THE FOSSIL FLORA OF SHETLAND AND SURROUNDING AREAS.

VOLUME 1.

A thesis submitted in candidature for the degree of Doctor of philosophy (2 Volumes).

Ian Perry.
Department of Botany.
University of Bristol.

MEMORANDUM.

The work described in this thesis was carried out in the Department of Botany, University of Bristol. It is the original work of the author, except where otherwise stated, and no part of it has been submitted for any other degree at this or any other University.

Ian Perry.

30:8:89.

SYNOPSIS.

The fossil flora of Shetland, Orkney, northern Scotland, Norway and Greenland of the Middle Devonian (Givetian age) was investigated. Extensive collections were made from new and established localities resulting in the re-description of Svalbardia scotica sp. emend., Thursophyton milleri sp. emend. and Dawsonites roskiliensis sp. emend. Other fossil localities are recorded. The plants described here are preserved as; compressions/impressions, permineralised and fusainised material. Although the high thermal maturity of the deposits has rendered much of the material unidentifiable, some localities yielded well preserved morphology and anatomy. This allowed a detailed correlation between the morphological and anatomical details. The flora consisted of two major elements represented by Thursophyton milleri, a zosterophyll and Svalbardia scotica a progymnosperm.

Anatomical preservation in pyrite and limonite was found and this represents the first of its kind from the study area. A polishing technique recently developed by Paul Kennrick was applied to investigate the anatomy. This provided high resolution images of anatomy comparable with that obtained by the Scanning Electron Microscope (SEM). An attempt was made to place the floral assemblage in Banks' (1980) stratigraphic zones, as well as interpreting the evolutionary significance of the plants found.

ACKNOWLEDGEMENTS.

I would like to thank Dr. Keith Allen for his supervision and encouragement during the course of this work. In addition I am indepted to; Dr. John Marshall for his comments and advice, Dr. Natascha Heintz of the University of Oslo for the loan of specimens from the Høeg collection, Dr Ølstein Jansen of the University of Bergen for the loan of type specimens from the Nathorst collection and the curators of the British Museum for their permission to inspect the Lang collection. Furthermore I appreciate the help and support of Diane Anstey while preparing this manuscript.

CONTENTS.

(Volume 1: text)

CHAPTER 1. ---------- 0.

Introduction. ---------- 0.

Early vascular plants a historical review. --------- 1.

Floral classification of early plants. ---------- 3.

Devonian plant stratigraphy. ---------- 11.

Devonian plant localities. ---------- 17.

Middle Devonian plants of the Orcadian Basin. ------ 21.

CHAPTER 2. ---------- 26.

Geology of the Orcadian Basin and the surrounding areas. 26.

Shetland geology. ---------- 27.

The Old Red Sandstone of Orkney. ---------- 38.

Geology of Caithness. ---------- 41.

Geology of Cromarty and the Moray Firth. ---------- 42.

Geology of eastern Greenland. ---------- 44.

Geology of western Norway. ---------- 47.

Palaeogeography of the Middle Devonian. ---------- 49.

CHAPTER 3. ---------- 53.

Techniques. ---------- 53.

CHAPTER 4. ---------- 66.

Major plant bearing localites. ---------- 66.
The South East Shetland basin. ---------- 66.
The Walls Basin. ---------- 69.
The Melby basin. ---------- 71.
The minor plant bearing localities. ---------- 73.

CHAPTER 5. Description of plants. ---------- 82.

Thursophyton milleri. ---------- 82.
Trimerophyton roskiliensis. ---------- 129.
Svalbardia scotica. ---------- 138.

CHAPTER 6. ---------- 177.

Discussion. ---------- 177.
Palaeoecology. ---------- 177.
The Svalbardia/Archaeopteris complex. ---------- 184.
Evolution of the leaf and Svalbardia. ---------- 187.
Evolution and Thursophyton milleri. ---------- 188.
Biostratigraphy. ---------- 190.
Taphonomy. ---------- 192.

REFERENCES. ---------- 195.

TEXT FIGURES.

Facing Page.

Fig. 1. ---------- 17.
Middle Devonian plant localities of the world.

Fig. 2. ---------- 26.
Devonian sediments of north east Scotland, Orkney and Shetland.

Fig. 3. ---------- 27.
Devonian sediments of Shetland.

Fig. 4. ---------- 28.
Devonian outcrop and locality map for south east Shetland.

Fig. 5. ---------- 31.
Devonian outcrop and locality map for west Shetland.

Fig. 6. ---------- 33.
Devonian outcrop and locality map for Foula.

Fig. 7. ---------- 36.
Devonian outcrop and locality map for Fair Isle.

Fig. 8. ---------- 38.
Devonian outcrop and locality map of Orkney.

Fig. 9. ---------- 41.
Devonian outcrop and locality maps for Caithness and Cromarty.

Fig. 10. ---------- 45.
Devonian sediments of east Greenland.

Fig. 11. ---------- 45.
Devonian sediments of east Greenland, cont.
Fig. 12. ---------- 48.
Devonian sediments of western Norway.
Fig. 13. ---------- 53.
Palaeogeography of the Middle Devonian.
Fig. 14. ---------- 117.
Reconstruction of a Metaxylem element from Thursophyton milleri.
Fig. 15. ---------- 119.
Reconstruction of Thursophyton Milleri.
Fig. 16. ---------- 119.
Anatomy of Thursophyton Milleri during branching.
Fig. 17. ---------- 129.
Comparison between the anatomy of Thursophyton milleri and related species.
Fig. 18. ---------- 133.
Reconstruction of Trimerophyton roskiliensis.
Fig. 19. ---------- 164.
Reconstruction of Svalbardia scotica.
Fig. 20. ---------- 164.
Reconstruction of the anatomy of Svalbardia scotica.
Fig. 21. ---------- 164.
Anatomy of some of the progymnosperms.
Fig. 22. ---------- 164.
Diagramatic reconstruction of secondary tracheids in Svalbardia scotica.

Fig. 23. ---------- 190.
Evolutionary relationships of Svalbardia and Thursophyton.

TABLES

Facing Page

Table. 1.1 ---------- 14.
Devonian assemblage zones.
Table. 1. ---------- 91.
Metaxylem element dimensions of Thursophyton milleri from Skersund.
Table. 2. ---------- 93.
Metaxylem element dimensions of Thursophyton milleri from Sandwall.
Table. 3. ---------- 99.
Metaxylem element dimensions of Thursophyton milleri from Foula.
Table. 4. ---------- 105.
Metaxylem element dimensions of Thursophyton milleri from Norway.
Table. 5. ---------- 108.
Metaxylem element dimensions of Thursophyton milleri from Greenland.
Table. 6. ---------- 108.
Comparisons of element dimensions for Thursophyton milleri.

Table. 7. ---------- 129.
Comparison of xylem cell wall structure of *Thursophyton* with other species.
Table. 8. ---------- 154.
Comparison of measurements for *Svalbardia scotica*.

CHAPTER 1.

INTRODUCTION.

During the past three decades there has generally been an increase in interest in the plants of Devonian age. This has been paralleled in the Orcadian basin by an increase in the study of the palynology of the area and in particular that of the Shetland basin, but not of the plants found in association with them. The Late Silurian and Early Devonian periods probably represent the age of greatest vascular plant evolution and radiation in establishing the beginnings of land flora. None of these early plants survive to the present day but they gave rise to several diverse lines which evolved in the Middle Devonian and saw the appearance of all the major groups of Pteridophytes; and by the Late Devonian the first platyspermic and radiaspermic seeds.

The investigation of Middle Devonian plants is thus an exciting and rewarding area of palaeobotanical study. The flora from the Orcadian basin has not been comprehensively studied since the work of Lang (1925, 1926.) and recent research into the palynology of the area has suggested that numerous plant localites are present, particularly within the Shetland Basin. The collections of John Marshall in particular have pointed to this area as being one worth further study. Other areas such as Western Norway and Eastern Greenland were thought to be worthy of inclusion within the study area because of the geographical proximity of the land masses during the Devonian and the similarity of the plant flora. Western Norway has long been known to have productive plant localites. While eastern Greenland has

recently been show to contain a limited plant flora.

EARLY VASCULAR PLANTS A HISTORICAL REVIEW

One of the earliest palaeobotanical contributions was the description of "fossil bamboo shoots" by the Chinese scholar Shen Kuo, published in 1086 (Li,1981). This may be the beginnings of descriptive palaeobotany and even now the science still relies heavily upon observation and description. Today the discipline has extended to include theoretical approaches such as modelling, statistical analyses (Alvin et al , 1982; Cichan and Taylor, 1982; Hill, 1980; Spicer, 1981.), studies of reproductive biology (Dilcher, 1979), and analyses of fossil plant communities (Scott, 1979).

J. W. Dawson 1859: Dawson published a description together with a reconstruction of a new genus Psilophyton, which at the time was regarded with much scepticism by his contemparies (Solms-Lombach, 1891) and despite his extensive pioneering collecting and work (1862, 1870, 1871, 1884) he had little impact on evolutionary thought at the time.

Kidston and Lang 1917: The prevailing attitude of comparision between the fossil record and extant plants persisted until the description of a beautifully preserved silicified flora from the Lower Devonian Chert beds at Rhynie Scotland (Kidston and Lang, 1917, 1920a, b, 1921a, b) which allowed the accurate description of the plants clearly

far more primative than any similar extant plant. This together with the publication of a Lower and Middle Devonian flora from Western Norway (Nathorst, 1913, Halle, 1916) and the discovery of sclariform tracheids in a spiny axis of Psilophyton ornatum Dawson (Halle, 1916) supported Dawsons claims that these plants were indeed vascular plants of great simplicity.

From these early works a series of floral classifications emerged, notably the concept of a psilophyte flora errected by Lang (1917) which included Rhynia and Psilophyton under the term Psilophytales. Lang suggested that these plants were "characterised by the sporangia being borne at the ends of certain branches of the stem without any relation to leaves or leaf like organs." The name was derived from the genus Psilophyton and was used to suggest a resemblence between plants of the class and the extant Psilotales.

Banks 1968: A great many fossils found during the period after 1917 were simply referred to as "psilophytes" a name that became firmly established and far too inclusive. Banks after reviewing the various earlier schemes of classification presented his own in which he confined the name psilophyte to the plants that he included in his subdivision Rhyniophyta. Since the plants included in the genus Psilophyton constituted the focal point of another subdivision it may have been better if the name had been dropped altogether. Banks work represented a significant step since in many cases the original morphology and the anatomy of these plants was poorly known (Banks 1975a), but

techniques developed or better preserved material was collected more imformation was obtained, making a redefinition of fossil classification essential.

FLORAL CLASSIFICATION OF EARLY LAND PLANTS

The most significant new imformation, highlighted by Banks (1968) review centres on sporangial structure, including size, mode of attachment, and, when preserved, the vascular anatomy. It became obvious that unrelated plants had been grouped together (Banks, 1968, 1975a; Hueber, 1964). Høeg in 1967 had already proposed the removal of the genera Drepanophycus, Baragwanathia, Protopteridium and Pseudosporochnus from the Psilophytales. Banks drew attention to the obvious discrepencies and replaced the taxon Psilophytales with three subdivisions; Rhyniophytina, Zosterophyllophytina, Trimerophytina, which together with the Lycophytina includes all the early land plant classes.

The Rhyniophyta: These were typified by two genera, Rhynia Kidston and Lang (1917) and Cooksonia Lang (1937). These are extremely simple and often very small branching more or less equally dichotomously and bear fusiform sporangia terminally that may dehisce longitudinally. The inclusion of Cooksonia as a land plant remains controversial since no species has been found with vascular anatomy. Edwards and Edwards (1986) exclude such plants erecting a term "rhyniophytoid" for plants of unknown anatomy. Rhynia major Kidston and Lang (1920a) has also been removed from

the class as it has been shown not to contain conventional tracheids. Edwards (1986) renamed it Aglaphyton major and considered it to be a possible byophyte.

Rhynia gwynne-vaughanii Kidston and Lang (1917) represents the type species of the genus and has been shown to be more complex than at first thought (Edwards and Edwards 1986). Axes consist of an epidermis with stomates, two zones of outer cortex very small centrally located protostelé, terete in cross section (Banks, 1968, 1975a). Branching is dichotomous, sporangia abcise after spore release, and this is followed by overtopping of the sporangia by lateral branches.

Taenocrada is often considered as a questionable rhyniophte (Banks 1975a, Edwards and Edwards 1986, Gensel and Andrews 1984). Fairon-Demaret (1985) has removed one species T. langii from the genus, erecting a new genus Stockmansella (incertae sedis), on the basis that its xylem elements are not tracheids. Similarly Heuber (1982) has discovered a new xylem structure for T. dubia with characteristic thickenings as seen in both Stockmansella (Fairon-Demaret 1985) and R. gwynne-vaughanii (Kidston and Lang 1920a, Edwards 1986) as well as Sennicaulis (Edwards 1981). If the Xylem structure is found to be the same it will have important implications for the vascular status of the Rhyniophytina. One futher species T. stilesvillenis Taylor (1986) investigated by Taylor (1986) shows similarities with the Zosterophyllophytina and it may well be that this taxon is an un-natural group.

The Zosterophyllophytina: These plants "Are more diverse and distinct from the original concept of the Psilophytales." (Banks, 1968). In contrast to the Rhyniophytina the zosterophylls are characterised by less equally branching axes that sometimes results in a pseudomonopodial appearance. Sporangia are borne laterally being globose or reniform, with dehiscence along the distal margin. In some genera axes are covered with emergénces in the form of teeth or spines. The anatomy where preserved shows an elliptical exarch strand (Banks, 1968, 1975a).

The Trimerophytina: This class has Trimerophyton Hopping 1956 as the type genus for the subdivision, which includes plants that branch pseudomonopodially. The lateral branches further dividing either trichotomously or dichotomously producing a more complex and often larger plant than either the rhyniophytes or zosterophylls. Large clusters of fusiform sporangia are borne at the tips of some ultimate axes. The anatomy is a terete centrach strand that is massive when compared to the Rhyniophytina (Banks, 1968, 1975a).

The Lycophytina: This includes lycopods and lycopod precursors such as Asteroxylon (Lyon, 1964) and Baragwanathia Lang and Cookson (1935) occuring from the Late Silurian and through the Devonian. The subdivision includes plants with a stelate exarch protostele and lateral sporangia associated with microphylls, the leaf traces extend to the leaves or only to their base, but are

characteristically typical leaf traces.

These subdivisions neatly encompassed the majority of groups representing the early vascular plants, any Banks was unable to include such as, Sciadophytaceae, Platyphyalles and Barinophytaceae he left as incertae sedis. Banks (1975a) considered that the Rhyniophytina evolved first and the Zosterophyllophytina soon after, but probably independently. This independent nature of the groups was questioned by Gensel. She postulated that Renalia hueberi (1976), which resembled Cooksonia, and it is generally thought to be a rhyniophyte, in sporangial mophology is akin to some zosterophylls and therefore may represent an intermeadiate in morphology suggesting that the distinction between the two groups is not great or as consistent as has been previously believed.

Crane (1989) questioned the basic assumption that the Tracheophytes are a monophyletic group, he saw two major groupings, the lycophytes and the rhyniophytes as representing a dichotomy of the Tracheophyte clade. Nothia (Edwards and Edwards 1986) was cited as showing some lycophyte characteristics but with primative endarch anatomy and no true tracheids. This suggests that similarly some lycophytes may not ~~of~~ have had true tracheids and so these characteristic cells may either have been lost in Nothia or more significantly been evolved within the lycophytes independently from the rest of the Tracheophytes in which a second group evolved tracheids. This implies that the Tracheophytes are not a monophyletic group.

Banks (1975a) also considered that the Zosterophyllophytina, because of their exarch anatomy, lateral reniform sporangia and emergences, may have given rise to the lycopods. With the emergences ranging from small hairs to spines or tooth like outgrowths of the stem cortex developing into microphylls. Their general habit of a partially creeping, partially erect axis also suggests a possible lycopod ancestory

For the Trimerophytina Banks (1975a) envisage a group that represented an evolutionary level that was advanced in comparision to the Rhyniophytina. Indeed the classification of the genus Psilophyton (Heuber, 1967, Heuber and Banks, 1968) established a generitype P. princeps which, together with Trimerophyton (Hopping, 1956), Pertica (Kasper and Andrews, 1972) represents a fairly natural group in which a considerable amount of evolution is going on. The Trimerophytina, Banks (1975a) saw as a group from which the Progymnosperms, Sphenophytina, Cladoxylaleans and Coenopterids evolved. Evidence to support this assumption comes from Andrews et al (1975) who suggested that Oocampsa was an intermediate between the Trimerophytina and some Progymnosperopsida such as Tetraxylopteris or Archaeopteris. Whether this is true or not it is clear that the Trimerophytina exhibit an early stage in the differentiation of axis or shoot systems, in particular overtopping and planation (Gensel, 1977). This in turn may represent an early stage in the evolution of the megaphyllous leaf.

The simplicity of Early to Middle Devionian plants means that the number of diagnostic characters is small and as a

consequence a range of material must be studied before an identification can be made. Often fertile specimens are required to determine which class or even family is involved since axes of these primative plants tend to initially resemble one another (Banks, 1980). Despite this the classification proposed (1968) and modified (1975a) by Banks has generally become accepted. The major disagreements arise over the rank of the taxa. Bold et al (1980) raised the subdivisions to divisional status, while Beirhorst (1971) reduced them to classes. The retention of the Psilophytina was proposed by Schweitzer (1983), as previously suggested by Høeg (1967), because he believed the subdivisions to be unrealistic as a result of the number of plants that showed simple and advanced characteristics in a mixture that he suggested were intermediate between subdivisions.

Progymnospermopsida: They represent the only other Class included in this thesis. It was proposed by Beck in 1960, closing the gap between pteridophytic and seed plants. The group was based on the demonstration that certain fossils with fern like foliage known as Archaeopteris were borne on stems of gymnospermous anatomy known as Callixylon (Beck, 1960a).

Beck envisaged the group to contain free sporing plants with a pteridophytic type of reproduction and foliage, combined with gymnospermous stem anatomy and secondary xylem. In 1960 he proposed three orders within the class; The Aneurophytales, containing Aneurophyton

(Eospermatopteris) Krausel and Weyland (1923) and Tetraxylopteris (Shenoxylon) Beck (1957), and characterised by their three dimensional unwebbed highly branched fronds, woody habit, pteridophytic reproduction, protostelic primary xylem strand,and crowded multiserate pitting on all tracheid walls; The Protopityales, represented by Protopitys Goeppert (1850) is typified by both pteridophytic reproduction and gymnospermic secondary xylem and is considered to be somewhat intermediate because of the distichous leaf arrangement, eliptical pith with a pair of almost endarch primary xylem strands at its extremities and elongated bordered pits on the radial walls of the secondary tracheids; The Pityales containing Archaeopteris (Callixylon) Dawson (1871), Pitys and Archaeopitys Scott and Jeffery (1914). This group was typfied by Archaeopteris with large planated compound fronds with webbed ultimate appendages, the presence of pith surrounded by mesarch primary strands and secondary tracheids with pitting restricted to the radial walls.

The Progymnospermopsida at its conception was clearly meant to include those plants showing pteridophytic reprodution with gymnospermous secondary growth, not one or the other (Beck, 1960, 1962, 1970, 1975). However like the Psilophytales before and in the case of the pteridosperms in 1904, the Progymnospermopsida became the repository for every genus that showed similarities to the six initially cited by Beck. Twenty seven genera were included in the new group by various workers (Barnard and Long, 1975, Bonamo, 1975), these showed either anatomical similarities in

primary or secondary xylem but with no indication of pteridophytic reprodution, or morphological form genera similar in some way to the external morphology of progymnosperms, or with only superficial resemblances. Only six of the twenty seven proposed fully conformed to Beck's orginal definition, these being Archaeopteris (Callixylon) Dawson (1871), Protopitys Goeppert (1850), Aneurophyton (Eospermatopteris) Krasuel and Weyland (1923), Tetraxylopteris (Sphenoxylon) Beck (1957), Rellimia Leclercq and Bonamo (1973) and Triloboxylon Matten and Banks (1966).

The restriction of criteria for true progymnosperms to the two dual characteristics of Becks (1960) original definition was put forward by Bonamo (1975), this limits the group to only five genera. If this restricted definition is accepted then the remaining twenty or so progymnosperms are placed in the category incertae sedis based on morphology or anatomy and await futher imformation as to their taxanomic classification. This definition is not widely favoured and the current status of the group acording to Beck (1975) includes fourteen genera within the three subdivisions, six are assigned to the Aneurophytales; Aneurophyton Krausel and Weyland (1923); Cairoa Matten (1973); Proteokalon Scheckler and Banks (1971); Rellimia Leclercq and Bonamo (1973); Tetraxylopteris Beck (1957); Triloboxylon Matten and Banks (1966).

The order Protopitales is represented by the single genus Protopitys Goeppert (1850). The remaining genera are assigned to the Archaeopteridales; Actinopodium Hoeg (1942); Actinoxylon Matten (1968); Archaeopitys Scott and Jeffery

(1914); Archaeopteris Dawson (1871); Eddya Beck (1967); Siderella Read (1936); Svalbardia Høeg (1942). Whichever classification is preffered it has to be kept in mind that some of the diversity within the group may be caused by ontogenetic variation although the majority is very likely the result of evolution through time.

In this thesis I intend to use the more open classification of Beck (1975) including in the orders well known plants which have progymnosperm morphology or anatomy based on the fact that it is generally accepted that they represent a natural group based on phenetic characters (Beck 1975, Bonamo 1975, Namboodiri and Beck 1968, Scheckler 1978). I also propose to retain Banks subdivisions of Zosterophyllophytina, Trimerophytina and Rhyiniophytina and Lycophytina on the basis that it has become widely accepted and is probably as equally well known as the Progymnospermopsida, representing another natural grouping among Devonian vascular plants. Their status as natural groupings is however questionable, particularly in the case of the Trimerophytes since most of our information comes from fertile specimens of Psilophyton, one genus which also shows preserved vascular anatomy.

DEVONIAN PLANT STRATIGRAPHY.

Halle (1916) working on Lower Devonian plants from Roragen, Norway, along with Nathorst (1913, 1915) working on the Middle Devonian flora of Western Norway attempted to order the plants they discovered with biostratigraphical

significance. This early work was followed by E. A. Arbers Devonian Floras (1921). Arber recognised two generally distinct floras, the Psilophyton flora of the Early Devonian and the Archaeopteris flora of the Late Devonian. Like Halle before him Arber recognised that the Devonian Archaeopteris flora was considerably more representative of a Lower Carboniferous flora than a Lower or Middle Devonian flora and importantly he supported the concept that Devonian land plants were characterised by evolutionary change. From this classic volume Devonian Palaeobotany has made tremendous advances in the last seventy years.

Kräusel (1937) added to Arbers work by describing three possible floras in the Devonian, that of an early Psilophyton flora, a Middle Hyenia flora and an upper Archaeopteris flora superimposed on the three classic divisions of Lower, Middle and Upper Old Red Sandstone. Leclerq (1940) basically agreed with this refinement but considered Protopteridium to be a more typical representative of a Middle Devonian flora because of the larger number of species and its wider distribution. However Leclerq and Bonamo (1971) reduced several species of Protopteridium to one and in 1973 introduced a new genus name Rellimia.

Clearly these early attempts at plant stratigraphy were hampered by the general lack of knowledge concerning the very plants that workers were trying to place within assemblage zones. It has however become clear as information increases that not only does the first appearance of many new structures rise through the Devonian

(Chaloner and Sheerin 1979, Knoll et al 1984) but there is a concurrent increase in the complexity of plants (Chaloner and Sheerin 1979, Edwards 1980, Banks 1980, Gensel and Andrews 1984) and a change in floral composition such that generalisations can be made about plant diversity or communities. Thus it is possible to recognise seven biostratigraphical zones (Chaloner and Sheerin 1979, Banks 1980). The assemblage zones proposed by Banks (1980) for megafossils and their statigraphic position are the most widely used and illustrated in Table 1. Each zone being named for an index fossil, he selected taxa at the generic level because many Devonian genera are monotypic and because species are often founded on minor differences that may have been insignificant to the plant.

Banks (1980) concluded that to be positive a collection represents a given zone a representative range of fossils must be analysed to show the relative state of evolution of their morphological features by this he meant having information on such important characters as presence or absence of microphylls or megaphylls, a root system, habit type, sporangial type, primary xylem anatomy and if present secondary xylem anatomy. This enables the establishment of genera that approach a natural classification which Banks proposed. Collecting on a large scale is therefore the only method in which a good fossiliferous lens can be discovered which will provide fossils with the necessary histological and anatomical details required and made available by the use of modern laboratory techniques.

Previous attemps at stratigraphic zonation were generally

TABLE 1.1 *Comparison of tentative megafossil generic assemblage-zones in Devonian strata with palynological zones suggested by McGregor (1977) and Richardson (1974).*

Series or Stage	Banks, 1980	McGregor, 1977		Richardson, 1974
Post Famennian Tn 1b Tn 1a	?—			
				V. *nitidus*
FAMENNIAN	*Rhacophyton* Assemblage—zone VII			*V. pusillites* *S. lepidophytus*
				L. cristifer
FRASNIAN	*Archaeopteris* Assemblage—zone VI			*optivus—bullatus*
GIVETIAN	*Svalbardia* Assemblage—zone V			*Triangulatus*
		devonicus—orcadensis		*Densosporites devonicus*
EIFELIAN	*Hyenia* Assemblage—zone IV	*velata—langii*		*Rhabdosporites langii* *Acinosporites acanthomammillatus*
UPPER	*Psilophyton* Assemblage—zone III	*annulatus—lindlarensis*	*Grandispora*	*Calyptosporites biornatus—proteus*
EMSIAN			*sextantii*	*Emphanisporites annulatus*
LOWER		*caperatus—emsiensis*		
SIEGENIAN				*Dibolisporites cf. gibberosus*
	Zosterophyllum			*Emphanisporites micrornatus*
GEDINNIAN	Assemblage—zone II	*micrornatus—proteus*		*Streelispora newportensis*
PRIDOLIAN	*Cooksonia* Assemblage—zone I	chulus—?vermiculata		Synorisporites tripapillatus

unsatisfactory (Petrosian 1968, Senkewich 1968, Krausel 1937, Leclerq 1940), Banks suggested that this was a result of the lack of precision of palaeobotonists when dating localities and the lack of correlation with international standards even when the locality is well known. A futher difficulty was in the correlation of the plant horizons because of the terrestrial or continental nature of most of the productive deposits. This results in the preservation of lenses lacking critical invertebrate fossils and being randomly scattered as in the case of Devonian lakes and ponds giving a general lack of lateral continuity, even when large areas are quarried, failure to arrange detailed mapping prevents precise location of the fossiliferous lenses.

Banks suggested solution to this problem was the use of palynological techniques for dating sediments and microfloral biostratigraphy has been proposed with some success for Canada (McGregor 1971), the Northern Hemisphere (Richardson 1974) and the Old Red Continent (Richardson and McGregor 1986) when attempts were made to correlate marine and continental sediments. The fragmentary nature of the majority of plant fossils and the variability of preservation (Beck 1970) has always led to the accumulation of form genera, this presents major problems to biostratigraphy. Banks (1980) therefore suggested the use of those taxa that are well documented, widely dispersed, with a moderately well known stratigraphical position and those taxa that are familiar to the worker. As a result of this the majority of his localities are grouped within the

Northern Hemisphere.

Morphologial features have been used by many workers (Banks 1980, Chaloner 1970, Chaloner and Sheerin, 1979). In particular Chaloner and Sheerin (1979) used the first appearances of anatomical and morphological characteristics plotted against the stratigraphy. While Banks (1980) favoured the use of such characters as the presence of seeds since they are found only in the Famennian stage they can provide an indication of Famennian, or later, strata. Similarly the presence of secondary xylem, lateral or adaxial sporangia have all been used to suggest the oldest assemblage zone to which they can be assigned.

Attempts at correlation between the plant megafossils and microfossils have recently centred on linking in situ and sporae dispersae (Allen 1980, Gensel 1980). Allen records sixty in situ spores from the Late Silurian and Early Devonian megaplant specimens. Most are poorly illustrated and not very well described, he emphasised that a number of spores in the Devonian were common and easily identifiable and have yet to be found in situ. Gensel (1980) suggests that by looking at the in situ spores it might be possible to explain the sporae dispersae. Thus enabling spore data to be used to interpret the floras of areas where megafossils are not preserved, as well as illucidating the evolutionary steps to heterospory.

Two classic floras remain problematical and refuse to fit in to any assemblage zone, in that faunal evidence (Garrat 1978, 1984, Garrat et al 1984) suggests an older age than the plants do. The occurrence of a plant assemblage from

Victoria Australia, containing the presumed lycopod Baragwanathia is regarded as Ludlowvian on the basis of Graptolites (Garrat et al 1984) rather than Early Devonian as the only other plant assemblage containing Baragwanathia would suggest. If correctly dated as is now being accepted, the presence of a fairly complex lycopod in the Late Silurian alters the ideas of plant phylogenies, supporting an earlier, separate origin of lycopods and altering the ideas on plant evolution in the Southern Hemisphere relative to what was occuring in the Northern Hemisphere.

Similar reports of lycopophytes and Psilophyton from presumed Lower Devonian sediments (Klitzsch et al 1973) from Aracus, Lybia which resembles forms found in Middle and Upper Devonian sediments elsewhere would, if correctly dated, have a profound impact on present evolutionary trends and biogeographic thought. The Lybian fossils are however poorly preserved and Banks (1980) uses this fact to suggest that there is not satisfactory evidence to assign the decorticated axes to a genus, similarly the specimens of Psilophyton are thought to show little of generic value. He therefore suggests that the axes may represent decorticated axes of Middle to Lower Devonian age. Banks (1980) thus declines to include these two formations in his flora until their age can be decided upon.

Text-Figure 1 Middle Devonian plant localities of the world.

Legend to Text Figure 1

1. Teichart and Schopf 1958
2. Banks 1966
3. Schopf 1964
4. Frenguelli 1954
5. Seward and Walton 1923
6. Hoeg 1942 Schweitzer 1968
7. Lang 1926 1927
8. Stockmans 1968 Leclercq 1939 1940
9. Krausel and Weyland 1926 1929 1948
10. Obrhel 1968
11. Reymanovna and Zdebska in Edwards 1973
12. Hoeg 1931 1935
13. Isenko in Petrosian 1968
14. Iurina 1969 Senkevich in Petrosian 1968
15. Petrosian 1968
16. Petrosian 1968
17. Lexique Stratigraphique 1963
18. Termier and Termier 1950
19. Plustead 1967
20. Harris 1929

e= Eifelian
g= Givetian

MIDDLE DEVONIAN PLANT LOCALITIES (see text fig. 1)

Few Eifelian floras are known except in the Soviet Union these frequently contain Lower Devonian elements such as Drepanophycus Taenocrada and Psilophyton (Gensel and Forbes 1984). In Siberia a flora originally considered by Ananiev to be Lower Devonian was later classified by Petrosian (1968) as Eifelian because of the presence of a small number of Middle Devonian elements. The Eifelian of this and other Soviet localities contains Protolepidodendron scharianum together with other species of Calamophyton, Aneurophyton and possibly Hyenia. These are also found in the Upper Eifelian of Germany and Scotland together with Protopteridium and Pseudosporochnus, Edwards (1973) considers these to be some of the commonest elements of Late Givetian floras.

By contrast many Givetian floras are known, Gensel and Forbes (1984) suggest that the well known floras of Belgium and Germany should be considered to be representative of the Givetian, they contain the following genera; Drepanophycus, Leclerqia (and former species of Protolepidodendron), Estinnophyton (and former species of Protolepidodendron), Cladoxylon, Hyenia, Calamophyton, Pseudosporochnus, Rellimia, Aneurophyton, Taeniocrada and certain vegetative, smooth and spiny axes referred to as Psilophyton but with unclear affinities. This plant assemblage they put forwad as a Givetian indicator.

Numerous and widespread localities in the Middle Devonian contain lycopods. With genera such as Protolepidodendron

and Leclerqia from New York State revealing the group to be well established in the Givetian. P. scharianun is only absent from Middle Devonian localities of the Northern Hemisphere from Norway, Spitsbergen and Scotland were the genus is represented by P. karlsteinni. In Protolepidodendron the leaf is forked at or near the tip while in Leclerqia the the leaves divide into five parts in a distinctive manner, unusually for a homosporous plant it bears a ligule. This plant is also widely dispersed geographically and has even been found in the Southern Hemisphere (Fairon-Demaret 1974) and again is only absent from Norway, Spitsbergen and Scotland in the Middle Devonian sediments of the Northern Hemisphere. Kasper and Forbes (1979) found Leclerqia from the Trout Valley in Maine while Kasper (1977) discovered a new species from Campbellton, New Brunswick. Lastly Fairon- Demaret (1980, 1981) identified specimens formerly Protolepidodendron scharianum from Elberfeld, Germany and Rorquiers and Goe Belgium as Leclerqia.

