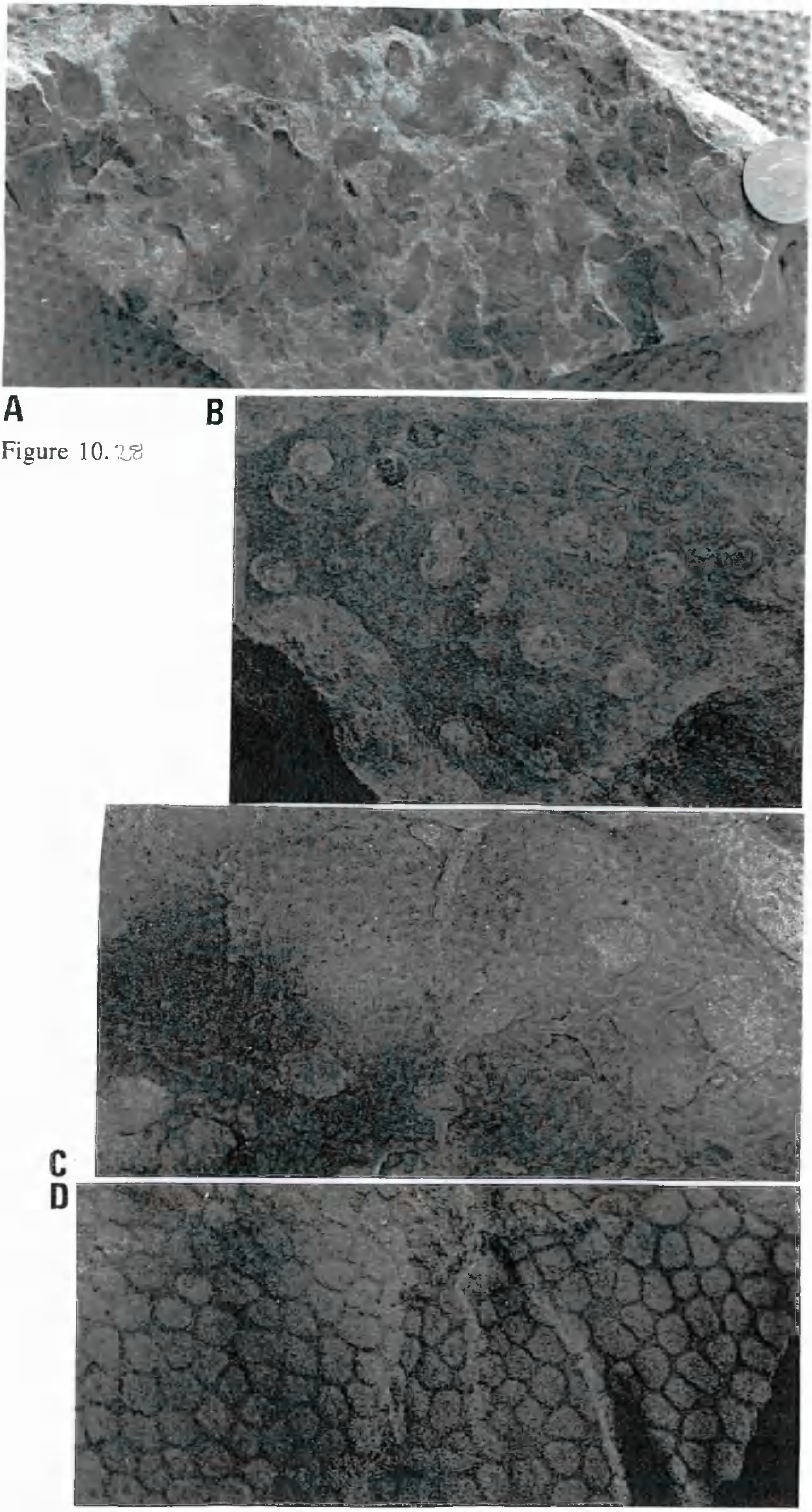


Figure 10.28

Figure 10.29

All specimens from GBLB locality *O spiralis* biozone age

Brachiopod *Erinostrophia undata*

a X 1.8; b Hunt. Mus. L 149168 X1.8; c Hunt. Mus. L 149168a X3.5;