In comparison to this rather limited Lycopod flora the extensively studied flora from New York State (Greirson and Banks 1963) shows a high proportion of Lycopods and provides the best illustration of a Middle Devonian Lycopod flora. An exclusive Lycopod flora also occurs in Kazachstan but contains less well known genera including Blasaria, Betpalaphyton and Lepidodendropsis and occuring with Lower Devonian representatives. In China the flora is again dominated by lycopods. While larger lycopods are found in the United States with Amphidoxodendron, in Spitsbergen with

Protolepidodendropsis and in Kazachstan with Lepidodendropsis.

In the Soviet Union many of the compression fossils represent unique and obscure genera being placed in the Primofilices by Petrosian (1968) but are considered to be Progymnosperms by Banks (1980). By contrast the petrified flora of New York State contains many Coenopterids and Cladoxylaleans not represented by compression material and so have an unknown morphology. In Europe and Russia the most widespread Cladoxyleans are Calamophyton and Pseudosporochnus once again being absent only from Norway Spitsbergen and Scotland. Progymnosperms on the other hand are widespread geographically, a particularly high number are found in the United States, Europe and Western Russia. This is a consequence of the large number of species of Rellimia, confined east of the Atlantic and Aneurophyton and Svalbardia, present on both sides of the Atlantic. Recent collections (Fiend et al 1983) from eastern Greenland suggests another Givetian flora and contain Svalbardia and Pseudosporochnus, the only other occurrence of Svalbardia east of the Atlantic is from New York State (Matten 1981).

The single most widespread sphenopsid in the Middle Devonian is Hyenia represented by H. elegans in Germany and Belgium H. sphenophylloides in Norway, H. banksi in America and H. vogti in Spitsbergen. H. Argentia is found in the Southern Hemisphere. The taxonomic position of Hyenia in the Sphenopsids is not absolute and Gensel and Andrews (1984) consider it to be a Cladoxylalean but do not discount the possibility that it might be a Sphenopsid ancester.

Allen and Dinely (1988) however consider it to be of unknown affinities with little if any relation to the Sphenopsids. Apart from this genus two further species, both of doubtful affinities, Sphenophyllum stylicium and a fructification Eupalaeostachya devonica from the Soviet Union have been found in the Middle Devonian.

The well documented German floras include Lycopods, the Cladoxylopsids, the Progymnosperms and a large number of "flabelliform leaves" placed in the Palaeophyales by Hoeg (1967) and includes Platyphyllum buddei and P. fuelingii, also present is Barrendenia kolderupii, Pectinophyton and Barinophyton, which occurs throughout the Northern Hemisphere.

The Southern Hemisphere has elements in common with the Nothern Hemisphere. The Australian flora in particular includes Protolepidodendron scharianum, a lycophyte, and Schizopodium davidii (Astralocculis davidii), a filicophyte, both found in New York State, Leptophloeum australe which occurs in South Africa at the top of the Givetian along with Dutoitia maraisia and Platyphyllum allerense. The Argentinian flora is characterised by being rich in lycopods, Drepanophycus (Protolepidodendron) exinus, Archaeosigillaria vanuxeni and Haplostigma species. South African and Argentinian plants are similarly inadequately dated and so of questionable accuracy. The remaining elements include Hyenia argentia and Haplostigma irregularis which is found on the Falkland Islands but both are very fragmentary.

From this review it can be concluded that there is

generally little difference in composition between the floras of west and east Laurassia or from north to south during the Middle Devonian. Representatives of both the Lycopsida, the Cladoxylopsida and the Progymnospermopsida are common. While the distinction between Northern and Southern Hemispheres is clearly present in the Middle Devonian but with a high proportion of northern types occurring in Australia.

MIDDLE DEVONIAN PLANTS OF THE ORCADIAN BASIN

Fossil plants of Middle Devonian age from Orkney and Shetland were first discovered among the sandstones of Lerwick and Bressay (Fleming 1811, Tufnell 1853). These were large fossil plant stems named Corduroy plants because of their characteristic longitudinal striations. The stems are usually found as compressions in the channel facaes of fluvitile sandstones and are now believed to be the stems of a larger progymnosperm (Allen and Marshall 1986). Other workers (Hooker 1853, Murchison 1853, 1859) found plant remains thought to belong to the Upper Old Red Sandstone (Upper Devonian). Later Peach and Horne (1879), Tudor (1883) and Geikie (1879) found plants of Psilophyton type in the Walls Sandstone and thus suggested that this formation is of Old Red Sanstone (Devonian) age.

On the Scottish mainland numerous fragments of plant material were discovered, the best of these early collectors being Miller (1841, 1849, 1857). He systematically made collections from Devonian localities around Northern

Scotland, Caithness and Cromaty and made attempts at identification and interpreting their significance. These early collections were reviewed by Salter (1857), he renamed specimens collected by Miller and Peach. In particular he redescribed specimens originally collected by Miller as Lycopodites milleri (This was later changed by Lang (1925) to Thursophyton milleri because it had nothing in common with the Carboniferous plant Lycopodites). After Salter further descriptions were produced by Penhallow (1892) and by Reid and McNair (1891). Penhallow also described a distinct species Lycopodites (Thursophyton) redi, a fertile specimen with globular sporangia 1mm in diameter occuring in the axils of scale like emergences.

The definition of the genus Thursophyton was produced by Nathorst (1915) based on Norwegian material identified with a plant common to Scotland; "plants probably with Psilophyton affinities with a large main axis" and "ramifications dichotomous in the distal axes and pseudomonopodial in the larger axes. Spines in the form of needles widening at the base, absent near the top". Nathorst (1915) regarded the fertile material described by Penhallow (1892) as being doubtful but this description began the association with the early lycopsids such as Asteroxylon even though Kidston and Lang (1925) confirmed that no fertile material had been found.

In the "Contributions to the study of the Old Red Sandstone flora of Scotland" (1925, 1926), Lang laid down the basis for an Orcadian flora. The paper published in 1925 began his examination of the Cromary flora, he

described Thursophyton milleri and several apparently fertile specimens of Hostinella. H. globosa represented by naked axes one specimen having a number of isolated oval bodies in close association which were demonstrated to contain spores. H. pinnata is based on numerous small fragmentary incurved axes which bore sporangia 3mm long and 0.5mm wide, these fragments are now referred to the genus Rellimia (Leclerq and Bonamo 1973). The last specimen was named H. racaemosa found from Stromness, Orkney, it consists of an axis 2mm wide and 14cm long and bears stout lateral branches each 5mm long terminating in an oval body 5-6mm long and 2mm broad, this illustrates the variety of fossil types placed in this genus. Hoeg (1967) transferred this specimen to the genus Dawsonites but it does not seem to fit the concept of this genus either which was erected by Halle (1916b) for fragmentary smooth axes bearing fusiform terminal sporangia not assignable to the genus Psilophyton. The genus Hostinella (Barrande and Stur 1882) itself remains one of no great significance representing specimens with naked dichotomous axes or pseudomonopodial branching with occasional bud like protruberances in the upper angle of the dichotomy. Many species within the genus have been reassigned including Pseudosporochnus (Leclerq and Banks 1959, 1962) and Rellimia (Leclerq and Bonamo 1973), thus the retention of Langs specimens in this genus is unsatisfactory. A futher plant described by Lang (1926) was Protolepidodendron karlsteinni, a herbaceous lycopod but the assignment of the species to this genus is by no means definite.

It was not until 45 years after the initial discoveries that our knowledge of the Orcadian flora was increased. Chaloner (1972) studied some fragmentary fossils from Early Middle Devonian rocks of Fair Isle, giving them the name of Dawsonites roskiliensis, this definition was based upon fragments 7cm long and 1-2 cm broad with sporangia borne terminally or on side branches, in pairs or in clusters. The sporangia, 4mm long and 1mm broad, have a close resembelence to Hedeia (Chaloner 1972, Gensel and Andrews 1984) and again it does not fit easily into the concept of the genus erected by Halle (1916b) as a form genus for fertile material of Psilophyton.

Chaloner described a second new species, Svalbardia scotica, from a Middle Devonian horozion on Fair Isle. The specimens were assigned to a genus established by Hoeg (1942) and now placed in the Progymnospermopsida (Bonamo 1975). Hoeg collected from a locality known as Planterggen in the Mimer valley of Spitsbergen, an Upper Middle Devonian or lowermost Upper Devonian locality. Devonian plants were first discovered here by Nathorst in 1882 and reported by him in 1884. More recently Høeg participated in expeditions (1924, 1928, 1939) to the area, this culminated in The Dowtonian and Devonian Flora of Spitsbergen (1942). In this he described Svalbardia polymorpha as a plant with a main axis at least 1m in height with primary branches bearing "pinnule like organs" which are several times divided to the point of being filiform and bear up to a dozen erect pear shaped sporangia in the middle region of the fertile branches. Chaloner's (1972) description of Svalbardia

scotica shows a plant of similar organisation but with structures interpreted as being flattened deeply divided wedge-shaped laminate ultimate appendages. The "leaves" divide twice in a dichotomous manner to end in four tapering lobes.

Høeg also published a series of papers describing the flora of Western Norway (1931, 1935, 1944) together with some lesser known species he found Pectinophyton norvegicum, Arthostigma species, Dawsonites ellenae, Thursophyton milleri, Hyenia ramosa and Hyenia sphenophylloides. Hyenia representing one of the most characteristic Middle Devonian genera is immediately suggestive of Banks (1980) stratigraphic assemblage zone IV representative of the Eifelian, while the presence of Svalbardia from Spitsbergen and Shetland correlate to Banks zone V representative of the Givetian stage.

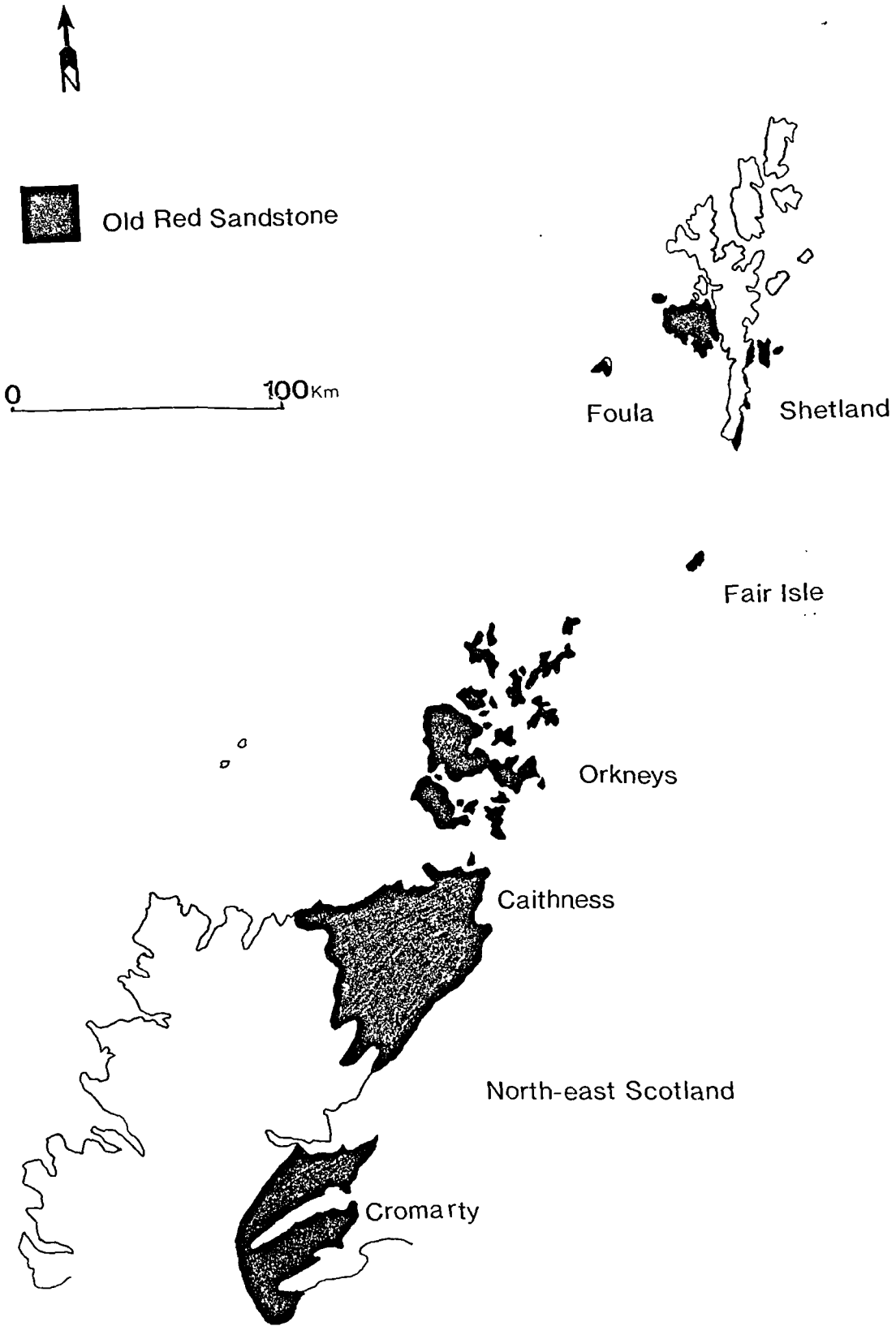
The most recent work of Allen and Marshall (1986) provides numerous localities of Svalbardia scotica from Fair Isle and East Shetland showing fertile material similar to that of S. polymorpha. The similarity of S. scotica, S. polymorpha and other Svalbardia species has been noted by many authors (Allen and Marshall 1986, Gensel and Andrews 1984, Hoeg 1942) and the almost identical nature of the fructifications within the genus and to that of Archaeopteris has long been known (Høeg 1942). Allen and Marshall (1986) saw no reason for separating the genus from Archaeopteris but retained the name Svalbardia until a thorough review of the species was carried out. They also emphasised the morphologial similarites between larger stems of Svalbardia and the

ribbed axes of the Corduroy plant. The affinities of this plant still remain unclear although Allen and Marshall (1986) suggested that it may represent the main axes of Svalbardia in a similar way as Callixylon represents the main stem of Archaeopteris.

CHAPTER 2.

Text-Figure 2

Map showing position of north-east Scotland Orkney and Shetland



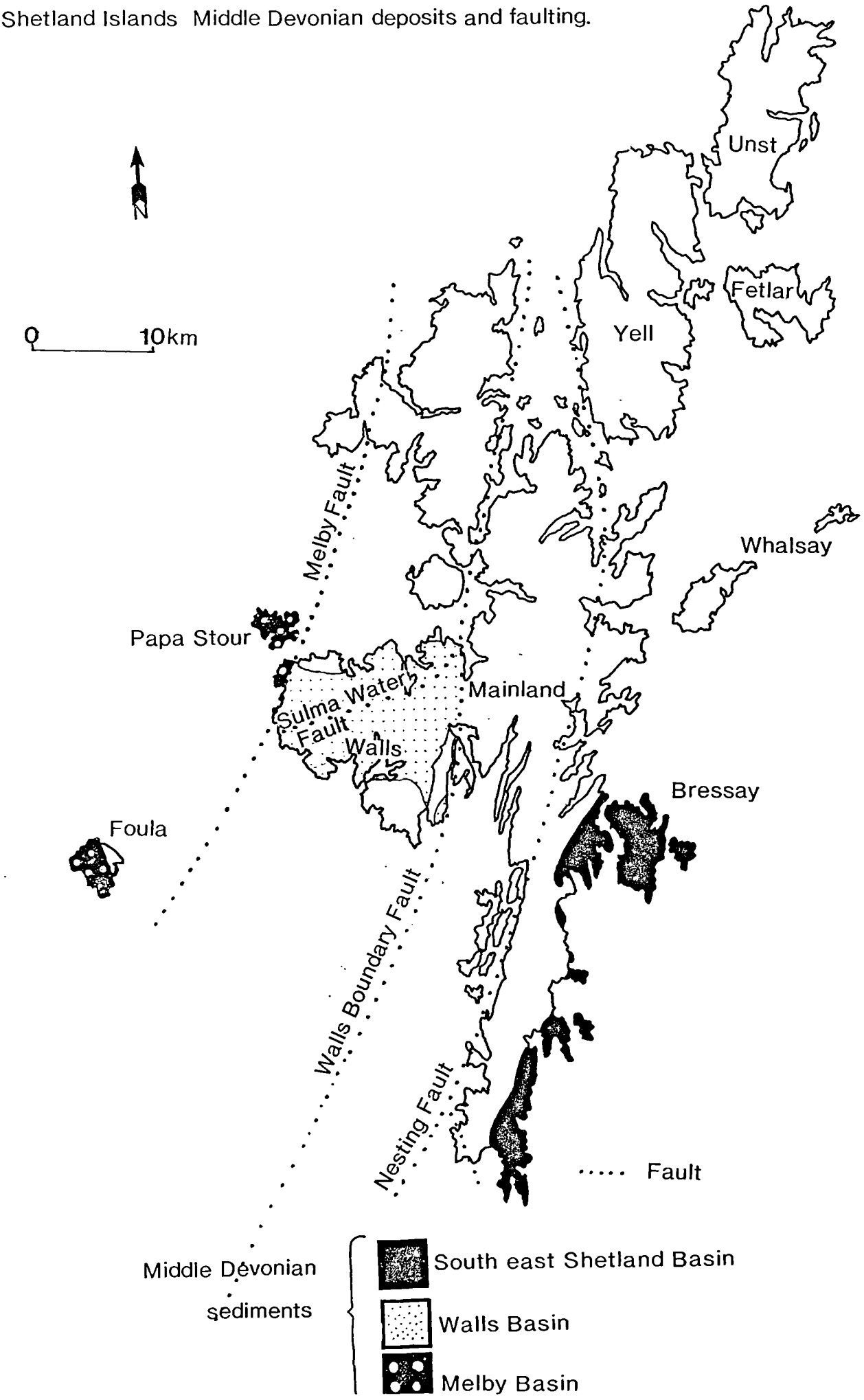
GEOLOGY OF THE ORCADIAN BASIN AND THE SURROUNDING AREA (see text fig.2).

Geikie 1879 recognised that the sandstones of South Ronaldsay in the Orkneys were the lateral equivalents of similar rocks near John O Groats and thus concluded that the Old Red Sandstone of Orkney, Caithness and Cromarty were laid down in the same intermontane basin which he termed "lake Orcadie" which has become known as the Orcadian basin. Rayner (1967) suggested that the lake extended from the northern part of the Great Glen Fault to Shetland a distance of over 240km. This veiw is not favoured by later workers and recent ideas (Allen and Marshall 1981) suggest that Shetland was connected to the basin possibly only by southward flowing streams.

Many remnants of this region are now separated by the North Sea and North Atlantic. In such areas as Greenland and Norway, deposits can be found that represent sediments laid down on the fringes of this region. The Orcadian basin is particularly well known for its thick fish-bearing Middle Old Red Sandstone, much of which is grey and fine grained. The idea that the Old Red Sandstones of Orkney, Shetland Caithness and Cromarty were connected by the Orcadian lake

Text-Figure 3

Shetland Islands Middle Devonian deposits and faulting.

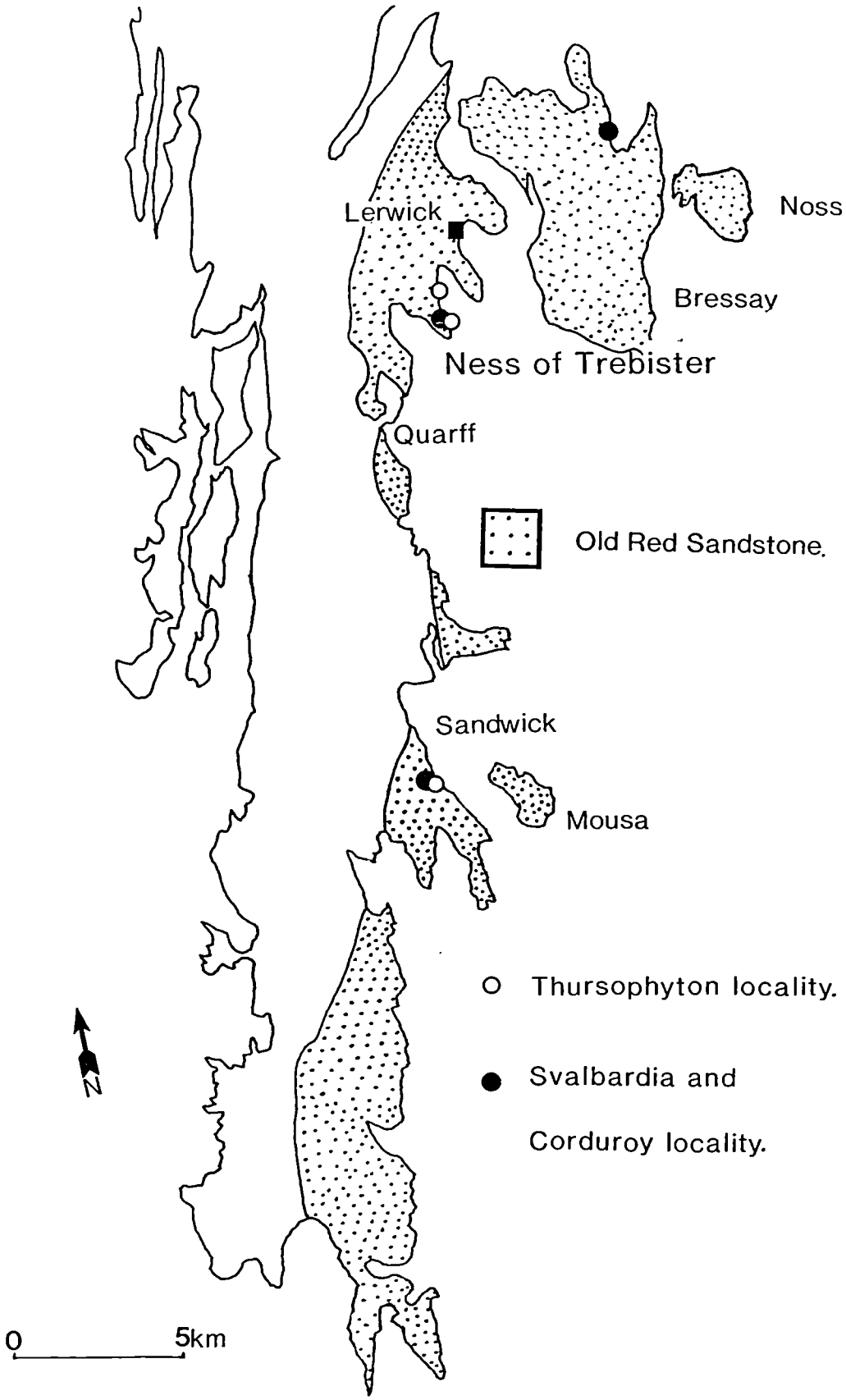


is suggested by the incursion of fish faunas and in particular the Melby fish beds. There is some lithological similarity in the sedimentary formations but the Caithness flagstones were seen by Rayner (1967) to be greatly different and he indicates that no clear palaeogeographic reconstruction can be extended to Shetland.

SHETLAND GEOLOGY

The Devonian rocks of Shetland were deposited in three distinct basins, the Melby, the Walls and the south east Shetland basins (see text fig. 3). Presently they are separated by north-south trending transcurrent faults. The present-day juxtaposition of the three basins has been produced by the lateral movement along the Walls Boundry Fault, which is a northerly extension of the Great Glen Fault (Flinn 1961, 1967), or a splay movement from the latter (Bott and Watts 1970). This point still remains controversial as does the timing of the movements along the fault (Smith 1977). There is general agreement that a post Devonian dextral shift of between 30 and 60km occurred on the Great Glen Fault and Walls Boundary Fault.

West of the Melby Fault the Devonian sediments contain fish bearing siltstones which correlate with the Achanarras Limestone of Caithness and the Sandwick fish bed of Orkney (Mykura 1976). East of the Melby Fault are the folded 1000m thick Sandness and Walls formations (Mykura 1976) and to the east of the Walls Boundry Fault the South East Shetland basin.



Text-Figure 4 Middle Devonian outcrop in south-east Shetland locality map.

The south east Shetland Basin.

This basin in Late Givetian times was a north north-west to south south- east elongated basin, possibly a defunct rift valley, which contained small lakes connected by major rivers flowing to the south south east. The schematic palaeogeography shows a lake shoreline in the east, present at times of fluvial and lacustrine dominance (Allen and Marshall 1981) the western edge of which is now exposed onshore. A reconstruction of the relative positions of the various Devonian basins (Donovan et al 1976) shows that South East Shetland was situated north of its present position close to the western Norwegian and eastern Greenland basins.

It appears that the Devonian sediments were deposited in a wide variety of environments, such as alluvial fan, aeolian and lacustrine (Allen and Marshall 1981). Mykura (1976) visualised two depositional systems separated by a palaeohill of metamorphic strata in the Quaff-Fladdibister region (see text fig. 4). He also suggested that the palaeohill separated a "deep south-east flowing river valley in the north from a more open river valley and later alluvial plain in the south".

The age of the sediments of south east Shetland comes from palynological and fish evidence. As a result of thermal destruction accompanying the formation of the steep belt (Mykura 1972) the preservation of miospores in the Shetlnds is generally poor (Marshall 1980) although abundant but stratigraphically restricted miospore assemblages have been

recovered (Allen and Marshall 1981, Marshall 1988, Marshall and Allen 1982, Marshall et al 1980). These have been useful in ageing the sequence as well as supporting some of the sedimentological conclusions. Age interpretations based on miospores are hampered by a lack of a miospore stratigraphy from possible correlatives on the mainland of Scotland. Also there are no faunally controlled assemblages available from above the Eday flags of Orkney (Richardson 1965) which is part of the Givetian Eday Group and the equivalent of the upper part of the John O Groats Sandstone of Caithness. This means that generally local comparisions are not available.

The presence of large camerate miospores (Richardson 1965) such as Grandispora spp. and Rhabdosporites langii together with Geminospora spp., Aneurospora greggsii, Ancyrospora langii and other elements typical of the Frasnian indicates an age for the sequence being younger than the Givetian close to the boundary with the Frasnian (Richardson 1974, McGregor 1979, Lodoziak and Streel 1980). The absence of Geminospora from Orkney and Caithness has been attributed to the Orkney and Caithness beds being deposited before the parent plant and therefore miospores of the Geminospora type migrated north westwards in the late Givetian (Marshall and Allen 1982).

Fish faunas disagree with the stratigraphical placing of the south-east Shetland Basin at the Givetian Frasnian boundary (except for parts of Bressay). Donovan et al (1974) places the sequence in Givetian fish zone 7 based on the presence of Microbrachius and Tristichopterus (Mykura

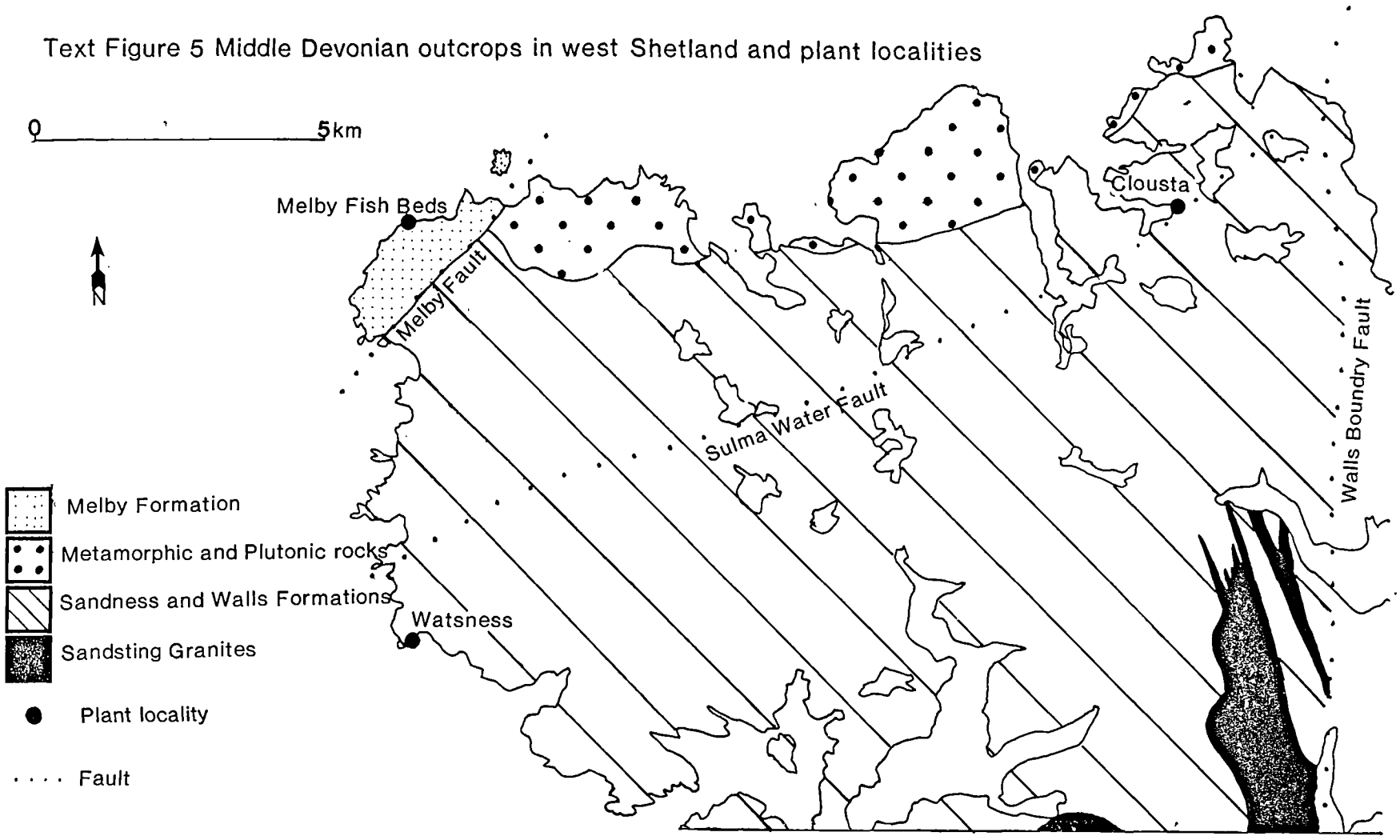
1976, Westoll 1937), which equates to the Eday Group and the John O Groats Sandstone. This discrepancy has been explained by the relative isolation of the basin and its tenuous lacustrine and fluviatile links with Caithness and Orkney and the presence of opposing currents flowing from the area (Allen and Marshall 1981). Donovan (1980) also sites the possibility that lower lake levels during this period would also restrict the flow of new fish into the area. Miospores however would not be restricted by such factors and they may have been aided by wind dispersal before the parent plant arrived in the area, or the plant may have had a distribution restricted to the upland areas and so only the miospores would be preserved in the fossil record.

Scottish equivalents on miospore evidence are reasonably good. For example the Upper Old Red Sandstone of Nairn and the Boghole on the Moray Firth (Westoll 1979). The stratigraphic link is strengthened by inland equivalents in the Baltic area from which miospores have been described (Ozolin'a 1963). Here the Amata and Gauya beds show a similar form of miospore assemblage to south east Shetland.

The Melby Basin

This basin west of the Melby Fault includes Papa Stour, the Melby Fish Beds (see text fig. 5) and Foula (see text fig. 5). The sediments appear to be predominately of fluvial origin with a dominant current direction from the west or west north-west, which changes in the upper part of the sequence to a predominately east north-east direction.

Text Figure 5 Middle Devonian outcrops in west Shetland and plant localities



This change is considered to have occurred after volcanic activity altered the topographical and drainage patterns (Mykura and Phemister 1976).

The rocks of the Melby formation consist of buff and red sandstones, pebbly sandstones and sandy siltstones intercalated at the top with two thick flows of silicified rhyolite or ignimbrite. Near the base of the exposed sequence are the Melby Fish Beds these are two beds of pale grey siltstone and shale with bands and nodules rich in carbonate. They contain both plants and fish (Mykura 1976). The fish includes Cheriracanthus species, Coccosteus cuspidatus, Dipterus valenciennesi and Glyptolepis c.f. leptopterus, Gyroptychius agassizi, Homostius milleri, Mesacanthus species and Pterichthyodes species. This assemblage is similar to that of the Sandwick Fish Beds of Orkney and they have been confidently correlated (Mykura and Phemister 1976). The lower part of the Melby Formation may thus be statigraphically equivalent to the Stromness Flags, and therefore ranges from the Upper Eifelian to the Lower Givetian. Fletcher (1975, 1976) studied the megaspores of the Melby Formation and from the spore assemblage concluded that it corresponded to other Middle Devonian assemblages, particularly those of Scotland and Spitsbergen. This endorses the view that the Melby Formation is of Eifelian-Givetian age and correlates with the Achanarras and Sandwick Fish Beds of the Orcadian Basin deposits.

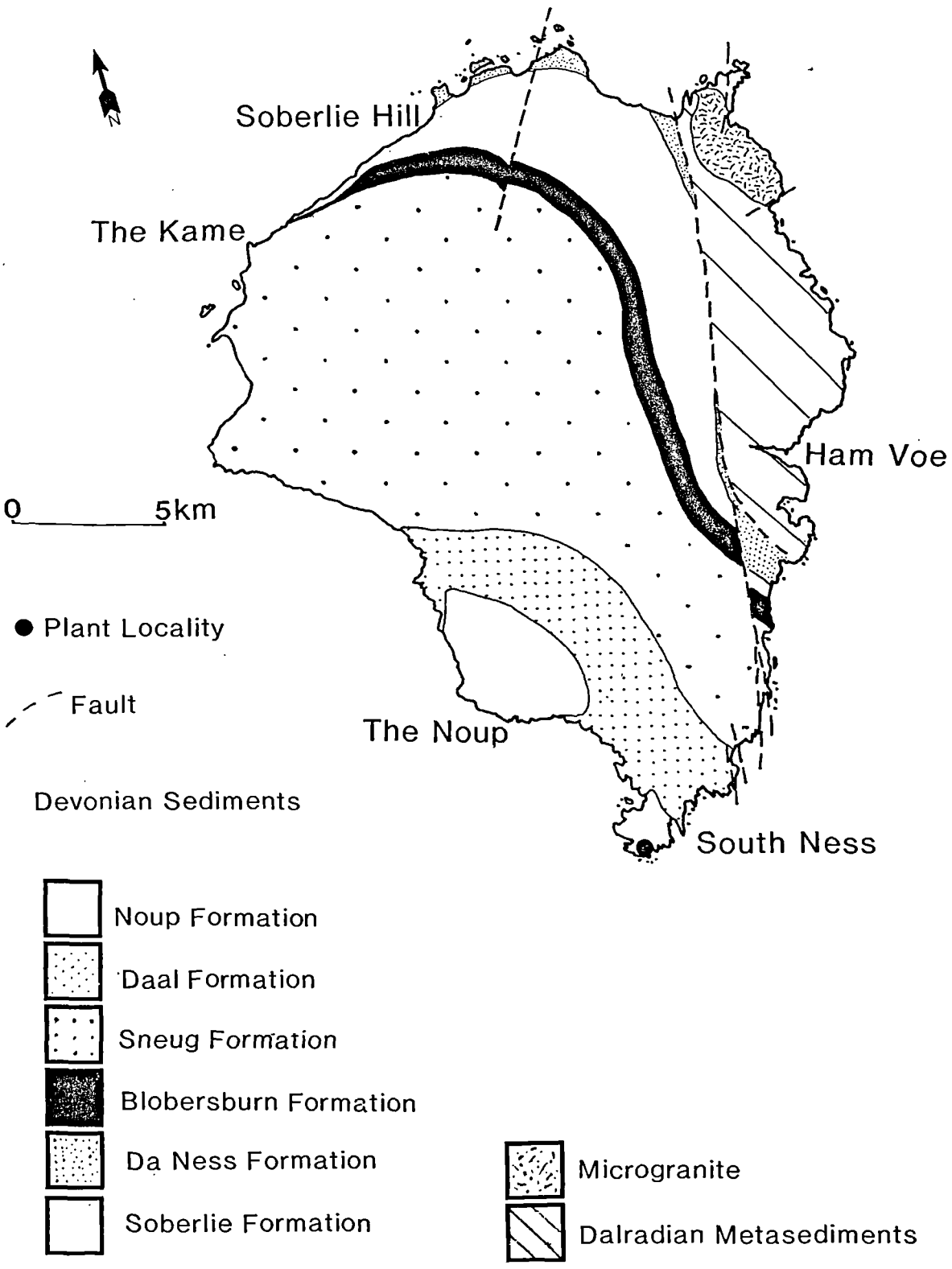
The sedimentary structures suggest that the deposits of the Melby Formation were laid down in the channels of straight or braided rivers (Allen 1965) flowing through an

alluvial plain (Mykura and Phemister 1976). The formation also contains two fish beds which show some resemblances to the lacustrine phases of the Orkney (Fannin 1970) and Caithness (Crampton and Caruthers 1914). Flagstone cycles which were deposited in shallow extensive lakes. Fannin (1970) has shown that the lacustrine beds of the Sandwick Fish Bed cycles are very much thicker than the equivalent beds within the Stromness bed cycles of Orkney and that in Western Orkney the fish bed lakes may at one stage have had a depth of 50m. The Sandwick Fish Beds therefore represent a major transgression, and it is just possible that one of the Melby Fish Beds was laid down near the north-western margin of the flat depositional basin which towards its centre contained the Orkney-Caithness lakes (Mykura and Phemister 1976).

The Devonian succession on Papa Stour has recently been found to contain miospores and fish fossils in fine grained dark shales and siltstones within the sandstones which are situated between lava flows (Marshall 1988). The age range of the miospores is Middle Eifelian to Early Givetian probably more specifically Late Eifelian and from a position close to the Achanarras horizon. This allows further correlation between the Melby Basin and that of the Upper Stromness flags of Orkney, and indicating a close similarity to other Orcadian Basin sediments, supporting the view that sediments west of the Melby Fault have a close affinity with the Orkney and Caithness successions (Marshall 1980, Mykura and Phemister 1976).

The island of Foula (see text fig. 6) provides the largest

Text Figure 6 Devonian outcrop and locality map from Foula



formation within the Melby Basin. It comprises over 1600m of Middle Devonian clastic sediments (Mykura and Phemister 1976) lying uncomformably on, and faulted against, a narrow strip of "Dalradian" metasediments (Mykura 1976, Wilson 1934). The sediments thin considerably towards the south-east and were deposited predominatly in sandy rivers infilling a subsiding north-east south-west half graben. Subsidence was related to extensional reactivation of major Caledonian thrusts (Marshall pers. comm. 1987). Sediments were initially transported from a local source in the north-east, these were rapidly swamped by the first of three major episodes of fluviatile sedimentation, with transport now coming from the direction of the major basin fault in the north-west and diverting along the basin axis to the south-west and south. The three major depositional episodes were separated by periods of reduced subsidence and sedimentation, during one of which up to 85m of organic rich lake sediments accumulated (Marshall pers. comm. 1987).

Miospore assemblages (Donovan et al 1978, Fletcher 1976, Mykura 1976) show species such as Rhabdosporities langii, Auroraspora spp., Ancyrospora ancyrea, Cristatisporities mediconus, Grandispora protea as well as other common species in the assemblage that are well known from the Middle Eifelian to Givetian. The formation thus covers the interval occupied by the lacustrine Achanarras horizon and the only lacustrine unit on Foula, may be equivalent to the Achanarras horizon occurring at about the correct position in the sequence and with a similar palynology. If a single lacustrine event penetrated as far west as Foula then it is

most likely to be the Achanarras since it is the only significant basinwide event (Marshall pers. comm. 1987). It has already been shown to occur in marginal deposits as far south as the Moray Firth and as far north as Melby (Mykura 1976, Mykura and Phemister 1976, Westoll 1979).

The walls Basin.

The greater part of the Walls Basin (see text fig. 5) is composed of the Walls Sandstone (Finlay 1930), which is of probable Middle Devonian age and consists of two major stratigraphic units, separated by the east-north-east trending Sulma Water Fault (Mykura 1976). The lower unit, the Sandness Formation, lies to the north of the fault; its thickness ranges from 1350-3000m. The lower part of the formation consists of sandstones and conglomerates derived from a north-easterly source (Mykura and Phemister 1976). There is a decrease in the overall grain size and in the proportion of conglomerate from north-east to south-west along the strike and Mykura (1976) after recording the sedimentary structures suggests that the sediments in the north-east were laid down in alluvial fans and by braided rivers. Those in the south-east may have been formed in flood plains of meandering rivers. Plant remains in the sediments interbedded with the Clousta volcanic rocks appear to be of Lower or Middle Devonian age (Mykura 1976).

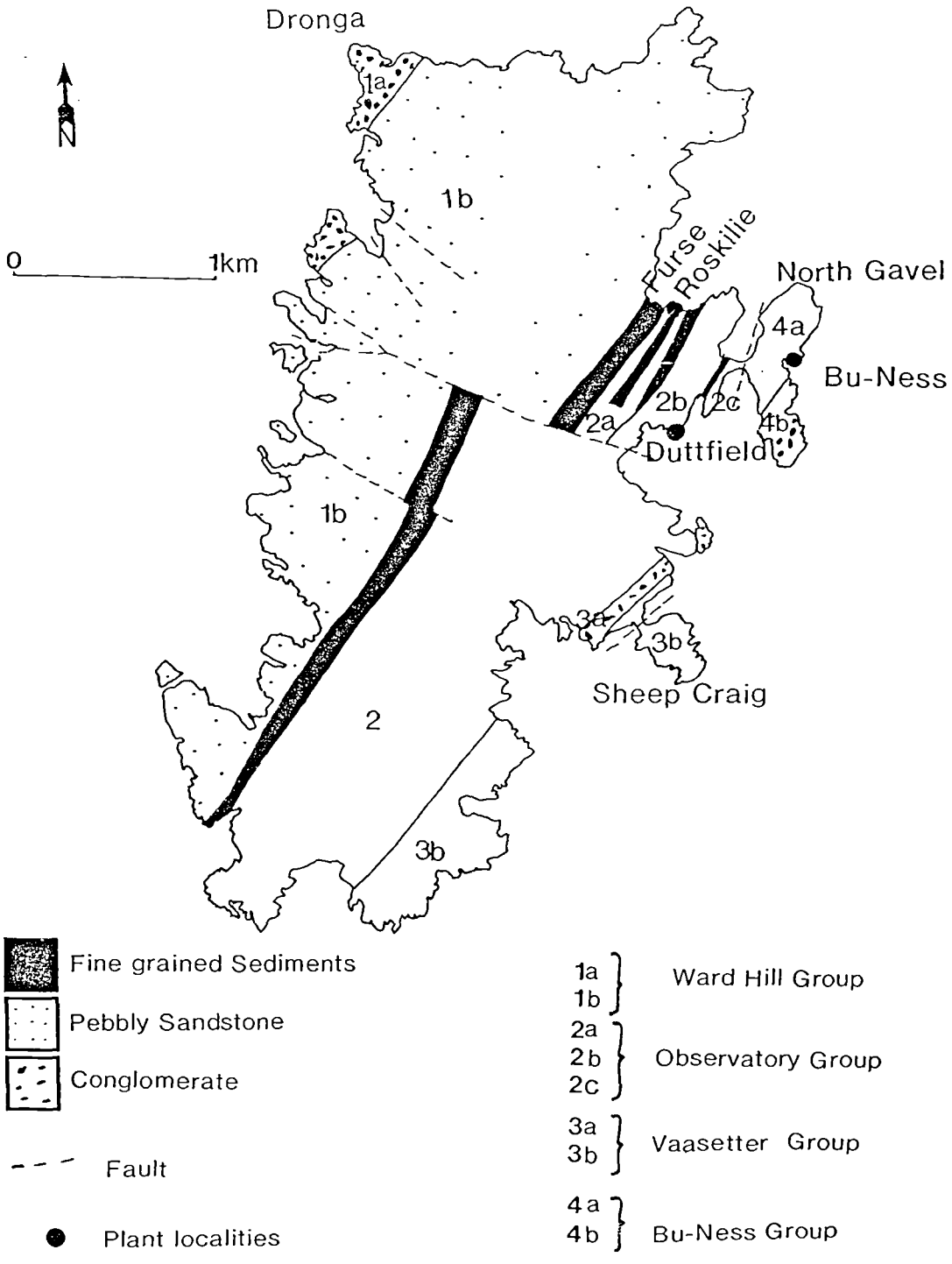
The upper unit termed the Walls Formation is south of the Sulma Water Fault and consists of 9000m of highly folded, generally dark grey, fine grained evenly bedded sandstone. The mode of deposition of these beds is not yet certain

(Mykura 1976) but many of the deposits are calcareous and some display characteristics found in the lacustrine flagstone deposits of Orkney (Fannin 1970) and Caithness (Crampton and Caruthers 1914). The absence of typical diagnostic sedimentary structures suggests that they may have been laid down in a fairly deep and extensive lake.

Poorly preserved fish remains determined by Miles (Mykura 1976) as being Cheiracanthus species, Crossopterigian and Dipnoan scales, of Acanthodian affinities and of a type associated with a Middle Devonian age. The miospore assemblage found in typical *Orcadian basin sediments by* Marshall (pers. comm. 1989) suggests an assemblage which contrasts with the Middle to Late Eifelian found in the Melby Basin. This is mainly because of a diagnostic Givetian miospore (Marshall 1988) Geminospora lemurata, together with other characteristically Givetian species. These include Ancyrospora langii, Cristatisporities triangulatus. All these species appear from the Early Givetian or younger strata and suggest an age similar to those of the South East Shetland and Fair Isle Basins.

The small Devonian outcrop of Fair Isle (see text fig. 7) lying to the east of the Walls Boundary Fault (Mykura 1972a, Mykura and Young 1969) has been considered to belong to the same sedimentary basin as the Walls Sandstone (Donovan et al 1976, Mykura 1976) and movements along the fault have placed it in its present position (Mykura 1975). Fair Isle is composed of at least 2700m of sediments of Middle Devonian age, which Mykura (1972) divided into four lithostratigraphic groups, the Bu-Ness Group, the

Text Figure 7 Middle Devonian outcrop and locality map of Fair Isle

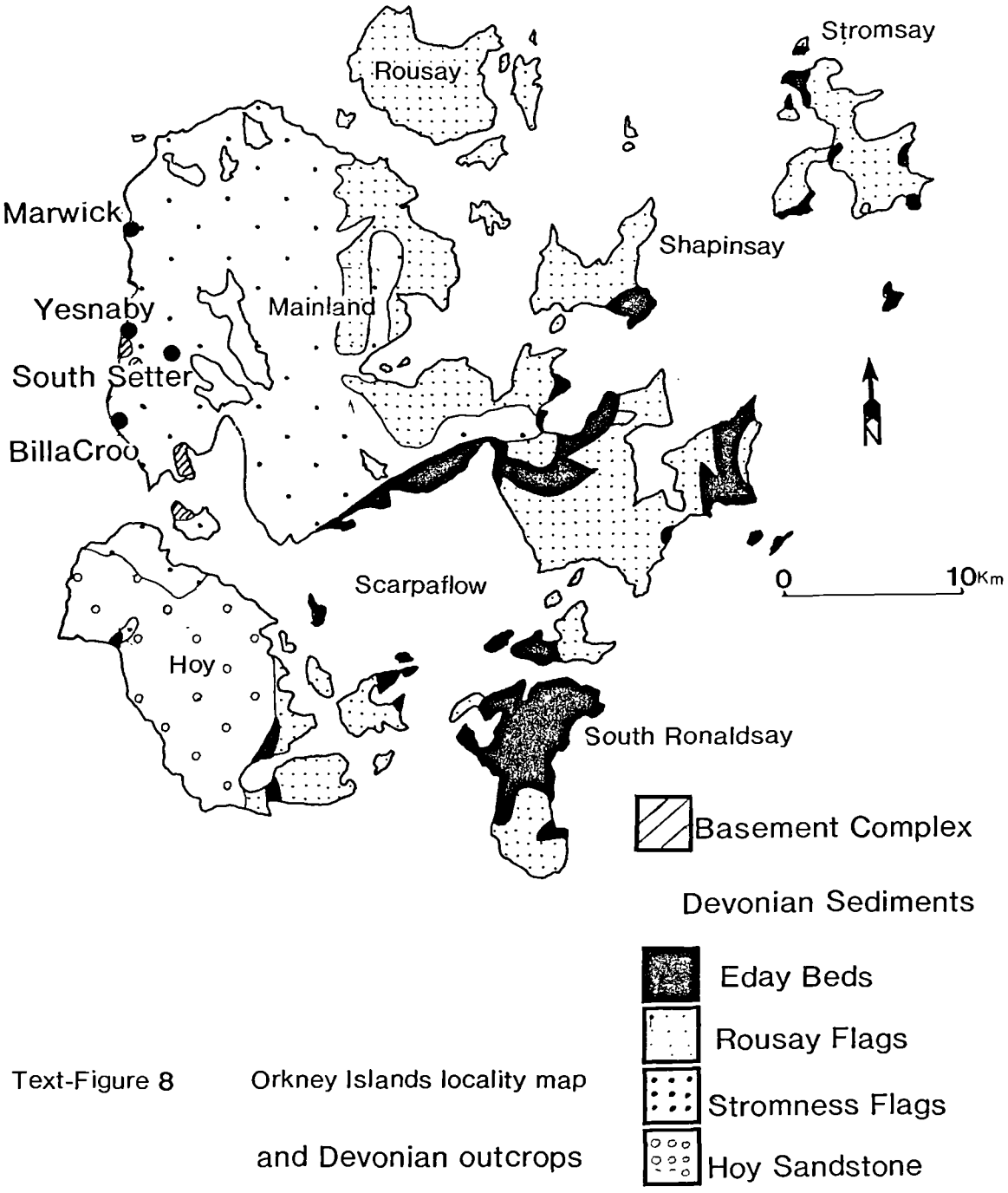


Observatory Group, the Ward Hill Group and the Vaasetter Group. The palaeoindicators suggest that the sediments were derived from a granite source carried by swift flowing currents moving in an easterly to north easterly direction. Pebbly sandstones and conglomerates present in all four groups were deposited by braided rivers in alluvial fans close to the western edge of a lake basin. The fine grained dolomitic beds found in the lower Observatory and Ward Hill Groups were probably laid down during periods of lake water encroachment. The rhythmic sequences of the upper Bu-Ness Group, or the shale and massive sandstone of the Observatory Group may be deposits from a river or rivers meandering over an alluvial plain (Mykura 1972, 1976). The shale units may represent lacustrine deposits with the massive sandstones laid down as a lake margin beach deposit (Austin in Allen and Marshall 1986).

Generally, Mykura (1972) believed that the rivers deposited their load in alluvial fans close to the margin of the lake or lakes which he suggested lay to the east of the area of deposition. The level of the lake fluctuated so that lacustrine beds were intercallated with alluvial fan or deltaic deposits. At certain stages the Fair Isle was well within the lake. The climate appears temperate and the inflow into the lake continuous. The lake came to an end after a period of uplift in the source area and a fluvial regime was re-imposed. Both the Observatory Group and the Bu-Ness Group have yeilded plant remains (Chaloner 1972) those from the Observatory Group could be of Lower Devonian age but the Bu-Ness fossils, which include Svalbardia

scotica suggest a Middle Devonian age. The animal fossils represented by Dipnoan scales, an Arthrodire plate and the brachiopod Asmussia (Mykura 1976) agree with this age assessment.

Studies of miospores from Fair Isle (Marshall and Allen 1982) give a Givetian age for the sediments. Marshall and Allen suggest that the best fit for the asemblages of the youngest Bu-Ness sequence is within the Givetian and Frasnian stages. In particular the diagnostic presence of Geminospora spp. presumed, to come from a local input, because of the presence of Svalbardia, a genus shown to contain the in situ spores of Geminospora (Allen 1980). This spore being totally absent from the Orcadian Basin's (Richardson 1969) lacustrine and fluvitile deposits. The spore sequences described by Richardson (1965) for the Orcadian Basin have the closest resemblance to palynofloras from the Eday beds. This supports the suggestion that a time difference exists between deposition of the Orcadian and Fair Isle deposits (Marshall and Allen 1982, Marshall 1988).



Text-Figure 8 Orkney Islands locality map and Devonian outcrops

THE OLD RED SANDSTONE OF ORKNEY

Orkney consists almost entirely of sedimentary rocks with subordinate lavas and tuffs of Middle Devonian age (see text fig. 8). The sediments fall naturally into two groups. The lower group comprising the Stromness Flags and the Rousay Flags made up of rhythmic sequences of thinly bedded and in part laminated grey and black carbonate rich siltstones and silty mudstones, alternating with generally thin beds of fine grained sandstone or sandy siltstone. The flags have yielded well preserved fossil fish (Miller 1849) and the Stromness Flags in particular contain the Sandwick Fish Beds, considered to be the equivalent of the Achanarras limestone of Caithness (Agassiz 1934).

The upper group, the Eday Beds, comprises the Lower, Middle and Upper Eday Sandstone, which are three thick sequences of yellow and red sandstones with pebbly lenses. These are separated respectively by the Eday Flags and Eday Marls. Beds ascribed to the Upper Devonian are confined to Hoy, although these may in fact prove to be Upper Middle Devonian age (Marshall Pers. Comm.).

The Stromness and Rousay Flags.

The Stromness Flags have been studied in detail by Fannin (1970) who showed that the flags could be divided into a succession of well defined rhythmic units or cycles. The Stromness Beds are made up of over 50 cycles which are thought to have formed by the fluctuations in the level of a single large lake in the Orkney-Caithness region (Mykura

1976). The cycles are similar to those described in the Caithness flagstone formation by Crompton and Caruthers (1914). It is believed that the Orcadian Basin at this time was a rapidly shrinking, and tectonically controlled, and the rhythmic sedimentation was regulated by tectonic and climate changes (Mykura 1976). By far the largest cycle is that containing the Sandwick Fish Bed, this cycle contains up to 55m of lacustrine sediments which have been correlated with the Achanarras and Niandt Fish Beds of Caithness and the Melby Fish Beds of Shetland (Miles and Westoll 1963). It represents a period when the lake was deeper and more extensive than at other times during the deposition of the Stromness Flags, the water depth may have been up to 50m.

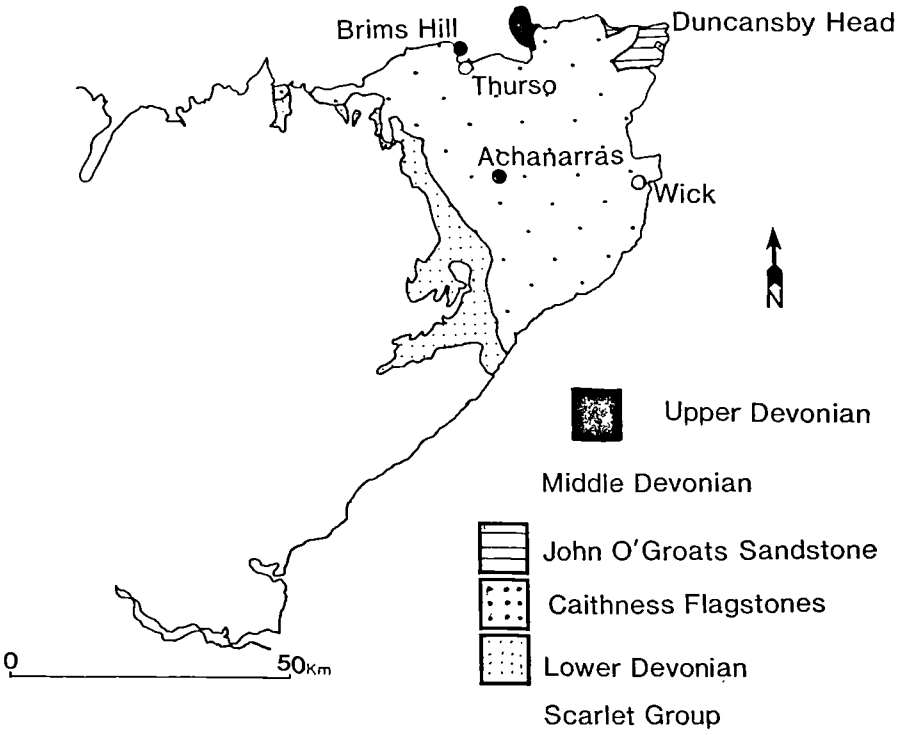
The Lower Stromness Flags are of Late Eifelian age and the beds above the Sandwick Fish are Early Givetian (Westoll 1951, Miles and Westoll 1963) based on the presence of fish remains. Large plant fragments are rare and poorly preserved the principle genera that have been recognised are Hostinella, Thursophyton and Protopteridium (Lang 1925). These however can not be used for accurate dating but do suggest a Middle Devonian age. Spores are abundant and provide a reliable source for dating. Richardson (1965) and Fannin (1970) recorded a large number of species, which have now been placed in spore zone 12 (Richardson and McGregor 1986), characterised by Densosporities devonicus and Grandispora naumovii. This dates the Stromness Group as Middle Eifelian to Early Givetian in age.

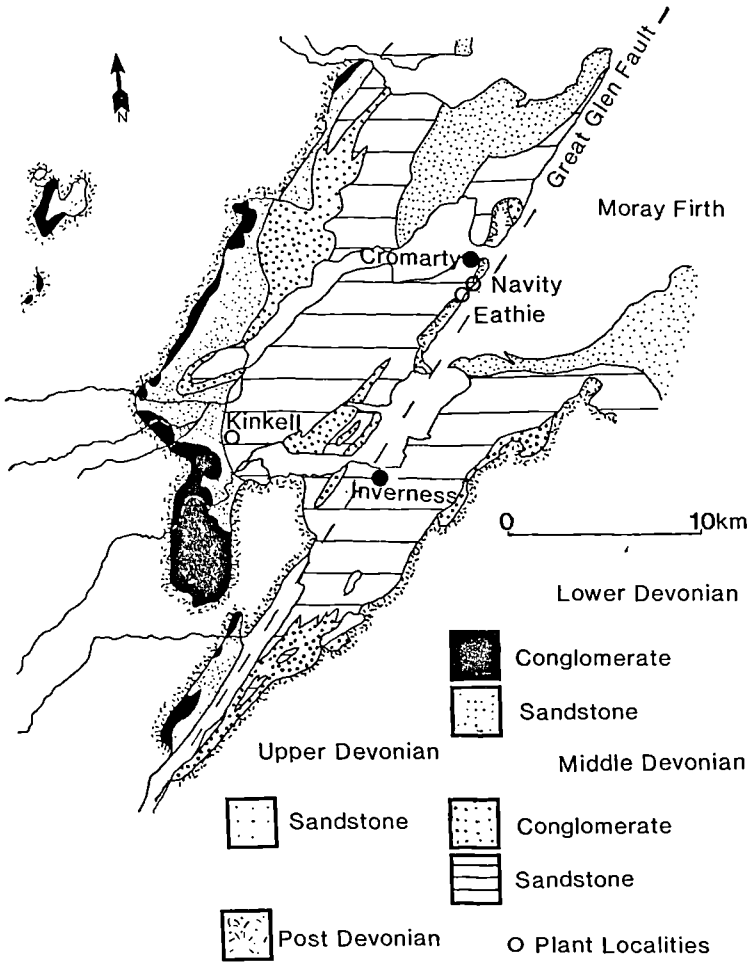
The Rousay Flags consist of 1500m of rhythmically bedded deposits, fine grained "flagstones" separated from the

underlying Stromness Flags by the presence of a less abundant fauna (Flett 1889) containing two distinct species of fish Thursius pholidotus and Millerosteus minor which together with the crustacean Estheria are unknown in the Stromness Flags. The Rousay Flags form the greater part of the northern Orkney islands and are believed to be the stratigraphical equivalents of the Mey and Ham-Scarfskerry groups of the Caithness Middle Old Red Sandstone succession (Donovan et al 1974) and have been dated as Givetian (Mykura 1976). Plant remains are even more fragmentary and poorly preserved than in the Stromness Flags. only "fossil wood", Thursophyton and Hostinella have been recognised (Mykura 1976).

The Eday Beds.

The thickness of the Eday beds exceeds 1000m. The lower half may be the equivalent of the John O'Groats Sandstone of Caithness and the entire goup has been placed in the upper half of the Givetian on the basis of fish remains (Westoll 1979). The fish are rare but highly characteristic and include, Microbrachius dicki, Pentlandia macroptera, Tristichopterus alatus and Watsonsteus flelti. This fauna has been found in fish beds at John O'Groats, and some species in common with beds in the south east Shetland Basin. Mykura (1976) suggested that the sandstones of Eday were deposited in the channels, alluvial fans and flood plains of fairly large rivers, which entered the area from the south-west and either filled the Orcadian lake or encroached up to its margin.





Text Figure 9 Middle Devonian outcrops and locality map for Caithness and Cromarty

Donovan et al (1974) suggested subdividing the Caithness Group (see text fig. 9) into the John O'Groats Sandstone Group, Upper Caithness Flagstone Group, Lower Caithness Flagstone Group and the Scarlet Group. The Scarlet Group was referred to by the geological survey (Crompton and Caruthers 1914) as the oldest strata of Caithness and called the Barren Group. Westoll (1951) considered the Barren Group to be of Lower Devonian age probably Siegenian-Emsian and the overlying flagstones to be of Middle Devonian age probably Eifelian-Givetian.

The Lower Caithness Flagstone group consists of 2330m of drab grey and dark green strata with a rhythmic pattern of sedimentation observed throughout the flagstone groups of Caithness. The distinctive Achanarras- Niandt Limestone although exposed in only a few places forms the best stratigraphic marker horizon by virtue of its distinctive fauna (Donovan and Westoll 1980) and lithology (Donovan et al 1974), and is taken as the top-most bed of the Lower Caithness Flagstone Group.

The Upper Caithness Flagstone Group consists of 1450+m of flagstones, most of the lithological types found in the lower group are also seen in the upper group. The upper group being more difficult to interpret than the lower group (Donovan et al 1974) and the passage from the lower group into the upper group is only seen at one locality. While the passage into the John O'Groats Sandstone Group is everywhere faulted. The John O' Groats Sandstone Group

shows an abrupt change from the underlying series consisting of red, yellow and buff cross-stratified medium to fine grained sandstone, occasional fine to very fine reddish silty and more rare grey green or red shales. Consequently the relations between the various sections are not clear. A characteristic feature of the Caithness series is the persistent repetition of sandstone, mudstone, calcareous flags and limestone. This repetition of cycles of sedimentation, the abundance of ripple marks, sun cracks and current bedding, the absence of marine fossils and presence of land plants (Mykura 1976) prove the land locked nature of the basin.

THE GEOLOGY OF CROMARTY AND THE MORAY FIRTH

The Middle Devonian deposits of Cromarty (see text fig. 9) were deposited in a great syncline, complicated by anticlinal folding and faults. The basal conglomerates and mudstones are exposed along the western margin, in the district south-west of Inverness and on the east side of the Black Isle. On the eastern flanks of the syncline the floor of metamorphic rocks reaches the surface at Rosemarkie and at the Sutors of Cromarty (Crompton and Caruthers 1914).

The strata shows the same lithological succession as in Caithness but is not as well developed, with the absence of dark flagstones. The highest group of the series contains the Edderton, Cromarty, Eathie and Killen Burn Fish Beds, which were first worked by Hugh Miller. The fauna closely resembles the Achanarras fauna of Caithness and is the same

as that obtained from the fish beds in Moray (Crompton and Caruthers 1914).

Friend and Williams (1978) in their field guide to the South Western Moray Firth suggested that the Early Devonian was deposited in a large intermontaine basin within the Caledonian Mountain chain, along or close to the line of the Great Glen Fault. Post Early Devonian movements and subsequent erosion removed many of these basinal deposits and by the time of the Middle Devonian depositional period a large alluvial plain covered an area centred on the Moray Firth. In the west and south this plain was bounded by mountains with large screes and alluvial fans at their base. In the north-east it was bordered by the extensive shallow Orcadian lake, which at times transgressed far across the plain. Middle Devonian sediments thus overlie the Lower Devonian sediments in the west but in the east the Middle Devonian sediments lie directly on the highly undulating crystalline basement. Thick lenses of coarse conglomerate and breccio-conglomerate are developed near the base of the Middle Devonian sediments in the southern part of the Black Isle. These may pass upwards and laterally to the north-east into medium grained locally pebbly sandstone of the Millbuie Sandstone Group of the Black Isle. The sandstones were deposited by predominantly braided rivers which drained the mountains to the west, south west, and south. Interbedded with the fluviatile sandstones are relatively thin beds of fish bearing calcareous siltstone with limestone nodules and some limestones. These beds represent periods when the waters of the Orcadian lake

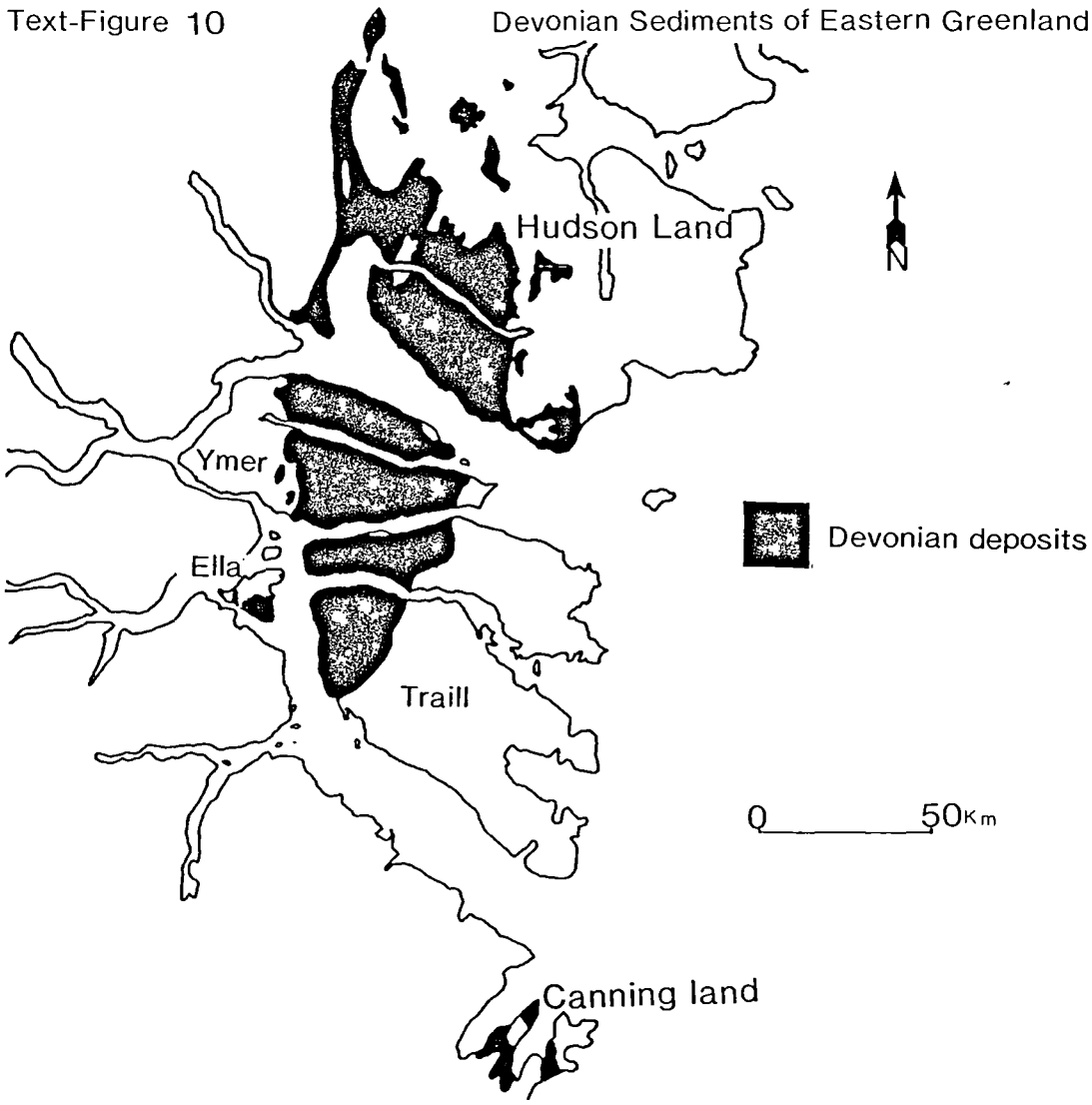
transgressed south westwards across the Moray Firth alluvial plain. The fish beds may have been laid down when the lake was at its deepest and most extensive, and at the same time as the Achanarras limestone was laid down.