d X 2.7; e Hunt. Mus. L 14917a X1.8; f Hunt. Mus. L 14916b X6

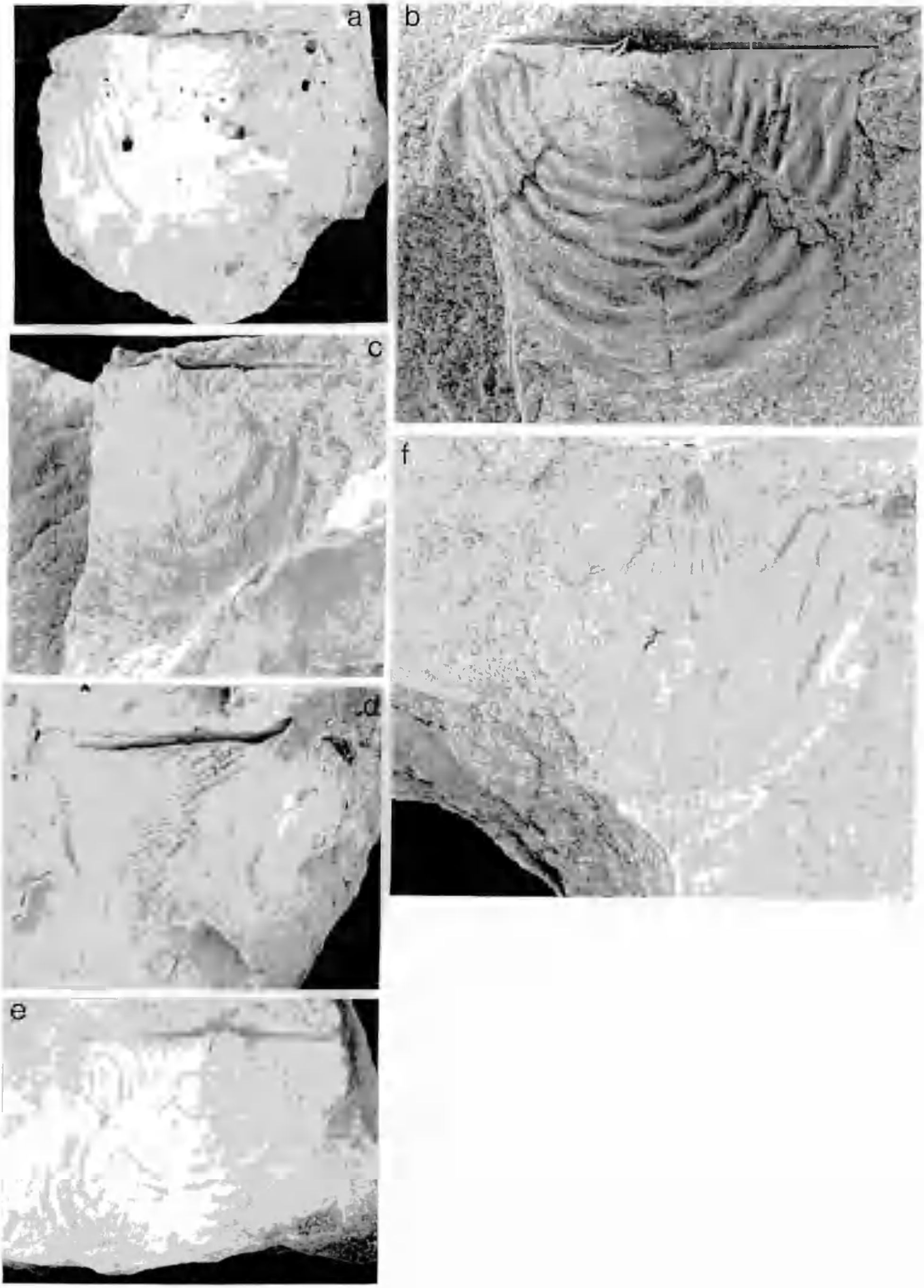

a
b
c
d
e
f

Figure 10.30

All specimens from GBLB locality *O spiralis* biozone age

Brachiopods

a, b, *Strophonella* sp. X2