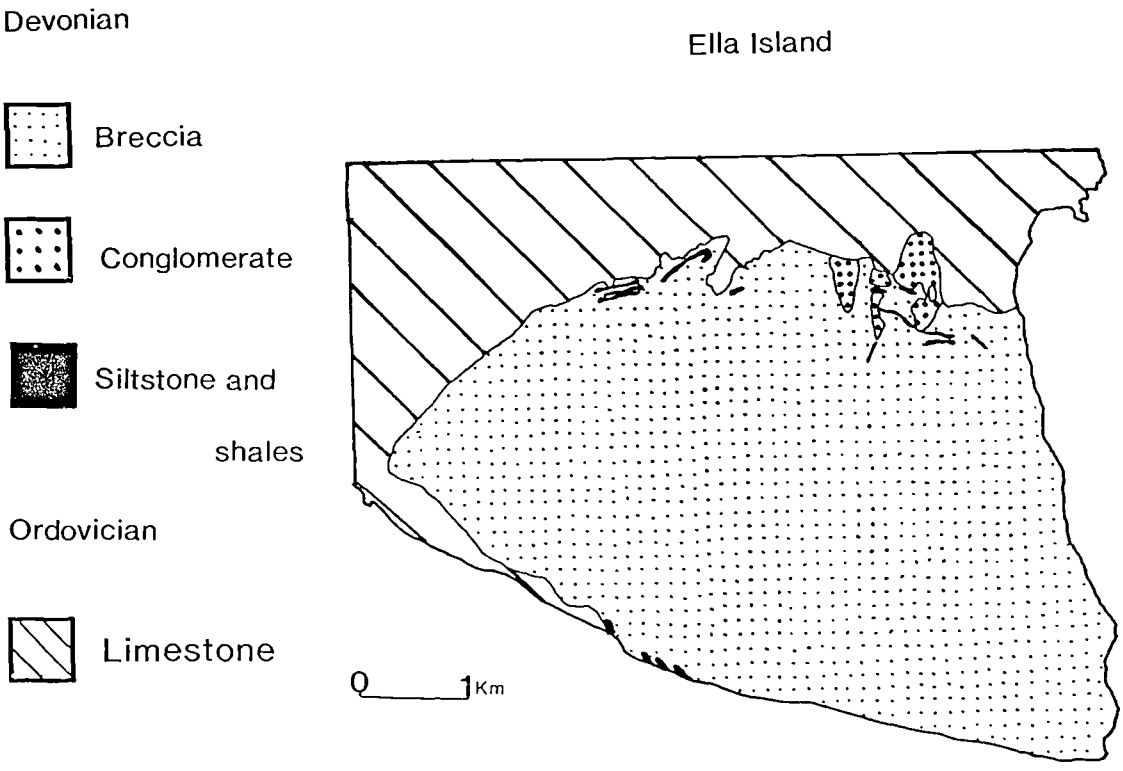
THE GEOLOGY OF EAST GREENLAND.

A 2km succession of Upper Middle Devonian and Upper Devonian fluvial conglomerates and sandstones outcrop north to south for a distance of 169km along the Western sequence of the Devonian outcrop area of East Greenland (see text fig. 10). Yeats and Friend (1977) have comprehensively studied the area and shown the thickness of the sediments varies considerably along this western margin. This is said to represent the growth of pebble and gravel fans. These coarse units range up to 1000m in thickness and locally lie on breccias. Thin limestone and siltstone units occur close to an uncomformity with the Ordovician deposits and are thought to have formed in lake hollows between the high gradient alluvial deposits and the basement topography.

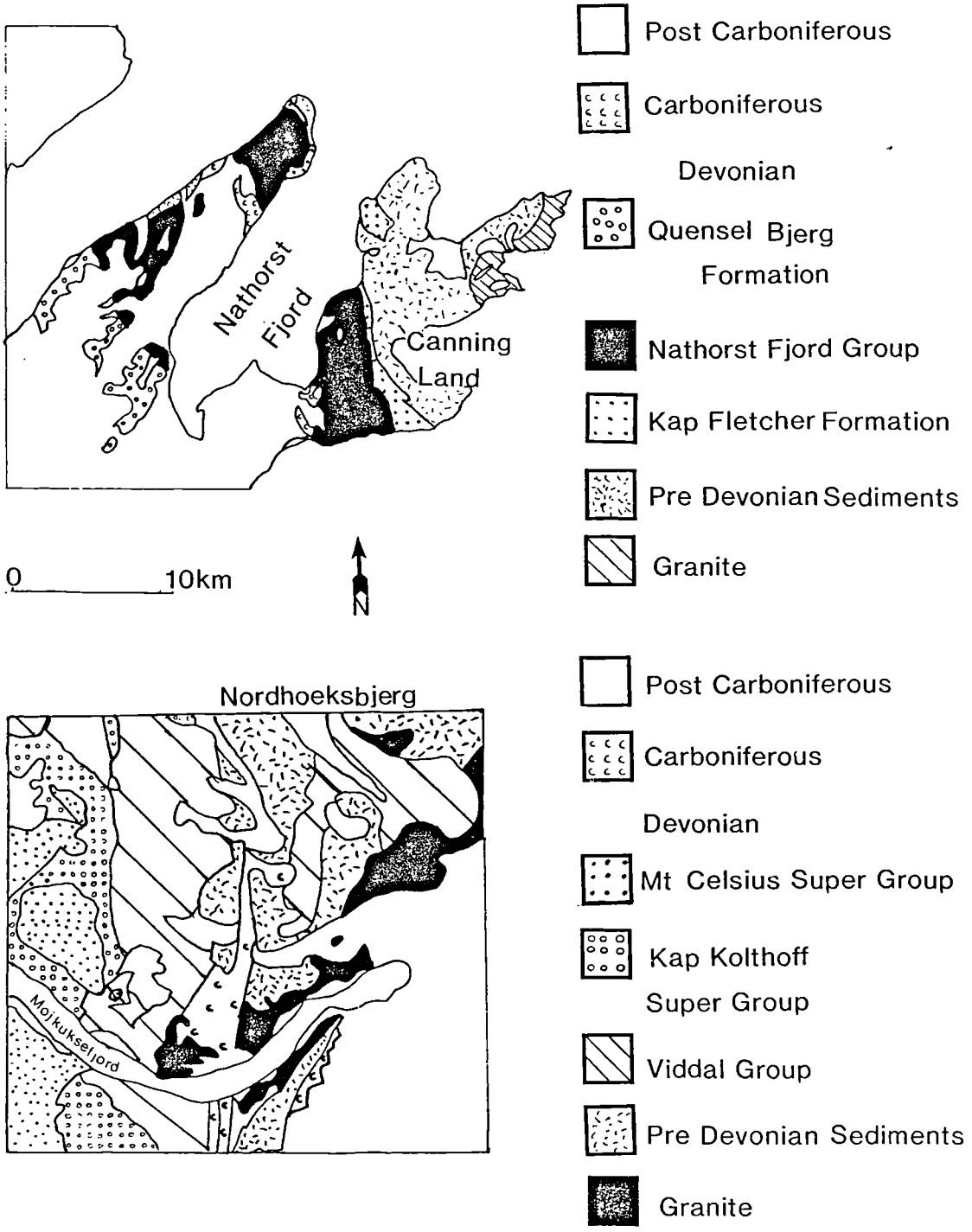
Most of the outcrops are of similar sandstone sequences, and palaeocurrent data and lithology interpreted by Yeates and Friend (1977) shows a number of distinct sandstone bodies deposited by broadly eastward flowing river fan systems at the margin of the Devonian outcrop area. A southward flowing river system deposited sands further east in the centre of the basin. The conglomerate on Ella is part of the Kap Kolthoff Super Group, and is 1000m thick and lies uncomformably on Cambro-Ordovician limestone

Text-Figure 10 Devonian Sediments of Eastern Greenland.





Text Figure 11 Devonian sediments of east Greenland continued



topography. Near the uncomformity four isolated siltstone and limestone bands, up to 7m thick, were found interbedded with the conglomerates (see text fig. 10). On Ella palaeocurrent indicates an eastward direction of flow (Yeats and Friend 1977). The juxtaposition of fine grained essentially low energy sediments within the high gradient deposits of breccias and fluvial conglomerates indicates an enviroment marginal to the main course of the alluvial conglomerate body (Yeats and Friend 1977).

Friend (1968), has collected a few plant remains, identified by Allen (Friend et al 1983) as Svalbardia and Pseudosporochnus, from the four fine grained freshwater limestone and siltstones low in the succession. Three of the deposits have yielded well preserved spores (Allen 1972). Allen (1972) suggested that the assemblage may be compared in part with the Triagulatus Formation in Spitsbergen Allen 1965, 1967), with the Wetherall Formation in Canada (Owens 1971, McGregor and Uyeno 1972), the Williams Island Formation in Canada (McGregor and Camfield 1976), with the Middle Devonian Old Red Sandstone of the Orcadian Basin (Richardson 1960, 1965, 1967)and the Melby Beds in Shetland (Fletcher 1976). Allen (Friend et al 1983) further suggested that a Middle Givetian age would be appropriate for the Ella conglomerate members of the Lower Rodedjerg Formation in which they were found. The presence of Svalbardia and Pseudosporochnus as well as fish remains identified as Glyptolepis and Asterolepis (Yeats and Friend 1977) also suggests a Givetian age.

Hudson Land yeilded Thursophyton milleri from the

Nordhoeksberg Group, part of the Viddal Supergroup (see text fig. 10). This Group rests unconformably on metamorphics and is over 2km thick (Alexander-Marrack and Friend 1976). Consisting of 1500m of red and green banded siltstones, 300m of green sandstones, 100m of sandstone and siltstone, in which the plant remains were found, and 300m of conglomerate. The mainly fine grained sediments of the group were deposited by streams flowing eastwards, and they correlate with the Viddal Group at Kap Franklin (Alexander-Marrack and Friend 1976). A Givetian age for the Group is suggested by the macrospores examined by Allen (in Friend et al 1983) which included Auroraspora macromanifestus, Rhabdosporites parvulus, Acinpsporities macrospinosus, Grandispora diamphida, and Samarisporites. The presence of T. milleri also suggests a Middle Devonian age for the Group.

The Nathorstfjord Group in the Viddal Super Group, from Canning Land has yeilded Rellimia sp. This Group is subdivided stratigraphically into four formations (see text fig. 11). The pre-Cambrian sedimentary rocks were eroded and unconformably overlain by intermediate volcanics of Lower or Middle Devoinan age. These were deeply eroded and small alluvial gravel fans deposited in the hollows. A relatively short phase of fluvial transport from the west was succeeded by the development of a silty flood plain with stream transport southwards. In the upper part of the Group drainage direction changed to flow northwards, with an influx of coarse sediments at the top indicating a possible uplift in the source area (Alexander-Marrack and Friend

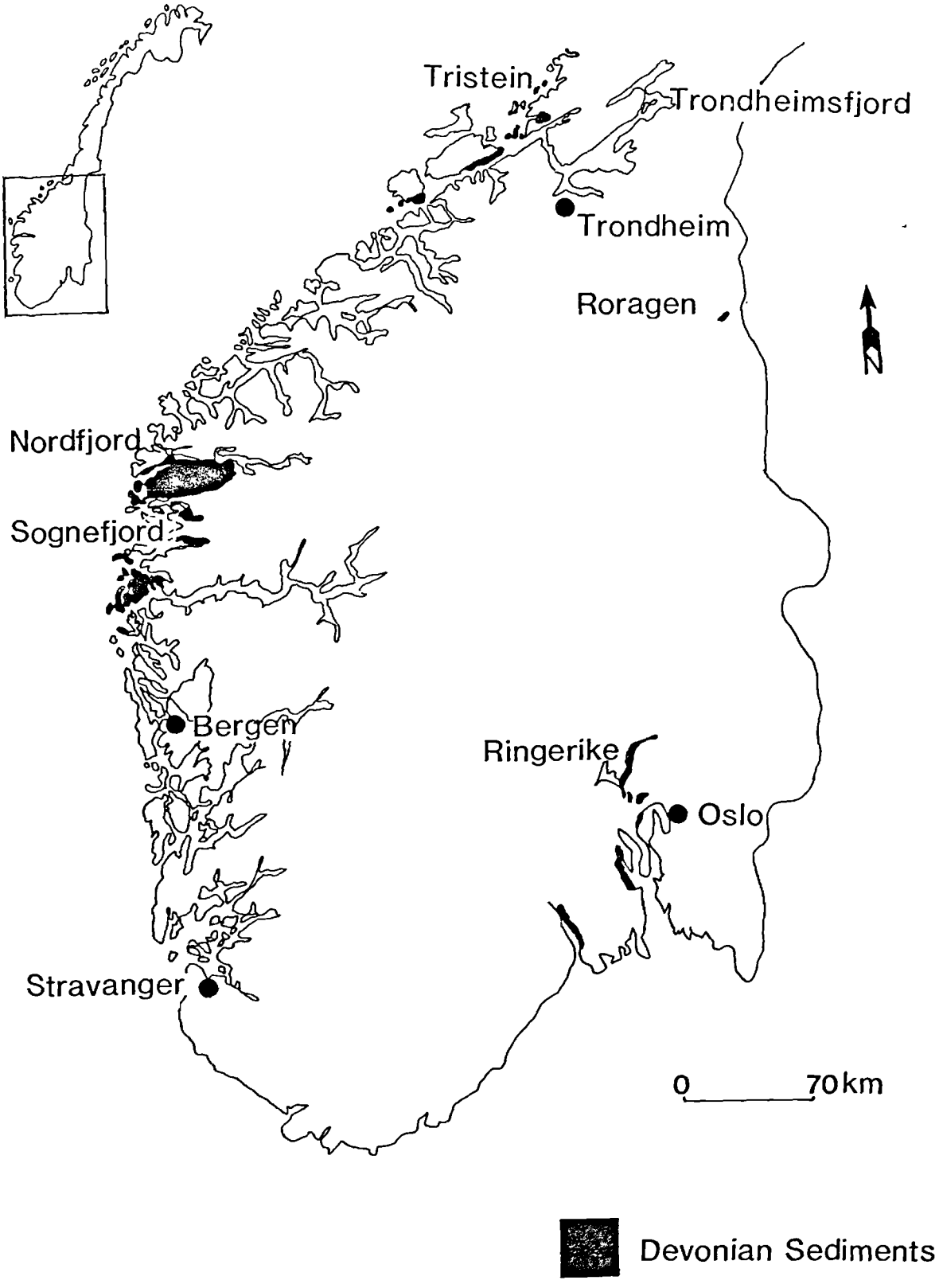
1976). Palynological studies by Allen (Friend et al 1983) failed to produce spores however Rellimia is considered a Middle Devonian plant.

GEOLOGY OF WESTERN NORWAY

Devonian continental deposits in Norway are of two distinct facies; vis coarse grained fluvial sediments deposited in a series of intermontane basins; and fine-grained fluvial sediments deposited on a broad extramontane alluvial plane. The sediments outcrop in four districts of Norway (see text fig. 12). Three of these, the Nordfjord-Sognefjord area, the Trondheimsfjord and Roragen districts are wholly terrestrial.

In the Nordfjord-Songnefjord district the Devonian rocks crop out in six separate sedimentary basins. These form part of the steep cliffs along the west coast of Norway. plant fossils have been found in the Hornelen area by C. Kolderup (1904) and additional fragments were later found in the Kvamshesten, Buelandet-Vaerlandet, and Hornelen areas (Kolderup 1925a, b, 1916, Nathorst 1915). The plant fossils together with fish remains of the Crossopterygian type, convinced Kiaer (1918) of the Middle Devonian age for the sediments, except those of the Buelandet-Vaerlandet areas which he thought were Early Devonian. Additional palaeontological studies were made by Høeg (1936)and Jarvik (1949). The Nordfjord-Songnefjord district consists of three northern basins containing Middle Devonian rocks that infilled separate grabens and were subsequently folded into

Figure 12 Devonian Sediments of western Norway



east-plunging synclines and thrust eastwards. Rocks in the southern area may be younger in age and have undergone less folding and faulting.

The Trondheimsfjord district has Devonian sedimentary rocks outcropping north and west of the entrance to Trondheimsfjord in a north-east trending series of exposures 20km south of the village of Vallersund. While north of the village small islands, including Tristein, have been shown to be of Devonian age (Reusch 1914) on the basis of fossil crustaceans. Vogt (1924a, b, 1929) collected Devonian plants from Strofosan and Høeg (1931, 1935, 1936) found many more fossils in this district. He also found plant fossils on Orlandet which were probably of Early Devonian age or possibly earliest Middle Devonian. In addition he found plant fossils on the small island of Tristein and many of the islands north of Vallersund. Høeg (1945) described these as being typically Middle Devonian. The Trondheimsfjord rocks appear to have been the remnants of a larger north-eastward trending intermontane valley, into which sediments were deposited by streams that eroded the highlands to the north and south. The sediments suggest this took place on alluvial fans, the valley may have originated as a post-orogenic graben following the main climax of the Caledonian orogeny (Richter 1958).

The third district is Roragen in Eastern Norway was suggested by Goldschmidt (1913) to be Devonian in age on the basis of plant fossils. These were examined by Nathorst (in Goldschmidt 1913) who suggested that they were of Middle Devonian age. Halle (1916) collected further specimens and

concluded that an Early Devonian age was more likely. Høeg (1936) confirmed this on the basis of a characteristic Psilophyton like flora. The fourth Devonian outcrop is in the Ringerike series of the Oslo district and consists mainly of marine sediments considered to be Late Silurian to Early Devonian on the basis of a well studied fauna (Heintz 1969).

The terrestrial Devonian rocks of Norway were deposited in intramontane basins and were most likely deposited in structural depressions of the graben or half graben type. The rocks are preserved in only three areas where Cambro-Silurian rocks outcrop adjacent to them. In the intervening areas, only basal gneiss is exposed. This implies that additional Devonian basins probably existed but have subsequently been eroded during uplift.

PALAEOGEOGRAPHY OF THE MIDDLE DEVONIAN

It has been almost two decades since the publication of the first Siluro-Devonian reconstructions based on palaeomagnetic data (McKerrow and Ziegler 1972). In the intervening years additional palaeomagnetic, biogeographical and palaeogeographcal information has become available. Reconstructions proposed by various authors share much in common. (Scotese et al 1979, 1985, Smith et al 1973, Turner and Tarling 1982, Van der Voo 1982).

For the palaeozoic six major continents are recognised (Scotese et al 1979, 1985, Smith et al 1973, Turner and Tarling 1982), these being Baltica (Northern Europe,

Tarling 1982), these being Baltica (Northern Europe, Scandinavia), Siberia, China (China, Japan, South Eastern Asia and Malaysia), Gondwana (South America, Florida, Africa, Arabia, India, Southern Europe, Australia and Antarctica), Laurentia (Central and North America, Greenland, Iceland, Spitsbergen, and parts of Ireland and Scotland) and Kazachstania (Central Russia). During the Devonian Baltica, Laurentia and Kazachstania and the small land masses of England and Avalonia (North Western North America) are believed to have collided (Scotese et al 1979), forming extensive mountain chains and resulting in the supercontinent Laurussia. Subsequent erosion of the mountain chains produced the fluvial sediments known as the Old Red Sandstone facies. Hence in early literature the continent of Laurussia is referred to as the Old Red Continent.

There is still no concensus over the position of the major continental blocks preceding the possible formation of Pangaea (Livemore et al 1985, Scotese et al 1985) and this remains a controversial point as to the configuration of Laurentia, Baltica, and England when the Iapetus Ocean closed between Laurussia and Gondwana with the resulting formation or absence of a Late Devonian Pangaea.

Whatever the exact positioning of the continents it appears that the plant-bearing Devonian rocks of the Northern Hemisphere were located within 20-30 degrees south of the palaeoequator on the most continental of reconstructions, Scotese et al (1979, 1985), with the exception of Siberia and part of Gondwana. During the

Devonian Baltica moved northwards so that by Late Devonian times it occupied a more equatorial position (Scotese et al 1985).

Climate for the areas with Devonian plant localities was postulated by Scotese et al (1985) to have been warm-hot in the low latitude areas and seasonally arid. The land masses in the higher latitudes are believed to have been cool temperate. Many palaeoclimate studies in recent years (Carroll et al 1972, Hodgson and Ramsbottom 1973, House 1975, Johnson 1981, Woodrow et al 1973) have shown that a monsoonal climate prevailed during the latter half of the Devonian. Laurussia probably lay within the tropical belt and had a fairly uniform climate (Allen and Dineley 1988). It also seems likely that sporadic heavy rainfall was common since fluviatile sediments abound (Rayner 1967).

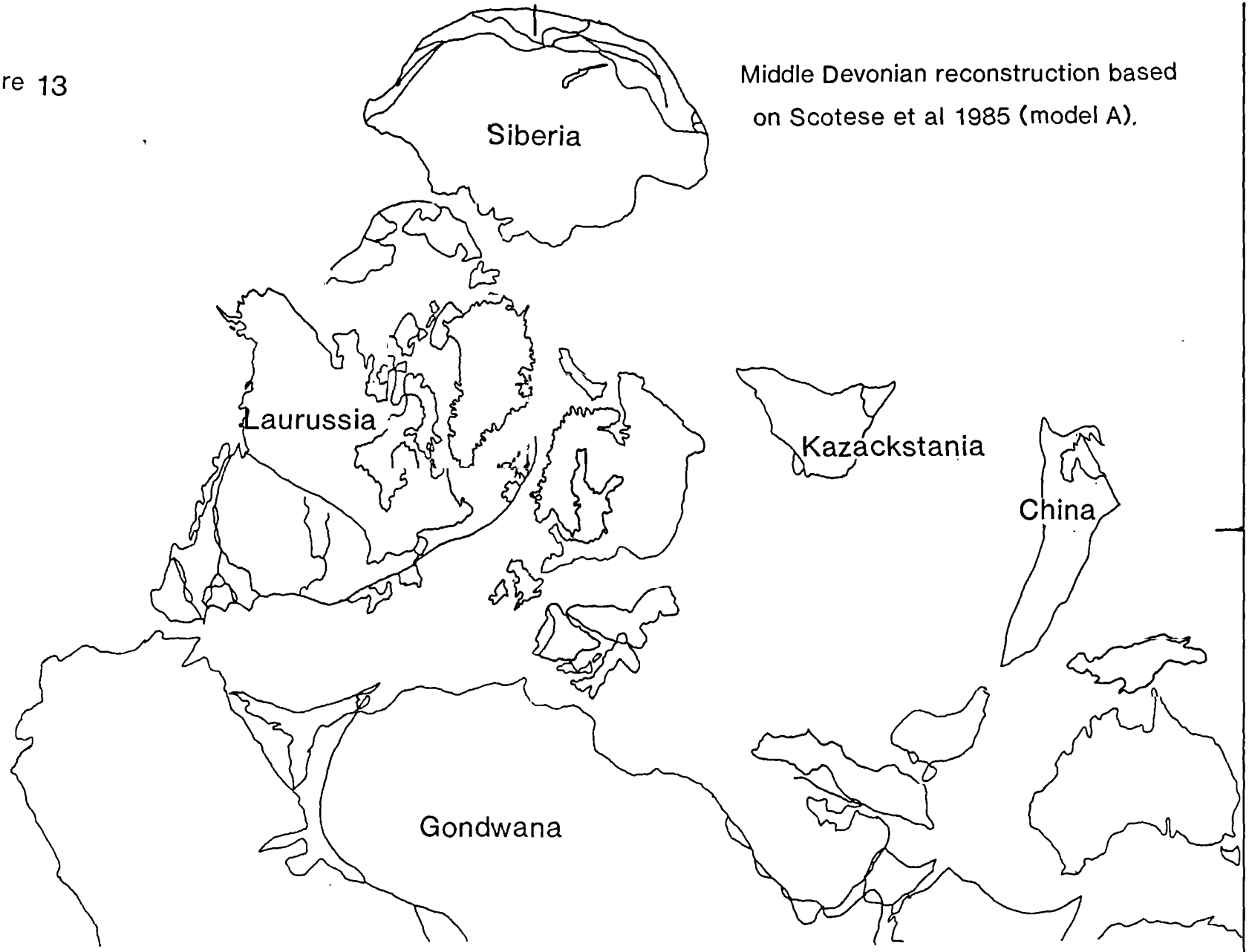
A widespread marine transgression in the Early Silurian reflects melting of the polar ice in Africa and South America, and several features combine to indicate generally warm and possibly dry climates during the Silurian and Devonian. Carbonates in general and reefs in particular seem to be more abundant than in the early Paleozoic. Devonian aridity is suggested by an abundance of red beds, though these are of uncertain environmental significance. Evaporites attain their greatest Paleozoic development in the Devonian, Early Silurian and Late Devonian evaporites being uncommon.

Devonian reefs occupy a wide zone, extending to more than 30' latitude. This may reflect a pole-ward extension of the subtropical belt, or it may have resulted from errors in

continental positioning. Coals of the Devonian demonstrate high humidity for areas of low latitude (35'). This may derive from unknown palaeoecological parameters governing the distribution of the early coal forming plants. There is some indication from faunas (Boucot 1974, Berry 1973) of warming in the Early Silurian, then gentle cooling in the Middle Devovian, followed by a warm Late Devonian (Frakes 1979).

The reconstruction favoured in this thesis is that of Scotese et al (1985), which shows some differences with earlier reconstructions (Scotese et al 1979). The more southerly positioning of Laurussia and the more northerly positioning of Gondwana. The map given in text figure 13 is based on that of Scotese et al (1985) and takes into account the more abundant palaeomagnetic data and information of palaeogeographic positioning from Devonian palaeoclimate studies.

Text-Figure 13



Middle Devonian reconstruction based on Scotese et al 1985 (model A).

CHAPTER 3.

TECHNIQUES.

Degagement: Preparation by degagement involves the delicate removal of matrix which commonly remains after splitting obsuring the part or counterpart. The specimens although highly compressed rarely remain in one plane of fracture and degagement allows the "development" of the fossil. The technique was perfected by Professor Leclercq (1960) in Belgium, she used a small hammer and various sizes of shoemakers needles, from very fine, for the removal of individual grains of sand to larger needles for less delicate work. Other forms of sharpened needle have been used including sewing needles and tungsten wire sharpened in molten sodium nitrate. It was found that the most effective needles were shoemakers needles resharpened on emery paper. These needles remained sharp for almost as long as the tungsten wire but did not bend when tapped with a hammer. In addition they proved easier to sharpen. Photographs were taken before and after degagement to retain a record of the specimen in the case of damage while uncovering. This techinque proved to be the most useful for revealing detailed information when working on coalified compression or impression fossils.

Embedding: A widely used pre-treatement involved the protection of specimens by embedding them prior to cutting. Suspected permineralisations, and material for sectioning and transfers were trimmed from the surrounding matrix using a diamond circular saw, and cut to fit in the base of a tin

foil mould. The moulds of various sizes had approximately 1mm of pre-catalysed resin on the base before covering the specimen with catalysed plastic resin (Metset S.W. Cold Embedding Resin N. 95-B136 Buehler Coventry P.O. Box 150 England). This completely hardened within 24 hours allowing rapid embedding and providing support during the subsequent treatments. For intricately shaped or porous specimens vacuum embedding was employed using a glass desiccator and a water type vacuum pump. Once the specimen is in the mould located within the vacuum vessel a vacuum is slowly applied. The resin then begins to "boil" as the air dissolved within it and within the specimen escapes. As the resin starts to gel atmospheric pressure is restored. This technique was infrequently used as normal embedding was found to provide adequate penetration for the majority of the specimens. It was however used on poorly preserved permineralised specimens containing air spaces within the fossil matrix.

Transfers: Attempts were made to reveal the presence of cuticle, spores or surface features (Banks et al 1972) by embedding the exposed surface of the specimen in resin, and dissolving away the rock matrix covering the remaining surface. This results in the retention of delicate spores, cuticle or other features on the resin surface. The specimens were cut to remove any excess matrix prior to embedded by the use of a diamond circular saw, described above, the specimens were then embedded with sporangia or axis placed at the base of the mould using the proceedure above. After the resin had set the top surface was cut away

to reveal the matrix. If necessary the specimen was demineralised in concentrated Hydrochloric Acid (HCL) for several days to dissolve any carbonates present. After thoroughly washing, the specimen was placed in 40% Hydroflouric Acid (HF) until the remaining matrix was dissolved away revealing the reverse side of the fossil attatched to the resin block. Repeated washings were carried out to remove any residual HF The dried block was then cut and mounted for observation under the light microscope or on the Scanning Electron Microscope (SEM). Alternatively, needles were used to prise any possible cuticle or sporangia off the block and on to a SEM stub. This technique proved to be of little value,revealing a few poorly preserved in situ spores and only one possi ble cutic ular fragment. The reason for this lack of success especially with Shetland material was considered to be the high thermal maturity of the sediments (Marshall pers. comm. 1987) and the consequential carbonisation of the organic material destroying any cuticle that may have been preserved. A large number of transfers were made in order to examine each likely locality for the presence of cuticle or sporangia and for the presence of spores but all proved unsatisfactory.

Thick sections: Permineralised specimens occurred usually in limonite, pyrite, or as a mixture of both. A number of techniques were employed in preparing the material for observation. These depended on the preservational state of the specimen but usually included embedding, sectioning,

re-embedding if necessary and polishing. A mineralogical polishing technique was also carried out for making highly polished sections, see later. Etching and demineralisation was carried when necessary. Both pyrite and limonite permineralisations once embedded (as described above), were cut using a diamond circular saw at 2-3mm intervals depending upon the friablity of the matrix. Saw marks were then removed by grinding with 600 and then 800 Carborundum Grit (BDH Ltd). The back of a photographic sheet of paper was used as a lap, by first adhering the emulsion side to a glass sheet. The sections were then fixed to a glass slide, with Metaset F.T. Fast Resin (N.95B137), after one side of the slide was frosted with 600 grit to help the adherance of the specimen. The specimen could now be polished.

Polishing: An initial polish was obtained with 800 Carborundum grit using the back of a photographic sheet as a lap. This ensured that the specimen was completely flat and ready for further polishing. It was found that Aluminium Oxide Polish (Gamma Micropolish N.3, Buehler Coventry P.O.Box 150 England) followed by a household metal polish such as Carr, Day and Martin Ltd. Metal Polish provided an adequate standard polish. A high polish was obtained by a one step procedure using 1um Hyprez Diamond Compound (Five Star Compound, Engis Ltd. Maidstone Kent England) with Hyprez Fluid as the lubricant. An appropriate 1um cloth lap was used (Hyprocel Pellon PAD-K Engis Ltd.) and a good polish obtained after 30-40 minutes, depending on the hardness of the material being polished. This provided

an acceptable polish. For the observation of pyrite permineralisations under incident light a metallurgical polish of high standard was required. This was carried out using sequential polishing with finer grades of diamond polish, starting with 6um and then 3um and finally 1um. Each polishing lasted for a period of 20-30 minutes. The sections were cleaned at the end of each polishing run by a 30 second immersion in a sonic bath. Polished sections tended to tarnish after several weeks and this was removed by a further brief 1um diamond polish with no serious deterioration. Both polished and highly polished sections were examined without a coverslip using reflected or incident light. Wetting the specimens with ethanol increased the contrast when a standard polish was used.