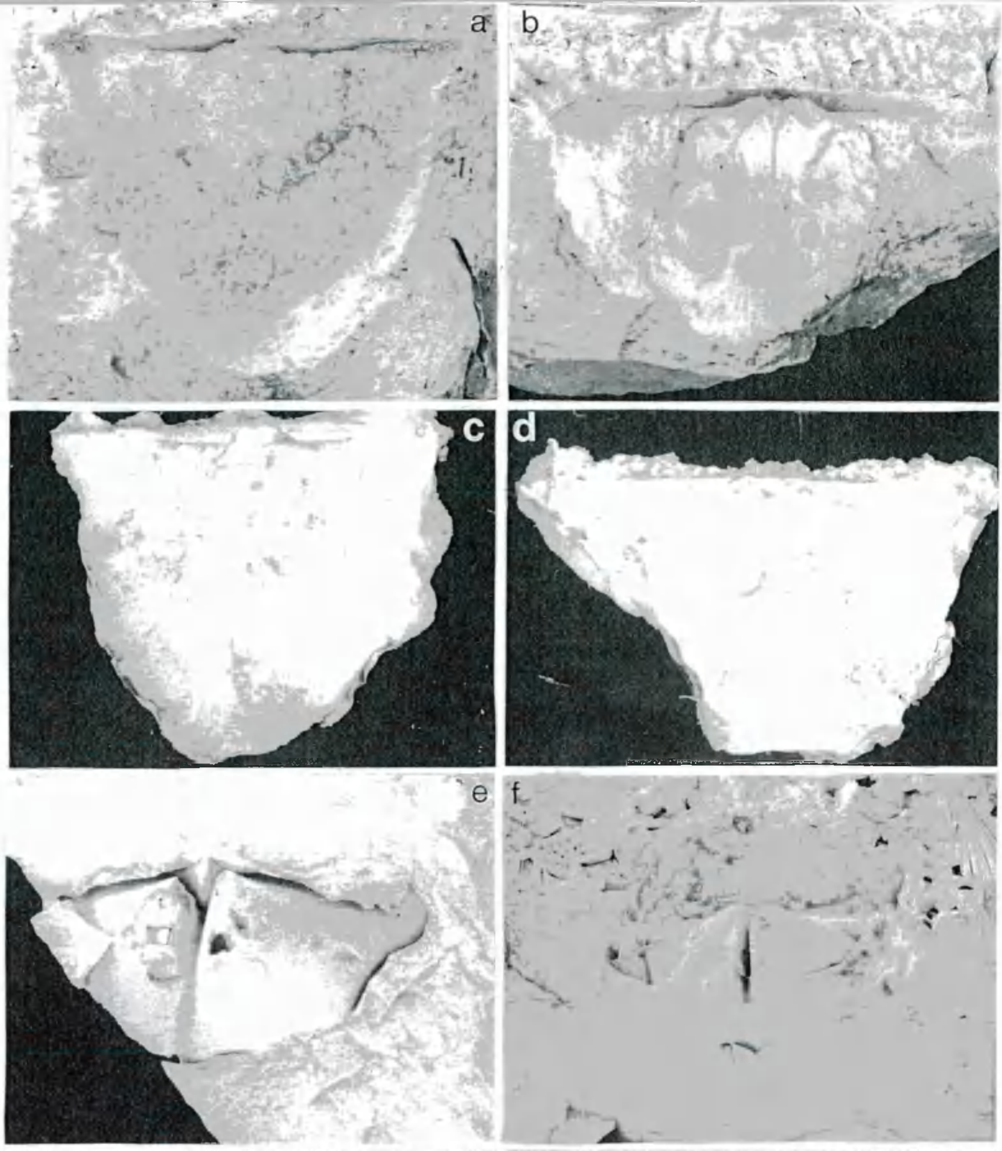
c, d, *Strophonella* sp. X2 Latex moulds.

e, Stricklandid X4

f, Stricklandid X 3

g, *Leptaena* sp. X3.8

h, *Orbiculoidea* sp. HML14919 X 8.3


a
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