Thin sections: This technique was first employed for limonite permineralisations by Beck (1967,1971), the technique adopted was that of Stein et al (1981) which includes a re-embedding stage. This was found to be essential in many cases, because of the soft nature of the limonite caused it to pill (pull out) and deform as it was ground. Embedding and sectioning was carried out as outlined above, but here sections cut at 1mm intervals. The best preserved face was determined, and after the removal of saw marks with 600-800 grit as before the favoured surface was polished with Aluminium Oxide polish. After thorough drying the sections were placed in uncatalysed resin (Metaset S.W.) for a period of 24 hours, each specimen was then placed preferred side down, in a pool of heavily

catalysed resin, on a glass slide roughened with 600 grit. Each section was weighted down to ensure a good contact with the slide thereby excluding air bubbles. If air bubbles were present once the plastic had cured then the section was removed by soaking in water to soften the plastic and after prising it away with a razor blade, the section could be remounted. Grinding was carried out by hand on a rotating grinder using 600 grit and finally 800 grit to an approximate depth of 15-25um or to a point when the limonite became slightly transparent. The sections were then fully demineralised in concentrated HCL and rinsed in water, and then dehydrated in an ethanol series and mounted in Elvercite dissolved in Xylene.

Etching and Demineralisations: The sulphides of iron are grouped under the generic term "pyrite" which is opaque and etchable in nitric acid (HNO3) but not hydrochloric acid (HCL). The oldest and most successful technique for preparing pyrite (Heard 1927) has been to produce polished surfaces followed by etching in reagents including oxalic acid, concentrated HCL, and concentrated HF. Etching and demineralisations removes the mineral layers leaving the coalified walls intact, thus allowing the examination of the coalified walls by light and electron microscopy and the preparations of etched surfaces prior to a cellulose acetate peel. limonitic permineralisations pose several problems, in that a number of oxides of limonite are present and proved to be insoluble. This leads to confusion between limonite and the coalified wall when using the SEM. In

permineralisations that contained both pyrite and limonite problems of this sort were avoided by examining the section before polishing to establish the positions of limonite and pyrite within the axis.

Pyrite permineralisations: An etching proceedure similar to that used by Stein et al (1981) produced excellent results. Initially, sections were immersed in conc. NHO_3 for a period of 10 seconds to 30 minutes depending on the nature of the material and the deepness of etch required. This was followed by neutralisation in concentrated (approx. 8M) sodium hydroxide (NaOH) for 1-2 minutes. The sections were re-acidified in concentrated HCL to remove iron oxides. This was neutralised in a weak solution of NaOH for a brief period followed by 30-60 seconds in a 5-10% solution of HCL to acidify any organic material present. Finally the sections were washed for several minutes in distilled water.

After air drying, care must be taken not to damage by contact the carbonised cell walls now exposed. For shallow etching to improve the contrast of standard and highly polished surfaces prior to photography, the sections were immersed in nitric acid for up to 30 seconds, the exact length depending upon the specimen. Washing in distilled water followed by brief examination before returning to the nitric acid gave some idea as to the length of time required. Deep and shallow etching was carried out before examination with the SEM, or before a cellulose acetate film pull. The amount of pyrite removed depended on the time of immersion, for a film pull, 2-5 minutes was normally

sufficient. The time required for deep etching of polished sections for examination in the SEM varied. If the carbonaceous wall was thin or tended to collapse during preparation, then an etch of 30 minutes was considered to be sufficient to reveal a suitable depth, however when the carbonaceous content of the walls was high they could withstand etching for a period of 1-2 hours and this completely demineralised the specimen.

Permineralisations in limonite: Specimens permineralised in limonite can be peeled, (Jennings 1972) but more commonly thick sections are cut and the surfaces prepared for observation with reflected light. Thin sections may also be prepared for observation with transmitted light, with (Matten 1966, Sheckler 1978, Brauer 1980) or without (Leclercq and Banks 1972, Fairon-Demaret 1969) surface etching. Both thin and thick section techniques were made with limonitic material. Surface etching with concentrated HCL was found to be the most effective way of increasing the contrast between cell wall and the limonite. The best effect usually occurred after 2-3 hours of immersion. Only brief demineralisation was carried out if the section was liable to collapse.

Permineralisations in pyrite and limonite: Preparations were carried out in a number of ways depending on the amount of pyrite or limonite present. Sections containing equal amounts of both minerals were etched in concentrated HCL instead of HNO3. Sections containing only a small

quantity of pyrite were thinly ground and partially demineralised in HCl and then observed with incident light over a white card to produce an image consisting of reflected and transmitted light. Thick sections were prepared etched and observed in reflected light. Sections with only small amounts of limonite were treated as for pyritised material. Demineralisations for SEM observation were carried by removal of pyrite in HNO3 and then complete demineralisation in concentrated HCL. Some of the limomite remained insoluble during all of these techniques and care had to be taken when interpreting the mineral and organic structures as seen by SEM.

Cellulose acetate film pulls: This was used in two ways to remove cuticle or spores adhering to a specimen or, to remove a thin layer of carbonaceous wall material from a deeply etched permineralised section. When removing any possible cuticle or spores a layer of cellulose acetate was built up over the specimen by applying numerous layers of cellulose acetate solution (Joy et al 1956, Lang and Cookson 1930). Each layer was allowed to dry before the next was applied, until a thickness was achieved great enough to allow the removal, of the film in one peel. The film pull could be mounted on an SEM stub, or on a slide in Elvacite which has been dissolved in xylene. The film pull solution was made by dissolving cellulose nitrate in amly acetate in a ratio of 1:3. Although this techniqe was used on several occasions only one cuticle and one group of presumed in situ spores were observed.

The second use of cellulose acetate film pulls was for the removal of carbonaceous wall material from an etched surface section of pyritised plant axes. This allows serial sections of a permineralised plant to be made. After deep etching of a polished thick section for up to 5 minutes. The section was dried and irrigated in acetone for at least 30 seconds allowing air bubbles trapped in the specimen to escape. A sheet a cellulose acetate film was then placed over the top of the section and allowed to dry. The main problem encountered was the occurrence of air bubbles in the film as it dried if this happened the section was repolished and a further film pull attempted. The peels obtained were mounted on a slide in Elvercite, and held in a clamp for up to a week while the mounting medium dried. This technique was reasonably successful so long as the percentage of carbon wall remaining in the fossil was high, otherwise the peels revealed little of the anatomical organisation of the plant. When it was successful, it provided a permanent record of the anatomy of the axis at that point along its length.

Fusainised material: This was either uncovered by the use of needles and lifted away or if delicate, dissolved out of the matrix by using HF acid. It was then washed for up to 8 hours and dried out at room temperature to prevent twisting and fracturing, although most specimens only survived for a short period in HF acid and degagement was the preferred method of removal. The fusain was mounted on an SEM stub and prepared for veiwing with the SEM. Many fusainised

specimens were destroyed during attempted degagement, or crumbled while in HF, or while being washed.

Scanning electron microscopy (SEM): Two techniques were used. The first was the secondary electron detector this was the most valuable while the second the back scatter detector was of only limited use. Preparation for both these methods was identical. Mounting specimens for the SEM was carried out using Cambridge Instruments Al uminium Stubs. Large specimens were adhered with Silver Conductive Paint (R.S. Ltd.) to ensure good electrical conductivity with the stub, thereby reducing any charging during operation. The paint was applied semi-dry to prevent the liquid invading the specimen and covering the fine detail. An alternative method of mounting for small specimens such as spores, involved using double sided tape. Both methods allow the specimen to be dissolved off in acetone and turned over so that both sides of a specimen could be examined.

All specimens prepared for the SEM were sputter-coated with gold for periods of between 5 to 20 minutes in a sputterer. Long periods of coating were found to reduce charging, and at the relatively low magnifications which were used no overcoating effects were seen. A further way to reduce specimen charging was to reduce the accelerating voltage (Kv). Low accelerating voltages of between 9 and 10Kv at magnifications of upto x2000 were found to be sufficient and up to 16Kv at higher magnifications. The material was examined using a Cambridge S4 and Philips P.504B stereoscan microscopes and photographs taken, using

Ilford FP4 220 film, to give a permanent record of the specimen.

Light microscopy: Observations were undertaken using a Wild Zlub 94a dissecting microscope with camera lucida attachments, an Olympus SX dissecting microscope (reflected light), an Olympus BH compound microscope (transmitted light), with a PM-6 camera attatchment, that could be used on either of the Olympus microscopes, and a metallurgical microscope (incident light) with a camera attatched. The Wild was used for making accurate representations of the specimens by using the camera lucida to make scale drawings thus allowing direct comparisons with similar specimens or with serial sections. The Olympus dissecting microscope was used for low power observations while the Olympus compound microscope was used to make observations at high power, photographs were taken with both microscopes . The specimens were illuminated using reflected light from an Olympus fibre optic light source or by transmitted light for thin sections.

Ninety five percent ethanol was sometimes applied to the specimen to increase the contrast between fossil and matrix. Photographs of highly polished sections of permineralised axes were taken with the mineralogical microscope using a fibre optic incident light source. The film used was 100 ASA Ilford FP4 black and white film. This provided good contrast and a fast film speed for use at lower light levels. Colour photography was carried out when the contrast between fossil and matrix or carbonaceous wall and mineral infill was low, but it proved to be little better

than black and white reprodution. Generally filtration did not enhance the contrast.

Photography: A pictorial record was taken at as many stages in the treatment of a specimen as possible to ensure a permanent record of the fossil in case the techniques used damaged it. Macrophotography was carried out with a Nikon F3 camera with Micro-lenses, obliquely orientated lighting was used from twin quartz halogen light sources on a standard enlarging platform. In some cases photography of specimens immersed in 95% ethanol produced a dramatic increase in the contrast of the specimen and was carried out when the rock matrix was not susceptible to disintegration. The black and white negatives obtained from macro and micro photography as well as from the SEM were printed on various grades of Ilford photographic paper using a Durst enlarger.

CHAPTER 4.

THE MAJOR PLANT BEARING LOCALITIES

Plant remains were collected and examined from documented localities on mainland Shetland, Bressay, Noss, Mousa, Foula and Fair Isle. Collections were made on the mainland of Orkney as well as on the Scotish mainland at localities in Caithness and Cromaty. New localities were also recorded from mainland Shetland. All the most productive localities were found within the Shetland Islands and included localities from the South East Shetland Basin at the Ness of Trebister on the Mainland and from Bressay. From the Walls Basin the most productive locality was Fair Isle, while the best specimens in the Melby Basin came from the small island of Foula. Each of these localities contained either fertile permineralised material together with good compression or impression fossils. The minor localities are included in this Thesis for completeness but rarely contained enough information to allow the identification beyond the generic level.

THE SOUTH EAST SHETLAND BASIN

Ness of Trebister: The Ness of Trebister (see text fig. 4) like much of the Lerwick area and northern Bressay consists of a pebbly sandstone sequence. Allen and Marshall (1981) consider this to be the equivalent to the Lerwick Sandstones described by Finlay (1926) and the sequence deposited in a braided stream environment. The fine grained alluvial deposits are scarce and generally represented by

red siltstones and mudstones on the southern shore of the Ness, while on the northern shore the sandstone facies are occasionally interbedded with predominately black and purple siltstones and shales. These sequences have been known to yield Estheria (Mykura 1976) while the thicker accumulations of fine grained alluvium filling abandoned channels has been found to contain rootlet horizons (Allen and Marshall 1981).

Two new localities at Sandwall (4592,3925) and Skersund (4609,3821) are reported here. These are exposed on the northern shore of the Ness facing the Voe of Sound. Both localities are readily accessable at low water. At Sandwall about 4m of a hard blue-grey fluviatile sediment is exposed above and below the high water mark. Various sizes and lengths of broken axes were found, many being permineralised in limonite or with some pyrite. The majority of the material being stained impressions with very little coalified compression material. The locality at Skersund is aproximately half a mile east of the previous locality and is represented by 2m of a soft dark grey siltstone which is probably an alluvial deposit infilling an abandoned channel. The fossil plants were preserved as faint coalified compression/impressions, or as permineralised and fusainised material. All the compression/impression material was randomly arranged and fragmented but all orientated on the same plane within the sediment. Material found at these two sites was assigned to Thursophyton milleri and Svalbardia scotica with the occasional presence of larger axes referable to the Corduroy plant.

Bressay: The major plant localities on Bressay have long been known (Unpublished 6" I.G.S. field maps, Mykura 1976). The sediments have been collected for palynology (Marshall 1981). The first extensive collecting was carried out by Marshall for his PhD thesis and later described fertile material of Svalbardia scotica and the Corduroy plant (Allen and Marshall 1986) from fluviatile and lake margin sediments. They also postulated that by association the Corduroy plant probably represents the main axis of the genus Svalbardia scotica.

The most productive localities were found along 800m of coast on the north east side of the Voe of Cullingsburgh in the flaggy sandstones and siltstones. Better preserved samples com ing from two fish beds (unpublished 6" I.G.S. field sheets) located south of Staves Geo (5165,4291) and North of the Sands of Bruntland (5150,4272). These are laustrine deposits which consist of grey siltstones and silty mudstones and contain the fish Asterolepis and Glyptolepis. An additional lacustrine deposit was found 100m further north at Seli Geo (5162,4300) and this also contained Svalbardia scotica. The original localities of Allen and Marshall (1986) were recollected but found to be less productive. The palaeoenvironment for these localities has been interpreted by Allen and Marshall (1986) as a lake margin with a fluviatile input. Other sedimentary facies present, include sandy banks, lacustrine shales and fluvial channel sands with deltaic margins into the lake. The larger "Corduroy stems being common in the fluviatile

and lake margin sandstones.

Axes and fronds of Svalbardia scotica occur as poorly preserved coalified compressions and rare permineralisations occurring at all three localities together with fertile fragments, usually preserved as detatched broken branchlets of various sizes. Occasionally they were found in connection with a portion of frond. The fronds occured in various sizes generally being in connection with flabelliform leaves. Ultimate appendages and fertile branchlets were usually found in isolation from the fronds but in the same bedding plane. Corduroy material was found in the coarse fluviatile sandstones above and below the Svalbardia localities. The preservation of the material was highly carbonised as a result of a local heating event of up to 200' C (Marshall et al 1986) and has caused significant change to the organic material, which now shows the development of close set orthoganal shrinkage cracks. Consequently no cuticle or well preserved permineralised material was found.

THE WALLS BASIN (see text fig. 7).

Fair Isle: The island is situated half way between Orkney and Shetland and is 124km north east of Duncanosby Head on the Scottish mainland. The collections were made from the eastern edge of the island, which has provided three well documented plant localities originally collected by Mykura in 1972. His specimens were studied by Chaloner (1972), who described three species, Dawsonities roskiliensis,

Svalbardia scotica and c.f. Thursophyton milleri. The Svalbardia locality (2279,7246) from the North Gavel Beds of the Bu-Ness Group (see Figure 7) was recollected by Allen and Marshall (1986). Here co-sets of massively bedded sandstones regularly alternate with thinner cosets composed of siltstone, shale and fine grained flaggy sandstone in which the plant remains were found. The most productive site being the last shale unit encountered before the cliff edge. Recent sedimentary facies interpretations (Astin pers. comm. in Allen and Marshall 1986) have shown the shale units to be lacustrine deposits, while the intervening sandstones represent a lake margin beach. The miospore assemblage from Fair Isle (Marshall and Allen 1982) suggests a Givetian age for the Bu-Ness, Group and more specifically a Late Givetian age possibly near the Givetian-Frasnian boundary.

The second major locality containing Dawsonites roskiliensis comes from several localities at Furse (2199,7282), all of which are within the argillite units of the Furse Argillaceaous Beds, Observatory Group (Mykura 1972a). Here the Ward Hill sandstone is overlain by a mixed series of sediments and is composed of three units, predominately a dolomitic argillite, separated by two thick units of massive sandstone. The argillites contain scattered plant fragments and are tentatively regarded as lake deposits formed in deep permanent lakes (Mykura 1972a). The third locality also within the Observatory Group contains material assigned by Chaloner to c.f. Thursophyton milleri and is found at the Heads of Duttfield (2195,7210).

The age of the Observatory Group is dated on the palynology as being Middle Devonian and probably Givetian (Marshall and Allen 1982).

THE MELBY BASIN

Foula: The specimens are preserved in a lens of hard, grey siltstone located approximately two metres above high tide mark at (493,612) Ness a Skerry on the island of Foula. This is the same locality (see text fig 6) from which J.E.A. Marshall (pers. comm. 1987) obtained miospores and plant fossils resembling Thursophyton milleri (Nathorst 1915), with its distinctive spiny axes and circinate tips.

The sediments, including the plant beds, represent the youngest deposits outcropping on Foula. They were deposited within a subsiding half graben, and there is strong evidence to suggest that currents flowing towards the south or south-east deposited the sediments. These are recorded by Mykura (1976a) as part of the Noup Formation, which is predominantly medium grained, cross-bedded, yellow sandstone in sets up to 2m thick. Scattered quartzite pebbles are common, some up to 6cm in diameter. Lenses of overbank deposits are frequent, and yield macroplants which at South Ness form a plant bed.

The age of the sediments has long been assumed as Devonian (Gibson 1877). Conclusive miospore evidence was provided by Fletcher (1976) and Donovan et al (1978), who determined the age as somewhere in the late Eifelian to early Givetian. The specific age of the Noup Sandstone Formation is suggested by

J.E.A. Marshall (pers. comm. 1987) as Givetian; indeed the microfloras are comparable with those from the Givetian Eday beds of Orkney. The presence of T. milleri supports this view as it is also found within the lower Upper Caithness Flagstone Group, see Lang (1925) and the Achanarras horizon which is widely accepted as Early Givetian. Compressions are the most common type of preservation, where organic matter is present on one part, or more commonly where organic material is present on part and counterpart. Plates 47-51 illustrate these two configerations and show the range of material collected. In both cases the line of cleavage passed through material originally represented by the plant axis.

Axes of various size, were present in considerable abundance within the 30cm thick plant bed. The broad vegetative axes lay parallel to one another, or were broken and somewhat randomly orientated. The main axes, being robust, always lay parallel to the bedding plane, rarely being bent or folded. It appears that the small axes and fragments of axes were either swept in from a distance or damaged during fossilisation; indeed many are randomly orientated. The majority of axes however were probably transported only short distances prior to deposition. Petrified material was common but only two specimens were found to reveal cellular detail. Isolated sporangia, containing spores, were found in association with the axes of T. milleri, however none were found in connection. Transfers yielded poorly preserved cuticlular fragments.

THE MINOR PLANT LOCALITIES.

The South East Shetland Basin (see text fig. 4).

Numerous localities were found mainly of Corduroy material from the coarse fluviatile sandstones on the island of Bressay together with some Thursophyton milleri and Svalbardia scotica localities and other unassignable plant axes from sites on the mainland.

Bressay

Hogs Kailyard (5158,4322): Large alligned plant stems of Corduroy type were found (Plate 33 fig 3). They were first recorded by Mykura (unpublished I.G.S. Field Maps 1976), from the sandstone bedding planes.

Quarry Bressay (5164,4308): Coarse grained fluviatile sandstone with abundant highly carbonised Corduroy material, one of which shows a pith cast (Plate 33 fig 2).

Brecks of Aith (5164,4308): Corduroy locality in similar fluviatile sediments, together with poorly preserved axes possibly of Svalbardia scotica (Plate 33 figs 4,5).

C3 (5165,4290): A few yards south of Staves Geo, further Corduroy specimens were found in a fluviatile lithology below the siltstone containing Svalbadia scotica (Plate 33 figs 6,7). This Corduroy locality was first found by J.E.A. Marshall (Pers. Comm. 1987)

C2(560,4279): Another repeat of the lithology containing Corduroy specimens (Plate 34 figs 1,2), first found by J.E.A. Marshall (pers. comm. 1987)

Sillock Geo (5138,4233): Original locality of Svalbardia scotica worked by Allen and Marshall (1986) now containing only poor quality fronds and axes which are preserved as impressions or stains, with little carbonaceous material remaining, in the fine grained sandstones and siltstones (Plate 34 figs 3,4).

Locality 90 (5150,4212): A fertile locality of Svalbardia scotica originally collected by Allen and Marshall (1986). Little was subsequently found except a few unidentifiable axes and fish scales (Plate 34 figs 6,7) assignable to Holonema ornatum (Loeffter pers. comm. 1989)

Blue Geo (5155,4200): A Corduroy locality together with abundant unidentified axes in a coarse grained sandstone which is similar to previous localities (Plate 35 fis 1,2).

Ullins Geo (5290,4135): plant remains assignable to Corduroy material, from which tracheids were recovered, found in a micaceous sandstone (Plate 35 figs 3-9).

Beas Pund (5199,3906): Unidentified small axes 3-4mm wide unbranched together with larger, possibly ribbed axes, in a

yellow medium grained sandstone (Plate 39 figs 1-5).

Skeo Back (5195,3882): Svalbardia scotica fronds found in a hard dark grey, fine grained sediment. Only sterile material was recovered, Corduroy material was also found from a locality close to the Svalbardia (5193,3882) in the typical fluviatile sandstone from which it has been found throughout the island (Plate 36 figs 6-10).

Kirkabister Ness (4886,3770) Fish scales belonging to Holonema ornatum (Loffter pers. comm. 1989), found in the same hard, dark grey, lithology as poorly preserved Svalbardia scotica fronds (Plate 37 figs 1-6).

Bay of Hoegan 1 (4755,4343): Unidentified axes preserved as red stained impressions on a green medium grained sandstone. One specimen possibly representative of a zosterophyll fertile axis (Plate 38 figs 2,3).

Bay of Hoegan 2 (4748,4345): Broken undifferentiated axes up to 1.5cm wide preserved as carbonised compressions in a hard grey, medium grained sandstone (Plate 38 fig 1).

Geo White Arye (4844,4466): Large possibly ribbed stem impressions of up to 3cm wide together with small broken portions of axis in a yellow medium grained sandstone (Plate 38 figs 4,5).

Noss: Plant fragments were found in three locations in the

siltstones and fine gained sandstones amongst cross bedded pebbly sandstones.

Gunstie (5308,4107): Small randomly arranged plant fragments found in a light grey, medium grained sandstone (Plate 38 fig 6).

Papil Geo (5367,4125): Small fragments of plant axes present in a dark grey/blue fine grained sandstone (Plate 38 fig 7).

Geo of North Croo (5398,4180): Plant fragments of apparently the same type as above but present in a yellow medium grained sandstone (Plate 39 figs 1,2).

Moussa: Two localities were found on this island lying just of the coast at Sandwick. These were originally recorded by Mykura (unpublished 6" I.G.S. Field Maps 1976).

Bard Sound (4592,2368): Dichotomously branching broken plant fragments, refered to Hostinella by Mykura (unpublished 6" I.G.S. Field Maps 1976) and preserved as compressions, above and within a calcareous shale (Plate 39 figs 6-8).

East Ham (4592,2461): Additional branching plant fragments of the same type as above and in the same calcareous siltstones (Plate 39 figs 3-5).

Mainland: Localities containing both Svalbardia scotica and Thursophyton milleri were found on the mainland together with similar blabrous, branching axes from a few localities in the south. These are similar in appearance to those found on Mousa and Noss but of little diagnostic value.

Leebotten (4343,2498): Material was collected from a dark-grey, fine grained sandstone, by Allen and Marshall (1986). They found only sterile specimens of Svalbardia scotica together with the Corduroy plant in associated deposits. This author also found fronds assignable to S. scotica (Plate 5 figs 1-8) with filiform leaves and flabelliform leaves, together with a small amount of fertile material in association with numerous axes some of which were identified as Thursophyton milleri (Plate 4 figs 1-9). Both plants were present in the same lithologies. An isolated sporangium was also found in association with the axes of T. milleri.

Wick of Sandayre (4344,2530): This locality is just north of the Leebotten site and contained numerous plant axes in a yellow fluviatile sandstone deposit. The axes were poorly preserved and the organic material like most in the south east Shetland Basin was altered as a result of a local heating event. The woody material appearing homogenised and showing orthogonal shrinkage cracks. Both c.f. Thursophyton milleri (Plate 40 figs 3-5) and c.f. Svalbardia scotica (Plate 40 figs 1,2) were tentatively identified from this

locality.

Hoswick (4187,2356): One productive locality was found from the two sites recorded by Mykura (Unpublished 6" I.G.S. Field Maps 1976). This contained branching axes and plant fragments in a hard, blue/grey fine grained sandstone (Plate 41 figs 6,7, Plate 41 figs 1-3).

Geo of Sloga (4075,1525): Branching and other fragments of plant axes were present in a yellow coarse grained fluviatile sandstone (Plate 41 figs 4-6).

The Waals (4040,0860): Dichotomously branching axes fragments together with isolated fish scales in a grey siltstone intercalated between medium and coarse grained sandstone (Plate 41 figs 7-10).

The Walls Basin (see text fig.5).

The first recorded record of fossil plants in the Walls Formation was by Peach and Horne (1879) in the hills between Gruting Voe and Bixter Voe. Unfortunately the records of this locality have been lost. Finlay (1930) recorded plants from sandy shale below one of the limestone depsits in Watsness. Lang (in Finlay 1930) decribed these and other plant reamins from unspecified localities as being of the Hostimellid type.

Voe of Clousta (309,573): This locality within the Sandness Formation produced fragments of axes showing

dichotomos and trichotomous divisions. The plant remains were present in the hard grey sandstone along the foreshore of the Voe and in front of the school house. Plants from this locality have been examined by Chaloner (in Mykura and Phemister 1976), and he identified Psilophyton species and a spinless axis of c.f. Hostinella. The author considers that thes specimens may be reassigned to c.f. Thursophyton milleri on the basis of the morphology of the newly collected specimens (Pate 46 figs 1-4).

Wick of Watsness (175,501): Unidentifiable branching fragments of axes were collected from this locality within thw Walls Formation. The locality was originally recorded by Mykura (in Mykura and Phemister 1976) and similar fossils preserved as a red film on the grey fine grained sandstone were found (Plate 46 figs 6-8).

The Melby Basin (see text fig.5).

The fish beds in the Melby Sandstone, whose fauna was shown by Watson (1934) to be similar to that of the Achanarras Limestone of Caithness, and of the Sandwick Fish Beds of Orkney. In associated sediments numerous plant beds are found in both lower and upper fish beds.

Melby Fish Beds (1732,5725): Numerous fragmented plant debris were present on the ripple marked medium grained sandstone, together with a few larger plant fragments showing pseudomonopodial or dichotomous branching, all axes were apparently glabrous. The plant remains were initially

recorded by Mykura (Mykura and Phemister 1976) and later by Fletcher (1976). They assigned them to Hostinellid type (Plate 46 figs 10-12).

The Orkney Basin (see text fig.8)

South Setter (2355,1615): Unidentifiable, glabrous pseudomonopodial branching fragments of axis were found from a soft, dark fine grained sandstone (Plate 3 figs 4-7).

Marwick (2261,2444): A few isolated Arthrodire plates identified as Homosteus milleri (Loffter pers. comm. 1989) were found from this soft, dark brown fine grained sandstone (Plate 3 fig 9).

Yesnaby (2205,1598): Unidentifiable plant fragments were obtained from a hard, blue grey fine grained sandstone (Plate 3 figs 10,11).

Billa Croo (2230,2561): A new locality from which specimens resembling the Corduroy Plant was found in the black hard medium-grained sandstone along the foreshore (Plate 3 fig 8).

Caithness (see text fig.9)

Brims Hill (0789,7100): Fish remains identified as Osteolepis panderi (Loffer pers. comm. 1989) found together with unidentifiable plant fragments in a hard blue-grey fine

grained sandstone (Plate 3 figs 1-3).

Cromaty (see text fig.9)

Eahtie Burn (7810,6415) and (7822,6415): Plant remains in a grey sandstone with limestone nodules and fragments of axes in a yellow medium grained sandstone. Dichotomous and pseudomonopodial branching was present and spines were identified along the margin of the axis. Localities in the Eathie Burn area were initially investigated and reported by Miller (1849), Giekie (1878), and Lang (1925). This locality is also a possible Achanarras equivalent. The plant remains were identified as c.f. Thursophyton milleri (Plate 2 figs 5-10).

Navity (7910,6521): Thursophyton milleri was identified from a locality initially recorded by Lang (1925). One axis was found showing a tricotomy, while others showed a pseudomonopodial habit. A large unbranched axis was also found in the medium grained red sandstone of this locality (Plate 2 figs 1-4).

Kinkell (565,535): A grey to buff medium grained sandstone with associated mudstone and two lenses of siltstone contained Thursophyton milleri with its characteristic spiny axes and occas ional tricotomy. The exposure is considered by Rogers (pers. comm. 1987) to be an Achanarras equivalent (Plate 1 figs 1-11).

CHAPTER 5.

INTRODUCTION

The morphology and anatomy of previously described plants from new and existing localities are described. The plants include Thursophyton milleri, Svalbardia scotica, and Dawsonites roskiliensis. Numerous localities were collected from but only those showing fertile, permineralised or good morphological information were extensively investigated. The remaining localities were figured to give some indication of the variety of preservational forms and the similarity between the plant assemblages of Scotland, Orkney, Shetland, Greenland, and Norway. After describing the plant species there follows an assessment of their systematic position.

Thursophyton milleri (Salter) Nathorst 1915.

Intoduction: Specimens assignable to this species were collected from numerous localities in the Middle Devonian of Northern Scotland and Shetland, comparisons were also made with material from previous collections in Greenland and Norway. The first account of this plant comes from collections made by Miller (1841, 1849, 1857) who described "lignite with structure preserved" from Millers Bay and Coal Heugh, Cromaty, and "smooth stemmed"and "turbercled fucoids" from Thurso and Stromness. The material was of reasonable preservation and initially recognised as a lycopod comparing it with Lycopodium and Lepidodendron. This view was upheld by Salter (1857) in a review paper in which he renamed the

plant Lycopodities milleri. Lang (1925) considered that a careful description based on specimens from western Norway by Nathorst (1915) was more accurate, and the plant was renamed ~~in~~ as Thursophyton milleri. Both Nathorst (1915) and Lang (1925) came to the conclusion that no fertile material had yet been found. Høeg (1967) in the Traite de Paleobotanique placed the genus in the Psilophyta along with numerous poorly preserved specimens from Siberia together with Thursophton (Asteroxylon) elberfeldense (Kräusel and Weyland 1923) Høeg (1967) a morphologically identical plant. The Psilophyta have been sub-divided by Banks (1965) and it became obvious that Thursophyton does not fit comfortably into the concept of any of the present Classes. Remy and Remy (1977) consider the genus to be within the Lycophyta on the basis of poorly preserved rhizome anatomy of T. elberfeldense, while they assign Euthursophyton hamperbachence Mustafa (1978) a similar plant with well preserved anatomy to the Zosterophyllophytina. Such is the uncertainty of the systematics that modern reference books (Gensel and Andrews 1984) ignore the genus totally.

The author has examined type material in the Nathorst collection from the Bergen Museum, the Høeg collection from the Oslo Museum and the Lang collection at the British Museum (Natural History) and material collected by Friend in 1968 from east Greenland. From the Høeg collection new information was obtained on anatomy at the point of branching and the morphology. Type specimens from the Nathorst collection were examined to enable comparisons with other collections, as was the Lang collection. Xylem anatomy

and morphological information was also obtained from the Greenland material.

Collections by the author were made from a number of well known localities and one new locality in Cromaty and unpublished localities from Shetland. Foula provided the most extensive material, containing large quantities of branched axes giving valuable information on gross morphology. Permineralisations in limonite were present but found to be of poor preservation. At Skersund and Sandwall on the mainland of Shetland permineralisations were common and well preserved in pyrite and limonite, together with limited but characteristic compression/impression material. Spiny axes referable to the genus were also found from Leebotton, Shetland , Navity and Eathie Cromaty and the new locality at Kinkell, which gave some useful information.

In the following section the specimens from each locality will be described under the locality name and at the end of the descriptions comparisons made between the material and the type specimens. An emended genus and species diagnosis will then be given.

CROMATY: Kinkell.

Morphology: Spiny and apparenty glaborous fragments of axes, varying from 1mm upto 6mm wide (x=3mm, n=20). Branching is predominantly pseudomonopodial (Plate 1, figs 2,3) but many were dichotomous or in one case trichotomous (Plate 1, figs 1,4). The largest specimen was 50mm long (Plate 1 fig 2). The branching angle was generally smaller

in the larger axes being 30 to 35' (x=34' n=12) but was never greater than 90' even in the smaller axes. Not enough complete specimens were found to determine the distance between branches. Spines were not found on the smaller axes but were present on the margin of the larger fragments. Where present, spines were dense (Plate 1 figs 5,6) being 1mm or less apart (x=0.5mm n=25). They taper from a wide base (Plate 1 fig 5), but the tips were never seen because the matrix is coarse and preservation poor. They are on average 1mm long (Plate 1 figs 5,6) and between 0.25 and 0.20mm (x= 0.22mm n=25) wide at the base. There is considerable variation in size and shape of the spines. This is considered to be a consequence of the poor preservational quality rather than any significant morphological variation. Although a variation in size and shape of the spines was noted by Lang (1925) in Thursophyton milleri from Navity. Specimens from this locality were identified as T. milleri.

Anatomy: No cellular details including spine bases or stomata could be seen on those axes examined, except in one specimen (Plate 1 fig 7). This axis was in a better state of preservation with possible cuticle and anatomy. The axis was sectioned and a portion embedded and macerated in HF. An apparent fragment of cuticle recovered was prepared for the SEM (Plate 1 figs 8,9). The cellular surface pattern shows ridges presumed to run vertically on the axis with a cellular pattern between. No guard cells were seen, but circular holes were present, which may represent simple

pores in the epidermis (Plate 1 figs 8,9). The remaining material was sectioned but no anatomy was visible. A section was demineralised in HNO3 and prepared for the SEM (Plate 1 figs 10,11). No tracheids were seen but their presence is suggested by the longitudinal furrows observed.

Navity.

Morphology: Apparently glabrous axes were found which varied from 20mm to 2mm (x=5.7mm n=10) in width, except for one exceptional specimen which measured 230mm (Plate 2 fig 4). Branching is pseudomonopodial with one specimen (Plate 2 figs 1,2) showing a trifurcation. The branching angle was smaller in the larger axes between 30-45' (x=41' n=8). The distance between branches could not be measured because of the fragmentation of the specimens. Spines were generally not present, but one specimen (Plate 1 fig 2) did show circular pits or spine bases, as noted by Lang (1925). These densely covered the axis and measured upto 1mm across (x=0.7 n=30). At high magnification no cellular detail was observed, and there was no permineralised material. Specimens from this locality were identified as c.f. Thursophyton milleri.

Eathie.

Morphology: Glabrous fragments of small axes were found which varied from 4.2mm to 0.6mm (x=1.8mm n=20) in width. The largest specimen (Plate 2 fig 5) measured 65mm long and

3mm wide and showed dichotomous branching. Branching where present was dichotomous and the angle of branching varied from 7-70' (x=55 n=18) being smaller in the larger axes. One specimen (Plate 2 fig 5) showed a possible permineralisation. This was sectioned but no anatomy was visible. A further section was demineralised and prepared for the SEM (Plate 2 figs 6,7) no celluar detail was visible except a faint longitudinal striation seen on the surface of the axis. The specimens from this locality were identified by the author as c.f. Thursophyton milleri.

SHETLAND: Leebotton.

Morphology: Spiny axes varied from 6.2 to 1.2mm wide (x=3.1mm n=21). The branching was predominantly pseudomonopodial in the larger axes (Plate 3 figs 1,2,3,4) and dichotomous in the smaller axes (Plate 4 fig 2). The largest specimen measured 115mm long and branched pseudomonopodially, the angle of which varied between 40-45'. While in the smaller axes the angle of branching was larger being 50 to 80' (x=58' n=20) but never exceeded 80'. The distance between branches ranges from 27mm to 39mm (x=30mm n=8). Spines were densely arranged on the margin of the axis and were between 0.33 and 0.5mm apart (x=0.45mm n=20). The spines taper from a wide base and were ascicular (Plate 4 fig 6), however the tips are not generally seen, the spines being between 0.54 and 0.70mm (x=0.6mm n=20) in length, but possibly greater (Plate 4 figs 5,6). At the base the spines measure between 0.23 and 0.1mm wide (x=0.18

n=20).

Transfers were carried out on one axis (Plate 3 fig 8) and no vascular connection was seen with the spines in this or any of the other specimens studied. No cuticular or anatomical material was found from this locality. One isolated specimen was found with a single apical sporangium (Plate 4 fig 7) in association with a spiny axis. The sporangium is fusiform (Plate 3 fig 8) 2.6mm long and 0.6mm wide. The mode of dehiscence was not visible. Cellulose acetate peels show (Plate 4 fig 9) numerous smooth black circular spore like bodies which averaged 54um in diameter. No fertile material of Thursophyton milleri has previously been recorded and the isolated nature of this specimen is not proof that T. milleri has erect apical sporangia.

SKERSUND

Morphology: A few poorly defined fragments of branching axes apparently glabrous were found and these show pseudomonopodial, dichotomous and in one specimen a trichotomous branch (Plate 6 figs 1,2,3). The widest fragment (Plate 6 fig 1) measured 3mm across, the smallest 0.5mm (x=2.5mm n=18). One specimen was 145mm long (Plate 6 fig 8) and was partly permineralised. The branching angle varied from 40-50' (x=45' n=10), the larger fragments generally had smaller branching angles. Spines were not visible on any of the axes. No cuticular material was recovered from transfers or macerations. Numerous axes were preserved as permineralised fragments. These were sectioned

and the anatomy examined.

Anatomy: No tracheids or preserved anatomy has previously been recorded for this species of Thursophyton although both T. elberfeldense (Krausel and Weyland 1923) and Euthursophyton hamperbachence (Mustafa 1978) have a terete exarch primary xylem. Høeg (1967) described the tracheids of T. elberfeldense as having sclariform thickening with circular perforations. He also gives measurements of the protoxylem as 14um wide and metaxylem as 130um wide. He records the absence of foliar traces, and a dense "polyhedral cortex with a hypodermis of elongated cells and an epidermis and cuticle without stomata". Høeg (1967) also describes the possible presence of elongated phloem cells.

These observations by Høeg (1967) and the original description by Kräusel and Weyland (1923) were made using reflected light microscopy from poorly prepared surfaces. Since this work was carried out techniques have improved, and in this thesis plastic embedding of permineralisations was carried out and transverse and longitudinal sections made. The specimens from this locality were preserved only in pyrite and treated as described in the techniques chapter. Etching was carried out in HNO3 to enhance the contrast of polished sections. A metallurgical polish was also used for examination under incident light. Cellulose acetate peels were also prepared to preserve a permanent record of the anatomy (Plate 11 fig 3,4, Plate 13 figs 4-8).

After polishing the transverse and longitudinal sections were prepared for the SEM and again after shallow and deep

etching in HNO3. One specimen showed excellent preservation and was sectioned both transversely (S38-40) and longitudinally (S37). Plate 11, (figs 1-7) shows a massive elliptical stele with protoxylem towards the periphery and metaxylem forming the majority of the stele located in the centre (Plate 11 figs 1-7). A thickened outer cortex (Plate 11 figs 1,2,3,6) can be seen consisting of large uniform cells. There is also a suggestion of a poorly preserved phloem (Plate 11 figs 6,7).

The classification of the stelar type was based on Schmid's (1982) review paper and in Thursophyton milleri it was determined to be a solid exarch protostelic column of vascular tissue which was ectophloic and haplostelic with the central eliptical xylem being all tracheary. In longitudinal section (Plate 13 figs 1-8) the tracheids appear to have annular thickening (Plate 13 fig 8, Plate 14 fig 1,2,3, Plate 16 figs 4,5) and a perforate wall between the bars of thickening. This was confirmed by the SEM (Plate 14 figs 5-7, Plate 15 figs 4,7, Plate 16 figs 1,6). In the protoxylem elements however helical thickening was also present together with annular thickening Plate 16 (fig 6) also shows branching of the thickening bars. The pores visible under the SEM indicate that those of adjacent perforate walls do not overlap (Plate 16 figs 1-3) and are randomly arranged. Connection between end walls of the tracheids is shown by Plate 17 (figs 1-3), in which the ends of the tracheary elements join with closely fitting tapering ends. In transverse section the maximum diameter of the protoxylem, from thickening bar to thickening bar was on

average 22.11um and of the metaxylem 35.14um. Table 1 shows a series of dimensions taken from the tracheary elements in transverse and longitudinal section.

Table 1. Metaxylem element dimensions of Thursophyton milleri from Skersund (sections S37-40).

	At.	Ap.	Ad.	dmax.	D.	Tw.	L.
x. um.	4.59	7.67	4.98	35.14	19.80	5.56	679.6
min um.	2.93	6.13	1.95	27.32	15.06	2.93	375.5
max um.	6.13	10.31	12.27	48.83	28.21	8.43	931.4

n=30

At. = thickness of annular thickening.
Ap. = distance annular thickening protrudes into lumen.
Ad. = distance between annular thickening.
dmax. = maximum lumen diameter.
D. = (dmax - 2Ap)= effective diameter for water conduction.
Tw. = wall thickness across adjacent cells.
L. = length of metaxylem element.
See text and fig.14 for explanation of measurements taken.

Sandwall.

Morphology: A few specimens of predominantly large, pseudomonopodial axes, which are poorly preserved as stained impressions (Plate 6 figs 4,5,6,7) were found from this

locality. Some were apparently glabrous (Plate 6 fig 4) while others showed robust spines (Plate 6 figs 5,6). The largest fragment measured 112mm long and 3mm wide (Plate 6 fig 7). The width of the axes varied from 1.5mm (Plate 6 fig 6) to 9mm (Plate 6 fig 4) (x=4.5mm n= 14). The distance between branching was determined on average to be 25mm in the smaller axes. The larger axes were too fragmented for measurements to be made. The branching angle varied between 35-50' (x=41' n=12) and was generally smaller in the larger axes. Rigid spines were found on the majority of axes (Plate 6 figs 5,6) and appeared to emerge from a thickened base 0.5-0.9mm wide (x= 0.6mm n=17). The spines were rarely complete, being broken or covered by matrix, and did not taper being 2-6mm long (x=4mm n=17), and 9-16mm apart. No cuticle was recovered from transfers or macerations of this material.

Anatomy: Numerous permineralisations in limonite were found (Plate 6 fig 5), but the majority were poorly preserved and showed little or no cellular detail. One specimen was reasonably preserved in limonite and pyrite. This specimen was sectioned transversely and longitudinally. Sections were made until the apex of the axis was reached (Plate 9 figs 1,2,3). The majority of sections crumbled when cut or when polished . Those that survived were polished for viewing under incident and reflected light as well as by the SEM. Cellulose acetate peels were unsuccessful and the sections treated as explained in the techniques chapter. Plastic re-embedding was found to essential be for this

material.

Stelar type was identified as an exarch protostelic haplostele. Plate 7 (figs 1-8) and Plate 8 (fig 1) show a circular stele partially preserved, but clearly visible is the protoxylem towards the periphery (Plate 7 figs 2,3, Plate 8 figs 2,5), and the larger metaxylem elements forming the majority of the central area of the stele (Plate 7 fig 8, Plate 8 fig 4). A thickened outer cortex is also present (Plate 7 figs 1,2,3,5,7, Plate 8 figs 1,3, Plate 10 fig 8). In longitudinal section (Plate 9 figs 4,5,6) the tracheids appear short and strap shaped, probably as a result of a slighty oblique section rather than a different xylem morphology. Thickening was seen to be annular (Plate 9 figs 5,6). This is confirmed by the SEM (Plate 10 figs 1,2,4-8), there is however a suggestion of helical thickening bars (Plate 10 fig 3). In the totally demineralised sections (Plate 10 figs 4-7), the annular nature of the thickening bars can be seen together with possible branching of these bars (Plate 10 figs 4,6). A perforate wall between the bars of thickening is present. Plate 10 (fig 6) shows that there is no alignment of these pores with adjacent tracheids and that the pores are therefore randomly arranged. The average maximum diameter of the metaxylem elements was 39.06um and the average protoxylem diameter was 20.66um. Table 2 shows a series of measurements taken from the metaxylem elements in transverse and longitudinal section.

Table 2. Metaxylem element dimensions for Thursophyton

milleri from Sandwall (SNT 007-001)

	At.	Ap.	Ad.	dmax.	D.	Tw.	L.
x um.	3.49	9.29	7.48	39.06	20.48	3.72	508.4
min um.	2.95	5.58	4.88	28.77	17.61	1.86	333.3
max um.	7.43	11.15	9.48	65.05	39.75	5.58	677.9

n=12

At. = thickness of annnular thickening.

Ap. = distance annular thickening protrudes into lumen.

Ad. = distance between annular thickening.

dmax. = maximum lumen diameter.

D. = (dmax - 2Ap) = effective diameter for water conduction.

Tw. = wall thickness across adjacent cells.

L. = length of metaxylem element.

Wick of Sandarye.

Morphology: Poorly preserved fragments of apparently spiny axes showing pseudomonopodial branching (Plate 40 figs 3,4,5). The largest specimen measures 50mm long and 5mm wide and shows spines preserved along the margin of the axis (Plate 40 fig 5). Width of axes varied between 1.5 and 6.4mm (x= 3.9 n=9). The spines were between 0.7 and 1.8mm (x=1.1mm n=12) long, the majority were poorly preserved and incomplete being damaged by the coarse matrix during deposition. Branching was pseudomonopodial with the distance between branches of 22 and 25mm (x=23mm n=4). The branching angle was acute between 10 and 25' (x=12' n=4). Plants from this locality were identified by the author as

c.f. Thursophyton milleri. No cutile or anatomy was found from this locality.

Voe of Clousta.

Morphology: A few rare fragments of glabrous axes were found but the majority did not show branching. One however showed a trichotomous division, and this specimen measured 3.3mm wide and 23mm long. On the basis of this morphology the fragmentary specimens were identified by the author as c. f. Thursophyton milleri. No cellular information was found from this locality.

Foula.

Morphology: A large number of well preserved specimens were collected from South Ness. These included large spiny axes showing pseudomonopodial branching (plate 47 figs 2,3,6, Plate 48 fig 3) and smaller axes showing dichotomous divisions (Plate 47 fig 5, Plate 48 fig 1). A suspected spiny rhizome was also found (Plate 47 fig 7), as were numerous circinately coiled tips (Plate 47 fig 4, Plate 48 figs 5,6,8). A few rare isolated sporangia were recovered present terminally on recurved glabrous tips, on average these measured 1.2mm long and 0.44mm wide (Plate 48 fig 4). One specimen (Plate 47 fig 1) showed two successive trifurcations, the axis being pseudomonopodial. The largest specimen measured 195mm long and 8mm wide (Plate 47 fig 6) and showed pseudomonopodial as well as dichotomous

divisions. The specimens measured 10-0.5mm wide (x=4mm n=30). The distance between branching in the larger pseudomonopodial axes was from 30 to 50mm (x=39mm n=20). In the smaller dichotomous axes branching was frequent and the distance between branches varied between 8 and 20mm (x= 14 n=25). The angle of branching was usually smaller in the larger axes, between 15-45' (x=25' n=25) and never exceeded 45'. In the smaller dichotomous axes the angle of branching was greater varying from 35-85' (x=40 n=25) and never exceeds 85'.

On the larger axes spines when present were dense (Plate 48 fig 6) and distally sparse or absent in the smaller axes. The spines on specimens from Foula varied from 0.8 to 2.9mm (x=1.6mm n=30) and were particularly dense and well preserved on the circinately coiled apical fragments (Plate 48 figs 5,8). These spiny coiled apical tips have been considered a characteristic feature of the genus (Hoeg 1967, Lang 1925, Nathorst 1915). The spines and spine bases were clearly visible on a number of axes (Plate 47 figs 5,2,3) and were often almost as long as the axis was wide. They were seen to emerge from a thickened base (Plate 48 fig 7) which varied in width from 0.4 to 0.7mm (x=0.6mm n=30). The circinately coiled tips were presumed to be the apical portions of axis arising from a rhizome although none were found in connection. A possible rhizome structure was found (Plate 47 fig 7), and this showed pseudomonopodial as well as dichotomous branching of spiny axes. An aerial portion arising from this structure was however glabrous.

Transfers were carried out for cuticle on well preserved

fragments of axes. The majority of these were unsuccessful, but one specimen did produce a possible cuticle (Plate 49 figs 5,6). This showed no cellular detail when prepared for the SEM. Numerous pores were visible and were considered to be possible primative stomata. Transfers were also carried out on possible sporangia (Plate 49 figs 1,2,3,4). Microspores were obtained and prepared for the SEM. These measured between 29.31 and 69.81um (x=47.45 n=8), and were smooth without a visible trilete mark. These spores were considered to be immature and of little diagnostic value (Marshall pers. comm. 1987). Spores of the trimerophytes range from 40 to 120um with a partially enclosed granular layer and a trilete mark, the spores being present in large numbers (Gensel and Andrews 1984). Spores of the Zosterophyllophytes are smooth trilete spores ranging from 36 to 90um with 50 to 100,000 spores per sporangia (Gensel and Andrews 1984). This would suggest that the spores found here may be of the zosterophyll type being smooth and smaller than the typical trimerophyte spore type.

Numerous suspected permineralised axes were found and the majority of these were poorly preserved in limonite and showed no cellular detail. One however (Plate 49 fig 7) was of reasonable preservation and when sectioned showed anatomy.

Anatomy: Transverse and longitudinal sections were made after plastic embedding of the specimen was carried out. Preservation was poor and re-embedding was necessary. Under reflected light the polished sections clearly showed

protoxylem elements towards the periphery, and metaxylem elements forming the bulk of the stele (Plate 49 fig 8, Plate 50 figs 1-9, Plate 51 figs 1-6). The preservation was almost totally in limonite and shallow etching in HCL was essential to increase contrast between the limonite infilling the lumen and that infilling the cell walls together with any carbon remaining. A section was prepared for the SEM, however because of the lack of contrast little cellular detail was visible (Plate 50 fig 1), but there is a suggestion of annular thickening, which can also be seen under reflected light (Plate 50 fig 4). When deeply etched in HCL (Plate 50 figs 2,3) the limonite was preferentially removed from the cell wall leaving a cast of the cell lumen.

Transverse sections were made closer to the apex (Plate 50 figs 5-9, Plate 51 figs 1-6), these showed identical preservation with little carbon remaining in the cell walls. Serial sections were taken and the polished sections etched in HCL. From these it was possible to conclude that the stele was an elliptical exarch protostelic haplostele, the section also revealed an incomplete dichotomous branch. Plate 51 (figs 1-4) illustrates the better preserved specimens in which two separate axes can be distinguished. Plate 51 (figs 5,6) shows the disrupted nature of the vascular tissues, but a clearly defined massive centrally located exarch protostele can be seen surrrounded by a thickened cortex. Deep etching of this material failed to enhance the contrast and caused the cell walls to collapse. Preparations for the SEM also failed to reveal any further information and no details confirming the presence or

absence of a perforate cell wall were found. Those measurements that were made are listed in Table 3. The average maximum diameter of metaxylem elements from this locality was measured in longitudinal and transverse section and was 41.01um, the average diameter of the protoxylem being 28.25um. Some difficulty was encountered in making accurate measurements because of the poor quality of the material.

Table 3. Metaxylem element dimensions for Thursophyton milleri from Foula (SNF 001-012).

	At.	Ap.	Ad.	dmax.	D.	Tw.	L.
x um.	2.93	5.65	8.47	41.01	29.71	3.39	542.8
min um.	2.82	3.39	5.58	33.90	27.12	2.26	356.7
max um.	3.95	7.34	11.72	64.97	50.29	4.52	721.9

n=14

At. = thickness of annular thickening.

Ap. = distance annular thickening protrudes into lumen.

Ad. = distance between annular thickening.

dmax. = maximum lumen diameter.

D. = (dmax - 2Ap)= Effective diameter for water conduction.

Tw. = wall thickness across adjacent cells.

L. = length of metaxylem element.

NORWAY

Specimens of Thursophyton milleri were examined from Oslo and Bergen Museums. The type specimens used by Nathorst (1915) were obtained for study from the Bergen Museum, these were originally collected from Gjegnalundsbreen, Gloppen, Nordfjord in 1910 by Omvik. The specimens are: p00009, p00020, p00023 illustrated on Plate 5 (figs 3,8,9) and Plate 6 (fig 1) in Nathorst 1915. Specimens p10001, from Bergen, and pa1236 from the Oslo Museum were used by Høeg in 1931 on Plate 11 (fig 3), and in 1944, on Plate 5 (fig 1), to illustrate the Devonian flora of western Norway. Specimen p10001 was collected by Omvik in 1910 from the Svartvatnet area in Nordfjord. While specimen pa1236 was collected from Tristein by Høeg in 1927 (locality 1) in the Trondenheimsfjord region.

These specimens were used to compare the type material from Norway with that found from Mainland Scotland, Shetland, Greenland and unpublished material from Norway. The specimens examined from Norway came from Tristein locality 3 (pa4443) and locality 5 (pa3797, pa3811, pa3812, pa1309, pa1317, pa1283), Høeg collected the material in 1927 and described the locality in his paper of 1944 identifing the specimens from the island as of the Psilophyton type, together with axes of Thursophyton milleri.

Nordfjord

Morphology: The type specimens (Nathorst 1915) showed pseudomonopodial branching in the larger axes and dichotomous divisions in the smaller axes closer to the apex (Plate 52 figs 1,4,5). One of Høeg's figured specimens (p10001) from this region (Plate 52 fig 2) showed a trichotomy of branching typical in this species found from other localities. The width of the axes measured varied between 2 to 7mm wide (x=4.1 n=7). The largest specimen (p00020) measuring 180mm long (Plate 52 fig 4), while another (p00009) showed a possible trifurcation (Plate 52 fig 1), a further specimen (p00023) was considered by the author to be a rhizome structure and showed pseudomonopodial branching and possible simple rhizoids emerging from the axis (Plate 52 fig 5) . The distance between branching varied from 36 to 62mm (x=41 n=10). While the branching angle varied between 30-50' (x=44' n=12) in the larger axes and between 45-80' (x=50 n=7) in the smaller dichotomous divisions. All of the axes examined were found to be covered with spines, these were especially dense on the larger axes appearing less frequent distally. Spines and spine bases were particularly well preserved on one specimen p00020 (Plate 52 fig 4) and in general measured between 1.0-2.5mm long (x=1.6 n=30). The spines were fine, rarely complete and emerging from a thickened base which appeared triangular on the margin of the axis. The bases varied from 0.1 to 0.4mm (x=0.3 n=30) in width. Permission to section or treat the material was not given because of their importance as type specimens.

Trondenheimsfjord

Morphology: Høeg in 1927 collected specimens from numerous localities on Tristien identifing them as being identical with the type specimens of Thursophyton milleri. These specimens (Plate 52 fig 3, Plate 53 figs 1-7) showed predominately pseudomonopodial branching in the main axes and dichotomous divisions in the smaller side branches. The width of the axes varied from 1.1 to 5.0mm (x=2.5 n=8). The largest specimen measured 165mm long and 2mm wide and branched pseudomonopodially followed by dichotomous branching of the minor axes (Plate 5 figs). The distance between branches varied between 65 and 22mm (x=35mm n=15), generally decreasing distally. The angle of branching was slightly greater in the larger axes, between 35-50' (x=39' n=8) while in the smaller dichotomous axes the angle varied between 45-60' (x=47 n=7). Robust needle like spines were present on all the axes, being less dense distally (plate 53 figs 1,2,3,4,6). Circular spine bases could also be distinguished (Plate 53 fig 2). The length of the spines were measured and found to be between 3 and 7mm (x=5mm n=20), and in many cases longer than the axis was wide. The fine asicular spines emerged from thickened bases (Plate 53 figs 3,4) which measured from 0.25 to 1mm wide (x=0.4mm n-20) they were rarely complete and possibly longer than stated. One specimen (pa4443) showed a typically diagnostic circinately coiled apex. When sectioned (Plate 53 figs 3,4) this specimen clearly showed the emergence of the spines

from the margin of the axis.

Transfers were attempted on other fragments of axis showing possible cuticle but none were successful. No fertile material was found from the limited number of specimens examined from this locality. Numerous permineralisations in pyrite were found (Plate 53 figs 5,7) these were embedded and sectioned. Most of the specimens were well preserved.

Anatomy: Specimens pa3812 (Plates 54, 57, 58, 59) and pa1317 (Plates 55, 56) contained the best preserved axes . These were sectioned transversely and longitudinally, the resulting sections were polished and etched in HNO3 as described in the techniques chapter. A metallurgical polish was also applied for viewing under incident light (Plates 55, 57 figs 2, 4-6,8, Plate 49 figs 3,4). SEM observations were taken after polishing (Plate 58 fig 1,2), shallow etching (Plate 56 figs 2-4, Plate 57 fig 3, Plate 58 figs 3-5) and deep etching (Plate 56 figs 5-7, Plate 58 figs 6,7,9, Plate 59 figs 5-8). Cellulose acetate peels were taken, where the amount of carbonised wall remaining was high, to preserve a permanant record of the axis (Plate 59 fig 2).

One specimen pa3812 was found to contain numerous axes , one of which (pa3812a) was sectioned serially in transverse section (Plate 54 figs 1-8) and showed a trifucation of the stele. Initially the stele is a massive, elliptical, centrally located protostelic haplostele, surrounded by an outer cortex of thickened cells (fig 1). This deforms (fig

2) by cellular development at one end of the stele, which then develops into two areas (figs 3,4). These are delimited by development of protoxylem and finally separate at the same time (fig 5). The two separate steles then diverge from the parent stele (fig 6) and a cortex begins to develop between the new steles (fig 7). The divergence finally ends when the cortex separates leaving three distinct steles two of which are preserved (fig 8). The division appears to be an unequal one, occurring simulaneously forming three separate axes. It is probably a development of two very close dichotomies, but the trifurcation appears to be a single dichotomy in which one stele undergoes a further dichotomy at the same time, forming three steles. Trichotomies and trifurcations are rare but present from the majority of localities and must therefore be considered a significant diagnostic feature.

An additional axis found in the same specimen (pa3812b) was sectioned longitudinally (Plates 57, 58) and transversely. In transverse section the exarch nature of the stele is confirmed (Plate 59 figs 1-8) and an outer cortex can be seen formed from dense thick walled circular cells. Occassinal spiral thickening of the protoxylem was seen (Plate 56 fig 6) From the longitudinal sections the xylem tracheids appear long with annular thickening (Plates 57, 58). Branching of the bars of thickening was seen in deeply etched material veiwed under the SEM (Plate 58 figs 6,7) and a porate wall between the bars of thickening was clearly visible (Plate 57 figs 4,6, Plate 58 figs 3,7,9). Adjacent end walls of the tracheary elements were seen when

observed using the SEM and the random nature of the pores was confirmed and there was no alignment with those on the adjacent cell (Plate 57 figs 4,5). Longitudinally sectioned cortical cells were also visible as thick walled elongated uniform cells (Plate 58 fig 8).

An additional specimen (pa1317) of excellent preservation was sectioned transversely and longitudinally, again clearly showing the massive elliptical stele (Plates 55, 56), with protoxylem (Plate 55 fig 2,4), with occassional spiral thickening (Plate 59 fig 7), situated towards the outside and the bulk of the stele being metaxylem, with annular thickening (Plate 55 fig 2,3). Cortical cells are also visible and occur as uniform, thick walled circular cells in transverse section. This is shown in greater detail by the SEM (Plate 56) viewed after shallow etching (fig 2-4) and deep etching (fig 5-7) with HNO3. From these sections the average maximum diameter of the protoxylem elements was 16.60um and the average metaxylem diameter was 55.76um. Table 4 shows a series of dimensions taken from the metaxylem tracheary elements in transverse and longitudinal section.

Table 4. Metaxylem element dimensions for Thursophyton milleri from Tristein Norway.

	At.	Ap.	Ad.	dmax.	D.	Tw.	L.
x um.	5.86	7.91	6.51	55.76	39.94	6.85	978.2
min um.	3.09	5.79	4.65	34.18	22.60	4.96	631.0
max um.	11.59	15.44	8.36	86.78	55.90	7.81	1141.3

n=30

At. = thickness of annular thickening.

Ap. = distance annular thickening protrudes into lumen.

Ad. = distance between annular thickening.

d max. = maximum lumen diameter.

D. = (dmax - 2Ap) = effective diameter for water conduction.

Tw. = wall thickness across ajacent cells.

L. = length of metaxylem element.

GREENLAND.

Numerous specimens were obtained and examined from east Greenland. These were collected by Friend in 1968, among the species identified were Svalbardia (Plate 60 fig 1,5), together with c.f. Pseudosporochnus (Plate 60 fig 4), From Ella. A fertile portion of c.f. Rellimia (Plate 60 fig 2), from Canning land and various unassigned axes (Plate 60 fig 3) and sporangia (Plate 60 fig 6). Hudson land yeilded Thursophyton milleri (Plate 60 figs 7-9), which was examined in detail.

Hudson land.

Morphology: Large spiny pseudomonopodial 2-12mm (x=6 n= in width. Dichotomous branching was not seen, possibly because only large axes were examined. The largest measuring 110mm long and 7mm wide. The angle of branching was determined to be between 45-50' (x=47 n=6), the distance

between branching could not be measured because of the fragmentary nature of the specimens. Long ascicular spines were present on all the axes examined and were 3 to 9mm (x=5mm n=20) in length. The spines densely covered the axes and emerged from spine bases 0.27-0.50mm (x=0.38mm n=20) wide, that could be seen as im pressions (Plate 60 figs 7-9). Transfers for cuticle were attempted but proved unsuccessful, and no fertile material was found. A large number of fragmented axes permineralised in limonite and pyrite were identifed. One of these was of reasonable preservation (Plate 61 figs 2,3).

Anatomy: The axis was embedded in plastic and sectioned as described in the techniques chapter. Re-embedding proved to be essential to hold the delicate axes together. Sections were polished and etched in HCL and NHO3 to enhance the contrast of the cell walls with the limonite/pyrite. Only one section provided detailed information (Plate 61 figs 6,7) in the form of a massive, centrally located, exarch, protostelic, haplostele. No cortex was preserved, this being represented by a bands of pyrite and carbonised material. Long, thin spines emerged from thickened bases in this carbonised layer (Plate 61 fig 4). Plate 61 (figs 6,7) shows the metaxylem and protoxylem tracheary elements, the average maximum diameter of which was 67.57um and 45.97um respectively. Metallurgical polishing techniques proved to be unsuccessful with this material, the stele pilling during polishing. Deep etching was also unsuccessful as it caused the collapse of the cell walls. Table 5 shows those

measurements that could be taken from the transverse sections, with some difficulty in determining the cell walls.

Table 5. Metaxylem element dimensions for Thursophyton milleri from Hudson land.

	dmax	Tw
X um.	67.57	5.75
min um.	40.54	3.52
max um.	108.11	9.87
n=20		

dmax. = maximum lumen diameter.
Tw. = wall thickness across adjacent cells.

COMPARISIONS BETWEEN THE TWELVE LOCALITIES.

The measurements and dimensions of Thursophyton milleri are presented in Table 6.

	1	2	3	4	5	6	7	8	9	10	11	12
bt.	p	pt	d	pd	pdt	p	p	t	ptd	ptd	ptd	p
ba.'	34	41	55	8	45	41	12	-	32	47	43	47
aw.mm.	3.0	5.7	1.8	3.1	2.5	4.5	3.9	-	4.0	4.1	2.5	6.0
bd.mm.	-	-	-	30	-	25	23	-	26	41	35	-
sl.mm.	1.0	-	-	0.6	-	4.0	1.1	-	1.6	1.6	5.0	5.0
sb.mm.	0.2	0.7	-	0.2	-	0.6	-	-	0.6	0.3	0.4	0.4
ss.	-	-	-	-	E	C	-	-	E	-	E/C	E

	1	2	3	4	5	6	7	8	9	10	11	12
sm.	-	-	-	-	ex	ex	-	-	ex	-	ex	ex
xt.	-	-	-	-	an	an	-	-	an	-	an	-
mx.um.	-	-	-	-	35	39	-	-	41	-	56	67
px.um.	-	-	-	-	22	21	-	-	28	-	17	46
sl.mm.	-	-	-	2.6	-	-	-	-	1.2	-	-	-
sw.mm.	-	-	-	0.6	-	-	-	-	0.4	-	-	-
sp.um.	-	-	-	55	-	-	-	-	47	-	-	-
At.um.	-	-	-	-	4.6	3.5	-	-	2.9	-	5.9	-
Ap.um.	-	-	-	-	7.7	9.3	-	-	5.6	-	7.9	-
Ad.um.	-	-	-	-	5.0	7.5	-	-	8.5	-	6.5	-
dmax.um.	-	-	-	-	35.1	39.1	-	-	41.0	-	55.8	68
D.um.	-	-	-	-	19.8	20.5	-	-	29.7	-	39.9	-
Tw.um.	-	-	-	-	5.6	3.7	-	-	3.4	-	6.8	5.7
L.um.	-	-	-	-	680	508	-	-	543	-	978	-

1=Kinkell. 2=Navity. 3=Eathie. 4=Leebotton. 5=Skersund. 6=Sandwall. 7=Wick of Sandayre. 8=Clousta. 9=Foula. 10=Nordfjord (type specimens). 11=Trondenheimsfjord. 12=Hudson land

bt=branching type. ba=branching angle. aw=axis width. bd=distance between branching. sl=spine length. sb=width of spine base. ss=stelar shape. sm=stelar maturation. xt=xylem thickening. mx=metaxylem maximum diameter. px=protoxylem maximum diameter. sl=sporangial length. sw=sporangial width. sp=spore diameter.

p=pseudomonopodial habit. d=dichotomous branching. t=tirfucations. E=elliptical. C=circular. ex=exarch. an=annular.

At=thickness of annular thickening. Ap=distance annular

thickening protrudes into lumen. Ad.=distance between annular thickening. dmax=maximum lumen diameter. D=effective diameter for water conduction. Tw=wall thickness across adjacent cells. L=length of metaxylem.

The mode of branching is predominatly pseudomonopodial, with occassional trifurcations becoming dichotomous distally. The branching appears planar in all localities, with no suggestion of a complex three dimensional habit. At Kinkell, Sandwall, Wick of Sandayre, and Hudson land the branching found was only pseudomonopodial. This is most likely to be the consequence of poor preservation, sorting prior to deposition, and lack of an adequate number of specimens. Branching angles are generally smaller in the larger axes and increase as the size of the axes decreases and branching becomes dichotomous. The range of axes widths is similar in all localities with only Foula (8mm) and Navity (20mm) showing axes significantly larger than the average. The average distance between branching is only slightly higher in Nathorsts (1915) type specimens and is elsewhere very similar. This may be caused by the selection of type specimens resulting in a sample of large well preserved axes, neglecting smaller axes.

Circinately coiled apical fragments were suprisingly uncommon since this is considered by Høeg (1967), Lang (1925), and Nathorst (1915), as a distinctive feature of the genus, which also occurs in other species of Thursophyton (Kräusel and Weyland 1923, 1930). They were however found on Foula, a locality where a large amount of material was

recovered. They were however absent from localities were limited numbers of specimens were found. This may suggest that they are not a common feature of the plant. There is a large variation in spine length from 0.6 to 5.0mm but similarity in base width. This variation may well be a consequence of poor preservation in some localities. Sandwall however showed spines that were not ascicular and did not taper. They appeared almost like rhiziods and it may be possible that the specimens from Sandwall represent rhizome material. It is here considered that variation in spine morphology is not significant enough to prove rhizomatous habit or to seperate the specimens from Sandwall from other localities. Variation in spine morphology was noted by Lang (1925) and the variation found at Sandwall and in the other localities may reflect natural variation, possibly under environmental control.

The reduction in spine number towards the apex is a feature seen in other species (Høeg 1967) and in other zosterophylls (Kennrick unpublished thesis University of Cardiff 1988), as well in the type material of Nathorst's 1915 description. A good case can be made for the fertile material found to be part of Thursophyton milleri on the basis of association and in the case of that found from Foula no other plant was identified from the locality. So there remains a possiblity that T. milleri has terminal erect or recurved sporangia containing smooth spores between 47 and 55um in diameter.

Anatomy: Bierhorst's (1960) terminology is used to

describe the tracheary elements of Thursophyton milleri. A primary tracheary element is defined as possessing a thin continuous unlignified first formed wall, the primary wall, and a relatively thick discontinuous lignified later wall, the secondary wall (see text figure 14). In extant plants the cellulose wall is capable of stretching. Because this can not be demonstrated in fossil plants Beirhorst has suggested that presumed primary wall should be used. His description of annular elements includes simple thickening where the rings are distinct, directly attached thickening where adjacent rings are joined directly to each other, and indirectly attached thickening where adjacent rings are connected by sheets of secondary material, partly covering the presumed primary wall. Beirhorst describes various helical thickenings but does not mention indirectly attached helical thickening as seen in T. milleri. The xylem measurements for T. milleri are given in Tables 1-5 and summarised in Table 6. A reconstruction of a xylem element and cross sections of the walls showing the measurements taken is given by text fig 14.

Plates 7-14, 50-51, 54-59, and 61 illustrate the anatomy which includes a central elliptical, often massive stele and a peripheral zone consisting of possible phloem and a thickened outer cortex. The area between probably represents the space occupied by the inner cortex. Controlled etching demonstrates layers of carbonised material outlining the cells and presumed to represent the remains of cell walls (Edwards 1980(b), 1981). Such carbonised walls are assumed to have been originally

lignified and hence comprise the secondary wall. The permineralised areas within the cell wall were therefore originally the cellulose primary wall. In well preserved specimens the primary wall has also been preserved together with other unlignified walls such as the phloem (Plate 14 fig 8).

From the majority of localities the elliptical outline of the stele seen in transverse section (Plate 12 fig 5, Plate 50 fig 8, Plate 55 fig 1, Plate 61 fig 4), is thought to represent the original shape of the xylem because individual cells show little or no signs of compression. The smallest cells interpreted as protoxylem (17-46um in diameter) form a peripheral layer. The bulk of the stele comprises indirectly attached annularly thickened elements interpreted as metaxylem (35-67um in diameter). The elements are polygonal in outline (Plate 7 fig 8, Plate 12 fig 8, Plate 51 fig 3, Plate 59 fig 8). The dimensions are given in Table 6. A few elements show direct connections between the annular bars (Plate 10 fig 6, Plate 16 fig 6, Plate 58 fig 7) and occassional elements with indirectly attached helical thickenings (Plate 16 fig 5, Plate 56 fig 7, Plate 59 fig 7) and these were seen predominatly in the peripheral elements.

In fossil plants the smallest elements are considered to represent the protoxylem. Apart from their smaller size they differ in this material from the metaxylem by having occassional helical thickenings. It is possible therefore that all the elements are metaxylem, the protoxylem having disintergrated before or during permineralisation. In some specimens a coalified layer remains surrounding the stele

(Plate 12 figs 6,7). This may represent the earliest remains of protoxylem elements or alternatively phloem cells. The smallest marginal elements are considered by the author to represent protoxylem where the inter-thickening lignified secondary wall was laid down after cell extension (Beirhorst 1960).

This description of xylem anatomy is almost identical to that given by Kennrick (1988) for Gosslingia breconensis, Deheubarthia splendens and Thrinkophyton formosum. The coalified remains of the wall of each element encloses a pyrite or limonite filled lumen. The coalified wall is often infilled by a layer of permineralised material shown in text figure 14 and is termed wall pyrite/limonite and is clearly visible in transverse and longitudinal section (Plate 12 fig 2, Plate 14 fig 2, Plate 51 fig 3, Plate 55 fig 2, Plate 58 fig 1,2). In longitudinal section the coalified remains of annular and more rarely helical thickenings protrude into the lumen as peg like structures (Plate 9 fig 6, Plate 10 fig 2, Plate 14 fig 3, Plate 50 fig 4, Plate 57 fig 4, Plate 58 fig 2). The surface of these thickening bars lacks perforations (Plate 10 fig 7, Plate 16 fig 6, Plate 58 fig 9). The thickening bars were never seen to be filled with pyrite or limonite, possibly indicating that they were formed from secondary wall only. Where a section passed through the annular thickenings, a ladder like appearance simulating sclariform thickening results (Plate 10 fig 3, Plate 14 fig 3, Plate 57 fig 4, Plate 58 fig 1). This effect would be heightened if the annular bars did contain pyrite or limonite. Sections such as these can

be seen in Euthursophyton hamperbacence (Mustafa 1978) and Thursophyton elberfeldense (Kräusel and Weyland 1923) and may have lead to the erroneous description of sclariform thickening in these species.

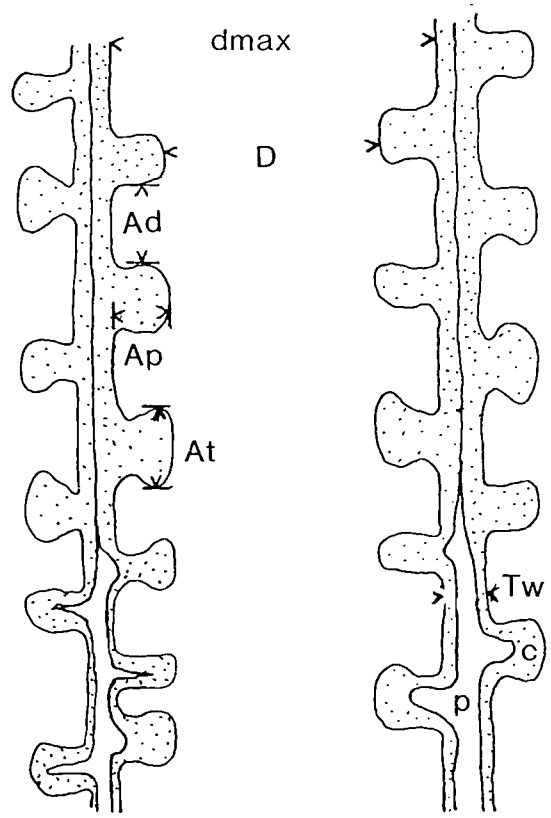
The coalified wall linking the bars of thickening is perforated by numerous round holes of various sizes (Plate 10 figs 6,7, Plate 13 figs 8, Plate 14 figs 5,6, Plate 15 fig 7, Plate 16 fig 7, Plate 57 fig 6, Plate 58 figs 3,7,9) and filled with pyrite (Plate 14 figs 5,6, Plate 57 fig 4,6). Perforations often appears to fuse with each other (Plate 10 figs 6,7, Plate 15 fig 7). A reconstruction of the coalified wall is given in Text Figure 14. The similarities in anatomical details was considered to be a significant feature confirming the morphological information.

Anatomy of peripheral tissues: A thick walled outer cortex is present in specimens from all the localities except Greenland. In transverse section the cells are of variable size but predominatly circular (Plate 7 figs 3,4,7, Plate 8 figs 5,9, Plate 11 fig 6, Plate 12 figs 5,9, Plate 51 figs 3,4, Plate 55 figs 1-5, Plate 59 figs 1,2,5,6), with a mean diameter of 67um. There is occassionally a layer corresponding to the wall pyrite/limonite of the tracheids (Plate 55 fig 5) but more often they form a continuous coalified layer (Plate 12 fig 9, Plate 58 fig 8). In lonitudinal section the cortex appears elongated (Plate 10 fig 8, Plate 13 fig 4,6, Plate 58 fig 8), on average 263um long. The walls appear to be on average 3,7um thick but

never greater than 5.5um, and frequently the walls are distorted (Plate 12 fig 5,9) probably before or during permineralisation. The cell walls appear smooth without ornamentation or perforation (Plate 12 fig 9, Plate 58 fig 8, Plate 55 fig 5). At one locality at Skersund a primitive phloem was tentatively identified consisting of large thin walled cells 2.6um thick and 52um in diameter. In appearance they were similar to parenchyma with no suggestion of seive elements.

The measured characteristics of the twelve localities are similar, except for Sandwall where spine morphology and the circular nature of the stele (Plate 7 fig 1) are different from the remaining localities. But a circular stele is seen after the division of an elliptical stele in a specimen from Tristein, Norway (Plate 54 fig 7). These differences were not considered significant enough to separate this locality from the species definition. Because of limited morphological and anatomical details, the localities at Eathie, Kinkell, Wick of Sandayre and Clousta were named as c.f. Thursophyton milleri and require further well preserved specimens for a positive identification to be made. The main problem encountered was small sample size which accounts for a considerable amount of variation. The following features, xylem maturation, xylem element structure, spine morphology and branching type are all considered important characteristics and on the basis of the presence of one or more of these specimens from the twelve localities are placed in the same genus.

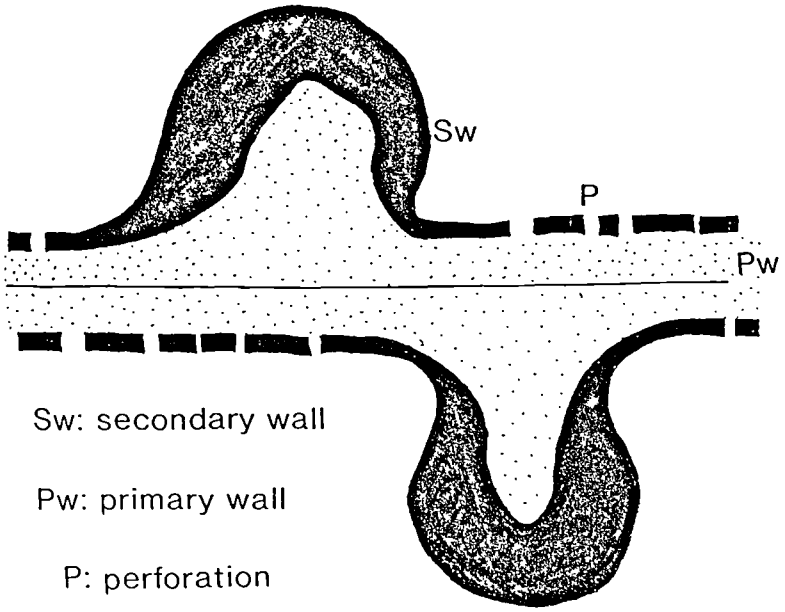
Text Figure 14 Metaxylem element of Thursophyton milleri



D=(dmax-2Ap)

c: carbon wall

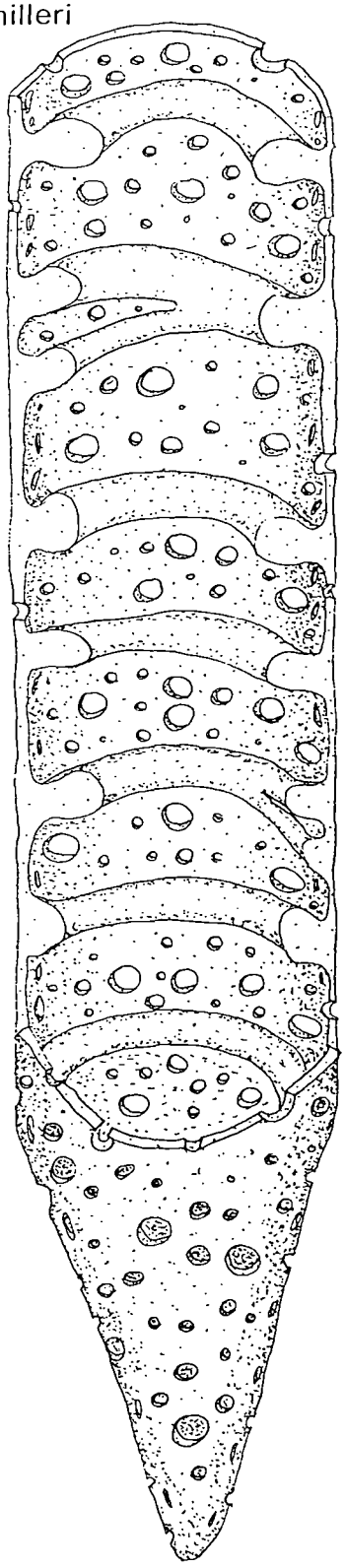
p: pyrite infill



Sw: secondary wall

Pw: primary wall

P: perforation



DIAGNOSIS

Genus: Thursophyton Nathorst 1915, emend:

Derivation: After a town in Caithness near which the plant was originally found (Salter 1857).

Plants with planar pseudomonopodial main axes, with occassional trifurcations or trichotomies, becoming dichotomous distally and terminating in recurved tips. Main axes originating from a rhizome system showing dichotomies and pseudomonopodial branching, with circinately coiled aerial projections. Robust ascicular spines present on rhizome and aerial portions of axis becoming less frequent distally and absent on minor axes. Stelar anatomy in the form of an exarch protostelic haplostele, elliptical to circular in cross-section. Tracheary elements long, having annular, occassionally spiral, bars of thickening, which may branch and all possess a perforate connecting wall. Extraxylary tissues including a thick walled outer cortex and a thin walled phloem.

Type species: Thursophyton milleri Nathorst 1915, emend:

Derivation: Hugh Miller an active C19th palaeontologist who worked on the Old Red sandstone of Scotland.

Identical to genus description, plants at least 50cm tall, with spines on the larger axes, and glabrous apical axes. Axes from 1.8 to 6.0mm wide (x=3.7). Branching angle from 12 to 58' or greater in the distal regions. Branches 23 to

41mm apart. Spines greater than 1mm long, their density decreasing distally. Emerging from a thickened base, between 0.2 and 0.7mm wide (x=0.4).

Stellar shape is elliptical, circular after a division and always exarch. Xylem elements have annular, or spiral thickening with occassional branches of the thickening bars, the thickness of which varies from 2.93 to 4.59um (x=4.22um). They protrude into the lumen between 5.65 and 9.29um (x=7.63um), the distance between the bars of thickening being from 4.98 to 8.47um (x=6.86um). Maximum metaxylem lumen diameter varies from 35.11 to 67.57um (x=47.70um) and the effective diameter for water conduction is from 19.80 to 39.94um (x=27.48um). The wall thickness across adjacent cell walls varies between 3.39 and 6.85um (x=5.05um).

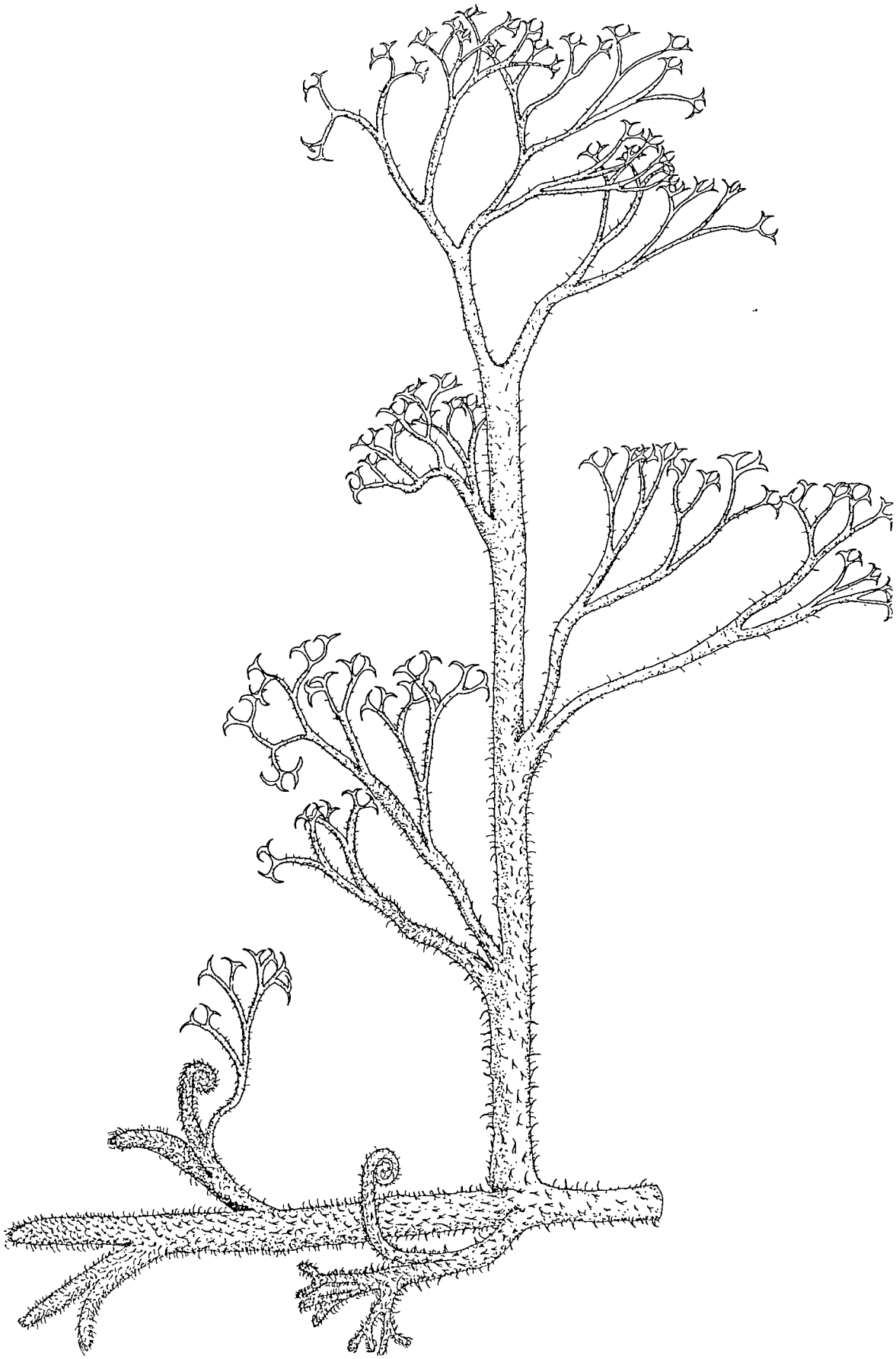
Holotype: Specimens p00009, p00020, p00023, p10002 (Plate 2 fig 5, Plate 5 figs 3,8,9, Plate 6 fig 1), Nathorst 1915.

Type locality: Gjegnalundsbreen, Gloppen, Nordfjord, Norway.

Stratigraphy: Middle Devonian, Givetian.

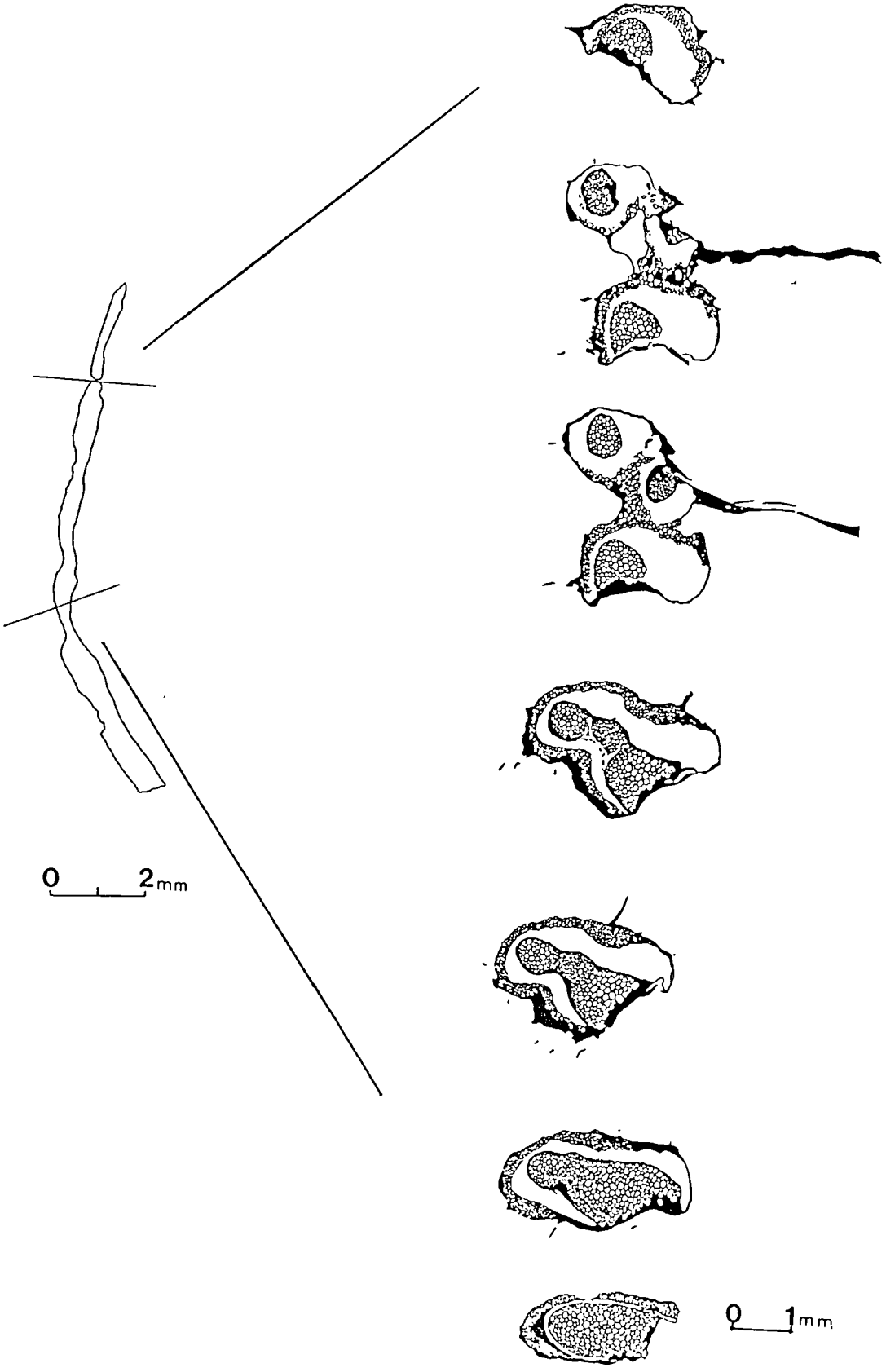
Other localities: Cromarty: Kinkell and Navity. Givetian.
Caithness: Thurso, Givetian.
Shetland: Lebotton, Upper Givetian and Foula, Lower Givetian (Achanarras).

Text Figure 15 Reconstruction of Thursophyton milleri



Text Figure 16 Anatomy of Thursophyton

during branching



COMPARIS ONS WITH OTHER SPECIES.

Thursophyton is placed in the Zosterophyllophytina (Banks 1968) on the basis of its elliptical exarch xylem anatomy. Since little is known about the fertile material the lack of lateral reniform sporangia is not considered significant enough to warrant exclusion from this class, even though there is a posibility that it may possess terminal fusiform sporangia. Miller (Salter 1857) was the first person to record the presence of this plant from a locality near Thurso, it was found by Lang (1925) to be identical to a plant from Nordfjord, Norway (Nathorst 1915) named Thursophyton milleri.

Trimerophytina:

The similarity with spiny axes of the psilophytes (Trimerophytina) was recognised by Høeg (1967) and morphologically Thursophyton milleri conforms closely to a trimerophyte. Characters which distinguish the genus Thursophyton from Trimerophyton and Pertica are the simple planar divisions that make up the plant, as opposed to the spirally arranged lateral first order branches as in Trimerophyton, the side branches arranged in a tetrastichos pattern as in Pertica grandifolia, or the decussate arrangement of successive subopposite pairs as in P. varia. The presence of robust spines, circinate coiled tips and the possibility of terminal recurved sporangia all suggest the close relationship to the genus Psilophyton.

Several recent studies of Psilophyton, especially those of Kasper et al (1974), Banks et al (1975), Gensel (1979) and Doran (1980) have resulted in an increase in our konwledge of the characteristics and extent of variability within the genus, particularly in those species found in North America. From these studies it is possible to draw comparisons between T. milleri and the Psilophyton genus.

Psilophyton crenulatum:

The New Brunswick species discovered by Doran (1980) with its variation in branching from pseudomonpodial to dichotomous or trichotomous divisions and the presence of emergences, whose abundace varies, up to 6mm long suggests similarities. However, the unique nature if these spines which bifurcate or trifurcate, together with the presence of minute crenulations and a main axis diameter of only 2-3mm clearly indicates the differences. The plant also possesses terminal fusiform reflexed sporangia not demonstrated in Thursophyton milleri.

Psilophyton dawsonii:

Banks, Leclercq and Hueber (1975) found petrified specimens of the genus from Gaspé. These showed glabrous three dimensional branching and possessed clusters of terminal fusiform sporangia. A terete centrach protostele was also found with spiral to sclariform thickenings of the tracheary elements. This is therefore a very different plant in branching and stelar morphology, from the spiny axes showing planar divisions and exarch anatomy, with

helical to annular thickening of the tracheids.

Psilophyton dapsile:

Kasper, Andrews and Forbes (1974) discovered this, the smallest and simplest species from deposits in Maine. The glabrous plant attains a height of 30cm and branches dichotomously, with dense terminal fusiform sporangia. P. dapsile shows little if any similarity to the genus Thursophyton.

Psilophyton forbesii:

First discovered by Andrews et al (1968) from Maine and then re-described by Gensel (1979) from Gaspé. This species shows obvious differences to the genus Thursophyton. It is glabrous and has a centrach protostele. It does however branch pseudomonopodially appearing very robust, reaching a height of 60cm or more and consequentely in branching morphology does show some similarities to Thursophyton.

Psilophyton charientos:

This North American species shows close morphological similarities, it was dicovered by Gensel (1979) from New brunswick and has a large main axis (33mm), pseudomonopodial tendency and abundant delicate spines 2mm long tapering to a sharp point. But with a centrach protostele and sclariform tracheids the anatomical differences are great.

Psilophyton microspinusum:

Kasper et al (1974) investigated this plant, which is a

superficially similar plant with a main axis 4mm in diameter, all axes bearing emerfences, which on the main stems are 2mm long, 0.4mm at the base and tapering to a needle point. The spines, unlike those of Thursophyton are never abundant, sometimes infrequent but always present although their size and number decreases until they may be absent distally.

Similar species found in Europe include Psilophyton goldsmidtii (Halle 1916) from Roragen, Norway (renamed as Margophyton, a Zosterophyll, by Zakharova (1981), P. pubescens Kräusel and Weyland 1938 from Elberfeld, Germany, P. arcticum Høeg 1942 from Spitsbergen, P. rectissimum Høeg 1945 from Orlandet, Norway, and P. krauselii Obrhel 1959 from Bohemia. These species represent a group of generally lesser known plants which all share common features, viz: a large pseudomonopodial to sympodial main axis, which may give rise to a dichotomously divided spreading habit; the presence of spines, the size and shape of which varies between 2-8mm in length but all have a thickened triangular base, narrowing to give a fine needle-like spine. The similarities between these species and T. milleri confirms the close morphologicl relationships of this plant to the genus Psilophyton. Indeed, if specimens were studied in isolation a good case could be made for placing those specimens within many Psilophyton spp., such is the variation of morphology found within the material. The anatomy however is exarch in Thursophyton and therefore distinct from the Genus Psilophyton with its centrach

anatomy.

Zosterophyllophytina:

Euthursophyton hamperbacence:

The genus Euthursophyton (Mustafa 1978) from Germany is a very closely related, if not synonymous with Thursophyton, is represented by only one species E. hamperbacense. The plant shows the typical characteristics of the genus Thursophyton in having stems covered with dense spines. The axes divide pseudomonopodially are up to 6cm wide in the basal regions. The spines are dense, but those nearer the apex are almost glabrous. The apical regions also show overtopping and frequent dichotomous divisions, with the ultimate appendages having recurved tips about 0.5cm wide. Stele maturation is exarch with a circular ring of protoxylem giving rise to centripetal development of metaxylem. Protoxylem tracheids measured 5.5-20um wide, about 1600u long with walls 2-3um thick, showing annular to sprial thickening. Metaxylem tracheids measured 60-80um, with walls 3-5um thick with sclariform thickening (which I belive may be interpreted as annular). The stele was surrounded by a cortex consisting of two layers, the inner consisting of thin walled cells, the outer of thick walled cells.

Mustafa separated this plant from the genus Thursophyton on the basis of the stelar anatomy which he considered a stylostele (sensu Remy and Remy 1977). It is does however appear as an exarch protostelic haplostele (Text Figure 17)

and is similar to those found in T. elberfeldense and T. milleri. The plant conforms closely to the anatomy of permineralised material from Shetland and Norway. The Norwegian material is particularly well preserved and shows the same exarch maturation of the stele, but with annular tracheary elements. The almost identical nature of this plant to Thursophyton both morphologically and anatomically suggests that they are in fact synonomous and Euthursophyton should be included within the genus Thursophyton. The major difference being the spine density which does decrease distally, but spines are seen terminally in Euthursophyton.

Thursophyton elberfeldense:

This species shows close similarity with T. milleri as would be expected from a member of the same genus. The branching morphology in particular is identical, while the stelar anatomy shows a terete exarch haplostele in the aerial portions. The tracheids are presumed to have sclariform thickening (which the author considers as annular), the protoxylem being 14um in diameter and the metaxylem 130um in diameter. The distinction between the species is based on poorly preserved rhizome anatomy which is an actinostele and considered by Høeg (1967) to be similar to that of Asteroxylon mackiei. No anatomy from rhizome material has been found in T. milleri and until its presence is confirmed, it remains a significant difference between the species. Other species of Thursophyton including T. vahlbergianum (Kräusel and Weyland 1930), T. uralicum (Zalessky 1937) and T. sibiricum (Ananiev

1959), are similar species showing axes densely covered with spines but too fragmentary for an accurate comparision to be made.

Zosterophyllum:

This genus is typified by Z. myretonianum (Penhallow 1892) which is well known. Edwards (1969, 1975) re-described the plant as having lateral reniform sporangia, axillary tubercles and a vascular strand which was terete to elliptical composed of sclariform tracheids in an exarch protostele. The absence of lateral sporangia, or axillary tubercles separates Thursophyton from this genus, as does the occurrence of sclariform and not annular thickening although other species such as Z. divaricatum (Gensel 1982) do possess annular thickening of the tracheary elements. The author considers that this genus may well have annular thickening similar to that seen in Thursophyton.

Gosslingia:

First found by Heard (1927) it represents a related species on the basis of anatomy only, it has been shown (Kennrick 1988) to have an exarch, elliptical, protostelic haplostele, with predominately annular thickening. The absence of spines, the presence of axillary tubercles and reniform lateral sporangia separate this genus from Thursophyton. Similarly Oricilla (Gensel 1982), and Hicklingia (Kidston and Lang 1923) are related but separate genera because of their lack of spines and the presence of lateral reniform sporangia.

Sawdonia ornata:

Hueber (1971) re-described and re-named this plant which was first found by Dawson (1871) from Gaspé. He gave it the name Psilophyton princeps var ornatum. It does have a resemblance to P. princeps (sensu Lang 1932) and is still referred to this genus by some workers (Ananiev and Stepanov). The plant is covered in spines 0.5 to 4.0mm long with slightly expanded tips, the density of which varies along the axis. It was shown by Heuber (1971) to possess an exarch, elliptical protostele, with annularly thickened tracheids and a thickened outer cortex. Sawdonia acanthotheca (Gensel et al 1975) is another species placed in this genus. It has spines ranging from, fine hairs to rigid deltoid structures between 0.15 and 1.8mm long, all of which taper to a sharp tip. The genus also has lateral sporangia as well as lateral branches occurring close to, but above, a dichotomy (Rayner 1983). These are glabrous structures and form into H-configurations or dichotomise frequently. Sawdonia is quite wide ranging stratigraphically and Geographically, having been found in, western Siberia, Gaspé in Canada, New York State (Heuber and Grierson 1961) and Poland (Zdebska 1972) and from Lower Devonian to Early Upper Devonian deposits.

Margophyton Goldschmidtii:

This plant was originally placed in the genus Psilophyton by Halle (1916) but was re-described by Zakharova (1981). The description includes axes densely covered with sharp

straight spines up to 4mm long, occurring on axes that branch in a manner reminiscent of the genus Psilophyton but with axillary tubercles as well as tubercles found on branches above dichotomies. Another unusual feature is a narrow marginal rim or groove. There is also no indication that the spines reduce in density distally. Lateral sporangia are also present on short straight stalks perpendicular to the main axis.

Anisophyton:

Vegetative axes of Thursophyton are similar to A. potonie (Remy et al 1986a) and A. gothapii (Remy et al 1986). However spines are present that do not become less frequent distally, and these posses a distinctive cup shaped end. Axillary tubercles are also present ocurring with isolated lateral sporangia attached at right angles to the plane of branching.

Konioria:

Zdebska (1982) described a plant with conspicuous tapering spines up to 4mm long and a branching pattern similar to Thursophyton milleri. However it can be distinguished from this genus by the presence of four longitudinal wings running down the axis. It also has lateral sporangia in an axilllary position.

Other genera such as Crenaticaulis, Serrulacaulis and Bathurstia have small, tooth like ennations arranged in one or two rows and like the other genera in the

Zosterophyllophytina can not be confused with Thursophyton milleri because of their different spine morphology. Sawdonia and Margophyton morphologicaly appear as close relatives of Thursophyton but the absence of fertile material makes comparisions difficult. Anatomically the stelar anatomy shows similarities with Gosslingia especially in the smaller axes. But the massive nature of the stele seen in Thursophyton is a further factor which separates this genus from other Zosterophyllopytina, as does the trimerophyte-like branching. The morphology may suggest relationships with the Trimerophytina but the anatomy being exarch rather than centrach separates it from all Trimerophytes for which anatomy is known. If the strict definition of Banks'(1968) classification is followed then Thursophyton milleri must be placed in the Zosterophyllophytina from stelar morphology alone, as this is likely to be a more conservative and therefore more important character than vegetative morphology. Text figure 15 shows a reconstruction of T. milleri, while text figure 16 shows the anatomy during a trifurcation and text figure 17 shows a comparison of the anatomy from various locations with T. elberfeldense and Euthursophyton hamperbacence.

TABLE 7 Table comparing xylem cell wall structure in *Thursophyton* with that in other selected species.

Taxon	Author	Preservation*	Techniques used†	Authors' description	Appearance in published photographs and comments
Zosterophyllum llanoveranum (Zosterophyllophytina)	Edwards (1969a)	P, L	I	"scalariform tracheids"	Polish not good enough to distinguish mineral within cell wall nor structure of coalified wall. Scalariform thickenings not clearly demonstrated; wall sculpture probably annular or spiral
Z. cf. *fertile* (Zosterophyllophytina)	Edwards (1969b)	P, C	I, T	"scalariform"	Wall pyrite occasionally seen between coalified walls of adjacent cells (Edwards, 1969b: pl. 3, fig. 21). Polish not good enough to detect pyrite within thickenings, nor a perforate wall. Scalariform thickenings not clearly demonstrated; wall sculpture probably annular or spiral
Z. divaricatum (Zosterophyllophytina)	Gensel (1982)	C	T, EMC	"tracheids 10–40 μm wide with annular, close annular and helical thickenings." "Among predominantly annular types a few adjacent thickenings occasionally converge" "The pock marks present in the area between wall thickenings (Fig. 13, 16, 17, 20, 21) are interpreted as resulting from degradation."	As in author's description. Wall thickenings do not appear hollow; no gap between adjacent cells. Pock marks confined to area between wall thickenings, fewer than the perforations of *T. milleri* but of similar size and shape
Crenaticaulis verruculosus (Zosterophyllophytina)	Banks & Davis (1969)	P	I	"Longitudinal sections demonstrated that most tracheids were scalariform (Fig. 31) and some of the periphery appeared to be annular or spiral (Fig. 29). A few seemed to have interconnections between the scalariform bars (Fig. 34) suggesting either a reticulate pattern or some variation of the Williamsons striations seen in several fossil lycopods."	Polish not good enough to see distribution of mineral within cell wall. The "reticulate pattern" suggests a perforate wall between thickenings. Scalariform thickenings not clearly demonstrated; wall sculpture probably annular or spiral
Serrulacaulis furcatus (Zosterophyllophytina)	Hueber & Banks (1979)	C	T	"Only helically thickened tracheids 26–38 μm in diameter have been described (Plate II, 2)"	As in authors' description, but some tracheids probably annular. Cannot see a perforate wall, nor hollow thickenings, nor a gap between coalified walls of adjacent cells

Kontorta andrychoviensis (Zosterophyllophytina)	Zdebska (1982)	P, C	I, T	"The metaxylem shows well-developed scalariform tracheids (Pl. 27, fig 7). Three different stems showed exactly similar scalariform tracheids with no round pits." "Yet another specimen (showing small spines), which was not pyritised, was unusual when macerated in Schulze's solution, in that it yielded excellent tracheids in longitudinal view, which showed round bordered pits in two rows in some of the tracheids (PL 28, Figs. 5, 6)."	Wall pyrite visible between adjacent coalified walls (Zdebska, 1982; pl. 27, fig. 7). Polish not good enough to detect pyrite within thickenings nor a perforate wall. In pyritized elements, presence of scalariform or reticulate wall sculpture not clearly demonstrated; it could be annular or spiral. *Kontorta* differs from other Zosterophyllophytina in having xylem cells with circular bordered pits, described from coalified elements
Saucdonia ornata (Zosterophyllophytina)	Rayner (1983)	P	I, EMF, EMD	"Secondary thickenings consist of transverse bars on the exposed inner tracheid walls, in an annular arrangement (Fig. 4h). The annular thickenings are about 4 µm thick and are connected by vertical elements in a reticulate manner."	As in author's description. Polish good but no wall pyrite. SEM of fine structure of "reticulate" wall unclear; cannot see whether wall sculpture is hollow. Reticulate wall may be equivalent to perforate wall of Thursophyton.
Baragwanathia longifolia (? Lycopsida)	Lang & Cookson (1930)	L, C	I, T	"Uniform tracheids with narrow annular thickenings"	As in authors description. Unable to see distribution of mineral within cell walls nor a perforate wall
B. abitibiensis (? Lycopsida)	Hueber (1983)	C	EMC	"Annular and secondary thickenings were the only forms observed. Irregular pits in the primary wall between the secondary thickenings are characteristic of all tracheids. The pits were thought at first to be the result of degradation of the primary wall; but the character seems to reflect the fibrilar structure of the wall and the pits are normal elements of the structure."	As in author's description. Not possible to detect a gap between coalified walls nor within thickenings. Hueber's perforate "primary" wall appears similar to the perforate coalified wall in Tmitteri but perforations may be a little larger, giving a reticulate appearance
Asteroxylon mackiei (? Lycopsida)	Lang & Cookson (1935)	S	I	"The middle lamella, secondary and tertiary layers can be distinguished in the walls separating adjoining tracheides. Further there seems to be no indication of a spiral course of the thickenings in most of the tracheides shown; they appear to have narrow rings of thickening projecting into the lumen."	As in authors description. Unable to see a perforate wall. Middle lamella and pale area of wall occupy a similar position to wall pyrite in Tmitteri Thin dark outer layer in a similar position to the coalified wall of Thursophyton
Drepanophycus devonicus (Drepanophycopsida)	Schweitzer & Giesen (1980)	L	EMF, EMD	"The scalariform tracheids of the metaxylem are hexagonal in cross section and have irregularly arranged pits."	SEM of fractured axes suggest annular or spiral thickenings as in Tmitteri (Schweitzer & Giesen, 1980: pl. 6, figs 1, 2). Irregularly arranged "pits" between thickenings similar to perforations in *Gosslingia*. Distribution of mineral within wall unknown

TABLE 7 *Continued*

Taxon	Author	Preservation*	Techniques used†	Authors' description	Appearance in published photographs and comments
D. spinaeformis (Drepanophycopsida)	Grierson & Hueber (1967)	Ca	T	"Tracheids with annular thickenings connected by a perforate membrane or system of reticulate fibrils." "pores have a border (about 0.5 μ) of different optical density, suggesting a pit border (Fig. 24, 25, 26). The openings in this connecting layer do not coincide in the walls of contiguous cells (Fig. 22 at arrow). They would seem to represent largely independent systems in the two cells." "Occasionally annular rings are joined vertically by a sharp angled connecting bar. Possibly some tracheids are spirally thickened for at least part of their length." "The bars are from 1.5 to 2.5 μ thick and about 7·5 μ apart."	As in authors description, except that the "pit borders" may just be shadows cast on the pit wall. Distribution of mineral within cell wall unknown. Many similarities to cell wall structure in T mitteri
D. spinaeformis (Drepanophycopsida)	Hartman (1981)	P	I, EMD	"Tracheids usually 6–7 sided, 20–70 μm in diameter (averaging about 40 μm), and more than 1 mm long. They bear annular thickenings (Plate I, 5) and low pitched helical thickenings (Plate I, 4, 6). The thickenings are occasionally branched (Plate I, 7)." "A perforate sheet or reticulum of strands, apparently in the position of the compound middle lamella, is evident between the secondary thickenings." "This indicates that the secondary thickenings were deposited inside the reticulate layer and demonstrates that the reticulum is part of the compound middle lamella."	Wall pyrite visible in polished longitudinal section between coalified walls of adjacent cells and within thickenings (Hartman, 1981: pl. I, fig. 4). Distribution of mineral reflected in gaps between coalified walls, and hollow annular thickenings seen in demineralized section (SEM) (e.g. Hartman, 1981: pl. II, figs 4–6). The "organic reticula" joins the annular thickenings forming a continuous wall as in T mitteri rather than underlying them. Where it appears to underly thickenings is simply where an annular bar is more extensively coalified. Cell wall structure appears similar to Thursophyton

D. spinaeformis (Drepanophycopsida)	Rayner (1984)	P, L, C	I, T, EMD	"Favourable sections show that the thickenings have a permineralised interior surrounded by organic matter (Fig. 4b —arrowed 3). In addition, pyrite occupies a narrow space between tracheids (Fig. 4c—arrowed)." "The micrograph in Fig. 4g illustrates the presence of holes in the region of primary wall between secondary thickenings. Each hole is round to subangular and about 4 μm in diameter." "The primary wall between thickenings is, *therefore, a reticulate sheet. The holes are* not bordered." The thickenings are annular and connected annular.	As in author's description. Tracheids appear very similar to those in Thursophyton
Periastron reticulum (? Lycopsida)	Beck (1978)	Ph	?T	"lateral wall sculpture of the tracheids is either helical (Fig. 11) or scalariform, with some tendency toward becoming reticulate (Fig. 12, 13). An outer wall layer on which the scalariform thickenings are deposited is characterised by a fine reticulate pattern (Fig. 12)." "Similar patterns have been observed on non-tracheary cells such as cortical parenchyma and the elongate cells of the bundle sheaths. This suggests that the fine, reticulate pattern may be a general characteristic of the primary and/or outer secondary walls of this plant and, further, one that may appear only on wall degradation, thus not a visible feature in the living plant."	Scalariform thickenings may be annular or spiral. Reticulate wall similar to perforate wall in T mitteri in that it joins annular thickenings (Beck, 1978; Fig. 24) and does not underly them. Perforations of similar size and distribution. Pale area between adjacent cell walls and protruding into wall thickenings (Beck, 1978: Fig. 24) has similar distribution to wall pyrite in T mitteri and overlying darker area of similar size and distribution to coalified wall in Thursophyton
Krithodeophyton croftii (Barinophytaceae)	Edwards (1968)	P, C	I, T	"The central strand of xylem was composed mainly of scalariform tracheids in which pits on adjacent walls were opposite (pl. 130, Figs. 8 and 9). A few elements showed reticulate pitting."	Polish not good enough to detect wall pyrite nor a perforate wall. Scalariform and reticulate elements not clearly demonstrated. Wall sculpture probably annular

TABLE 7 *Continued*

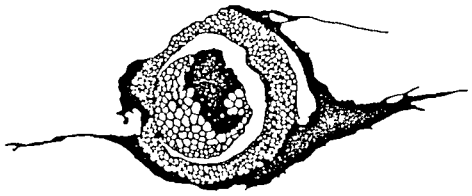
Taxon	Author	Preservation*	Techniques used†	Authors' description	Appearance in published photographs and comments
Barinophyton citrulliforme (Barinophytales *Incertae sedis*, Barinophytaceae)	Brauer (1980)	L, C	I, EMF, EMD, T	"the tracheids have a basically annular pattern with some connected annular thickenings" "The presumed secondary wall is a continuous layer which, when seen in longitudinal section, has U-shaped protrusions into the lumen of the tracheid" "the presumed continuous secondary wall between the protrusions bears numerous small openings." "Each opening resembles a small pit (0.4–3.0 μm wide)" He also recognizes limonite between the coalified walls of adjacent cells.	As in author's discription. Distribution of mineral within wall and structure of coalified wall suggest a similar cell wall structure to Thursphyton
Stolbergia spiralis (*Incertae sedis*)	Fairon (1967)	L	I	"En section longitudinale, le métaxylème apparait formé longues trachéides à épaississements scalariformes dont les barres font de 5 μ a 10 μ d'epaisseur." "Nous n'avons pas observé de trachéides spiralées ni annelées." She also notes mineral between tracheids and mineral within thickenings.	Polish is longitudinal section very good, the following features can be seen: wall pyrite between adjacent coalified cell walls, wall pyrite within annular thickenings, a perforate wall between thickenings. Illustrated xylem cells bear striking similarity to those in T milleri suggesting a similar structure; i.e. annular or spiral not scalariform
Hostinella heardii (*Incertae sedis*)	Edwards (1980)	P	I, EMF	"Tracheidal secondary thickening is annular with bars 1–1.5 μm wide and 3–6 μm apart." She also recognises wall pyrite but disputes the presence of a coalified wall.	As in author's description; but coalified wall probably present. SEM of small knobs of pyrite on lumen casts and wall pyrite on fractured elements suggests a perforate coalified wall between lumen and wall pyrite as in T milleri

Taeniocrada stilesvillensis (*Incertae sedis*)	Taylor (1986)	P, C	I, T, EMF	"a continuous secondary wall, laid over a template which seems to include annular (Plate IV, 2) and spiral (Plate IV, 4: at arrows) patterns. In a few areas connections between thickenings are found (Plate IV, 3: at c). On average the thickenings are 3.0 μm thick and spaced 5.0 μm apart." "small, usually paired, bordered pits (c) are found in the continuous secondary wall, inbetween ridges of discontinuous wall." "In Plate V, 6 two coaly, entombed tracheids can be seen, with the area between the tracheids filled with pyrite. This probably indicates pyrite between tracheids."	Annular or spiral thickenings as in author's description. Wall pyrite in core of annular thickenings visible on SEM. Polish not good enough to see how consistent a feature wall pyrite is. If consistent, it rules out paired bordered pits of type described by author. Knobs of pyrite seen on SEM of fractured lumen casts fill pits of type seen in perforate coalified wall of *Tmitteri*. Knob shape formed by fortuitous fractures. Small, usually paired, bordered pits not clearly demonstrated; cell wall structure probably identical to *Thursophyton*
Euthursophyton hamperbachense (*Incertae sedis*)	Mustafa (1978)	P	I	"Protoxylem-Tracheiden englumig, etwa 5, 5 bis 20 μ weit, etwa 1600 μ lang, mittlere Wandstärke etwa 2 bis 3 μ, Wände ringförmig bis spiralig verdickt. Metaxylem-Tracheiden weitlumig, etwa 25 bis 140 μ (meist jedoch etwa 60 bis 80 μ) weit, im Querschnitt polygonal, mittlere Wandstärke 3 bis 5 μ, Wände treppenförmig verdickt (z.T. mit schräggestellten Leisten), etwa 2400 μ lang."	Metaxylem probably annular not sclariform. Polish just good enough to see wall pyrite between adjacent coalified cell walls. Polish not good enough to see pyrite within wall thickenings nor a perforate wall between thickenings. Some metaxylem tracheids considerably larger than those in *Thursophyton*

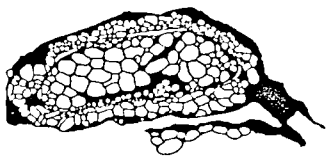
*Preservation: P = Pyrite + coalified cell walls. L = Limonite + coalified cell walls. C = Entirely coalified cells. Ph = Phosphatic nodules. Ca = Calcareous concretions + coalified cell walls. S = Silica.

†Techniques used: I = Incident light microscopy of polished surfaces (standard polish). T = Transmitted light microscopy of coalified cell remains. EMF = Scanning electron microscopy of fractured permineralized cells. EMD = Scanning electron microscopy of partially or fully demineralized cells. EMC = Scanning electron microscopy of coalified cells.

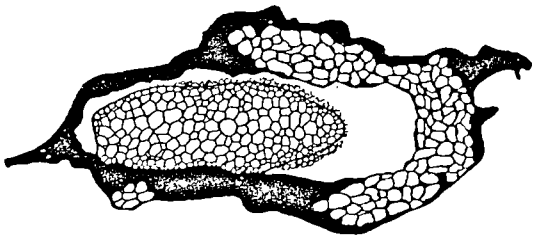
‹t Figure 17 Comparison between Thursophyton milleri and related species



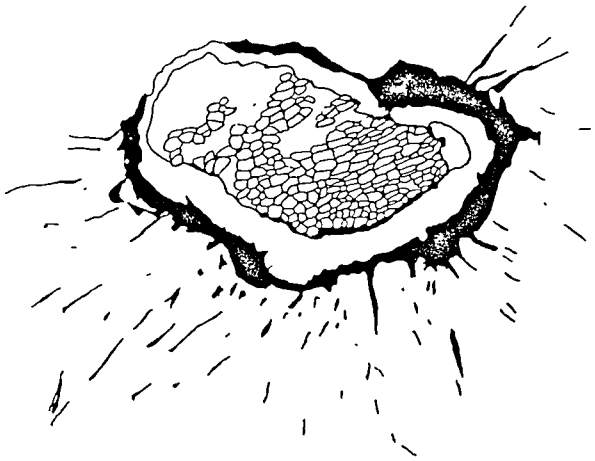
Sandwall



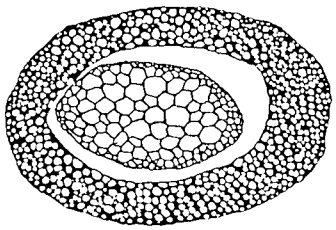
Foula



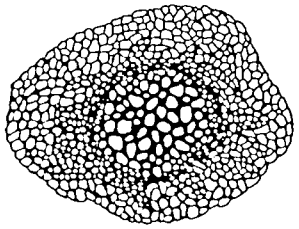
Skersund



Greenland



Euthursophyton hamperbacense



Thursophyton elberfeldense

Introduction.

Specimens assignable to this species were collected from a single group of localities near Roskilie, Fair Isle, Shetland initally by Mykura (1976) and later by Marshall (1980). Those collected by Mykura were identified by Chaloner (1972) as Dawsonites roskiliensis. Chaloner described pseudmonopodial branching of the main axes and fertile portions bearing lateral and terminal erect fusiform sporangia in pairs or dichotomising corymbose clusters. This immediately suggests a trimerophytic relationship although there is a similarity to sporangia of Svalbardia which occur in different deposits on Fair Isle.

The generic concept of Dawsonites was established by Halle (1916) while studying Psilophyton princeps. It now represents a form genus for fragmentary smooth axes bearing terminal fusiform sporangia, Halle used this to name fertile portions of Psilophyton for which a species identification was not possible because of the lack of vegetative specimens. The genus has become widely used for fertile material of a variety of sporangial types (Høeg 1967). Høeg follows the usage by Kräusel and Weyland (1935), Stockmans (1940) and Ananiev (1959) extending the concept of the genus, to include lateral as well as terminal sporangia. Hueber and Banks (1968) offered well documented evidence that sporangia of Dawsonites arcuatus were in fact borne on spiny axes of Psilophyton princeps. Indeed, it has been suggested by several workers that all sporangia not of the Psilophyton type should be excluded from Dawsonites (Gensel

and Andrews 1984).

In 1972 Chaloner assigned the fragmentary specimens from Fair Isle in the sense used by Høeg (1967) and commented that the plant had affinites with Hedeia corymbosa (Cookson 1935), which is characterised by sporangia of varying sizes in erect corymbose clusters. He also compared the sporangia with those of Trimerophyton and some progymnosperms. The author has examined type material housed in the I.G.S. Museum, Edinburgh (specimen GSE 12815), as well as other Dawsonites species including Dawsonites minor from the Institute Royal des Sciences Naturelles de Belgique and Dawsonites racemosa (Lang) Høeg (1967) from the British Museum. Those specimens collected by Marshall from Fair Isle were also examined and included well preserved fertile material. A limited amoumt of vegetative axes were collected by the author. Plates 44 (figs 1-6) and Plate 45 (figs 1-7) illustrate the range of material studied.

Morphology of the vegetative axes:

Only fragmentary glabrous axes were recovered, these showed simple dichotomous divisions (Plate 44 fig 3,5), together with pseudomonopodial branching (Plate 44 fig 1) and a more complex axis showing spirally arranged lateral branches (Plate 44 fig 2a,2b). These gave rise to lateral branch systems which divided dichotomously and pseudomonopodially up to three times. The axes were between 0.5 and 3.0mm (x=1.9mm n=14) wide. The distance between branching was difficult to measure as only one specimen was large enough (Plate 44 fig 2a). On the main axis the

distance between branches was from 4.0 to 7.5mm (x=5.8mm n=5) and in the lateral branches between 2.0 and 7.4mm (x=4.9mm n=9). This specimen is also the largest measuring 55mm long and 3mm wide. Longitudinal striations were also seen on this specimen (Plate 44 fig 2a part and fig 4 counterpart). The branching angle on the main axis and in the laterals was between 40-80' (x=72' n=8).

Morphology of the fertile axes:

The fertile specimen was collected by J.E.A. Marshall (Plate 44 fig 6 part and Plate 45 fig 1 counterpart). The sporangia appeared as erect fusiform clusters, singly or up to three on the ends of glabrous, dichotomising axes (Plate 45 fig 1,2 part and fig 6 counterpart). The sporangia are between 1.8 and 2.9mm (x=2.4 n= 10) long and between 0.50 and 1.06mm (x=0.76mm n=10) wide. A longitudinal dehiscence line was seen (Plate 45 figs 3,4,5). This was considered to be questionable in many cases. In Plate 45 fig 4, it appears that two sporangia might be present. However the adjacent sporangium does show a similar but much narrower line interpreted as a definite dehiscence line. Degagement would have revealed if the sporangia were singular or consistently occurring in pairs. The apparent pairing may have been caused by widening of the dehiscence line, during deposition or after release of the spores. However only limited degagement was attempted because this specimen represented the only fertile material apart from that in the Royal Scotish and I.G.S. Museums Edingurgh. Transfers were attempted on a few sporangia cut from a fragment of the

counterpart and on fragments of axis but no spores or cuticular material were recovered.

In summary the specimens revealed a plant with a striated, glabrous main axis, with spirally arranged lateral branches which branched frequently dichotomously or pseudomonopodially. The terminal portions of which carried fusiform erect sporangia in dichotomising clusters with a longitudinal dehiscence line.

Diagnosis.

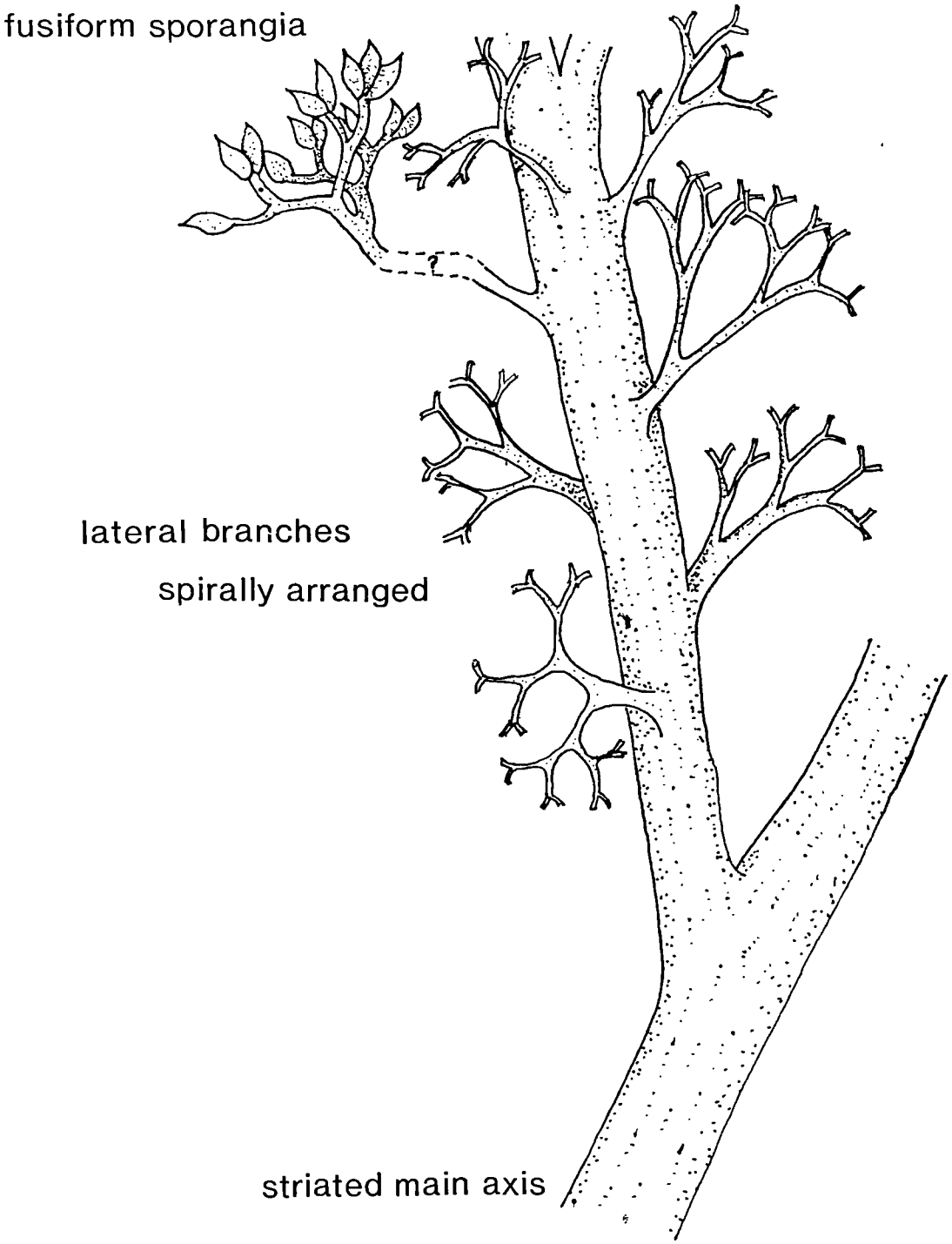
Genus: Trimerophyton Hopping 1956.

Derivation: from trifurcations seen in the lateral branches. The glabrous main axis bears lateral first order branches which are spirally arranged. They trichotomise close to the main axis into second order branches of apparent equal thickness. These divide again dichotomously or unequally. The fertile stalks or pedicels bearing terminal clusters of erect fuisform sporangia on dichotomising axes.

Species: Trimerophyton roskiliensis comb. nov.

Derivation: Roskilie, Fair Isle, the type locality. Characteristics as for the generic description, except dichotomous instead of trichotomous branching in the lateral first order branches. Main axis with longitudinal striations. The lateral branches smooth leaving the main

Text Figure 18 Reconstruction of Trimerophyton roskiliensis



axis at an angle of betwen 40-80'. Branching equally or unequally close to the main axis. Each fertile ultimate branch bears clusters of up to three sporangia, usually in pairs. The sporangia are small with an average size of 2.4mm long and 0.76mm wide.

Synonymy: Dawsonites roskiliensis. Chaloner 1972. Devonian plants from Fair Isle Scotland, Rev. Palaeobot. Palynol. 14: 49-61.

Holotype specimens: Dr011, Dr012, Dr013.

Type locality: Roskilie Fair Isle (Observatory Group Mykura 1976).

Stratigraphy: Givetian (Marshall and Allen 1982)

COMPARISIONS.

Trimerophytina:

Erect terminal fusiform sporangia are found on a number of species including Trimerophyton robustinus (Hopping 1956), Pertica quadrifaria (Kasper and Andrews 1972), Pertica varia (Granoff et al 1976), Hedeia ssp. (Cookson 1935), Dawsonites minor (Stockmans 1940) and Protohyenia ssp. (Ananiev 1957). Fusiform sporangia are one of the significant features present in the Trimerophytina (Banks 1968) and immediately suggests a relationship with this Class. However the erect

nature of these sporangia provides a significant difference from all species of Psilophyton the dominant genus in this Class.

Trimerophytina robustius:

This plant described by Hopping (1956) on the basis of one specimen has as its most distinctive feature trifucations of the lateral branches. These lateral branches are spirally arranged on the main axis. After trifurcating close to the main axis they divide again unequally and then dichotomously ending in dichotomising tips which bear pairs of erect sporangia, 4-5mm long, in clusters. T. roskiliensis does not show the trifurcations of the lateral branches; these appear instead to dichotomise or branch unequally. The sporangial morphology is however close to that seen in this species. The difference in size of the sporangia (being only 1.8-2.9mm long in Trimerophyton) is significant and this together with the trifurcations of the lateral branches separates the two species. The lack of trifurcations is not considered to be important enough to prevent inclusion in this genus since both species are based on fragmentary material and occassional trifurcations do occur in other genera such as Psilophyton, Pertica, and Thursophyton. It is considered that further collections would probably reveal the presence of trifurcations from T. roskiliensis.

Pertica:

This Lower Devonian genus represented by Pertica quadrifaria (Kasper and Andrews 1972) as the type species

for the genus, is based on a large collection of specimens from Maine. The plant attained a height of at least a metre. The main axis upto 1.5cm in diameter. The stem bore side branches in a tetrastichous pattern which forms a clockwise spiral and does appear similar to Trimerophyton roskiliensis. Similarly the lateral branches dichotomise frequently, but successive divisions are at right angles to each other, some being fertile others sterile. This results in a dense three dimensional structure not seen in this material. Another distinguishing feature are the minute papillae less than 0.4mm long present on the main axes and the laterals. The fertile branches terminate in dense clusters of sporangia which are 3mm long by 1mm wide they are also ovoid rather than fusiform. The number of sporangia per cluster being 32 to 256 is quite distinct from anything seen in Trimerophyton roskiliensis. This plant therefore represents a similar genus but, is clearly separated by different vegetative and fertile morphology.

Pertica varia was found by Granoff et al (1976) from Gaspé and is another well known species being up to 3 metres tall, the main axis bearing lateral branches in a decussate arrangement with subopposite pairs rotating through 90'. The sterile branches are similar but distinct in that they tend to be psedomonopodial with occasional dichotomies or trichotomies. The presence of small papillate to conical hair like emergences also separates this species from T. roskiliensis. The fertile branches however show close similarities, since they are more uniformly dichotomous and terminate in clusters of 8 to 16 paired sporangia. The

individual sporangia being 3 to 5mm long with a longitudinal dehiscence line, the sporangial walls however bear minute emergences 200um long. This species therefore represents another closely related plant but again the presence of spines and a different branching pattern being the major points of separation.

Dawsonites minor:

This plant was discovered by Stockmans (1940) from the Lower Devonian of Belgium is again only represented by fragmentary but quite diagnostic material. *Fertile axes are* preserved in which whorls of lateral branches emerge and dichotomise at least twice and terminate in paired erect fusiform sporangia 1.75mm long. The nature of the sporangia suggest a relationship with Trimerophyton but the whorled nature of the lateral branches indicates a closer relationship with the sphenopsids and the author considers that this plant represents a probable Protohyenia type.

Protohyenia janovii:

This little known species was found by Ananiev (1957) from the Lower Devonian of west Siberia. The plant possess dichotomously branched or unbranched whorls of lateral axes which terminate in pairs of erect fusiform sporangia 2.5 to 3mm long and 1.5 to 2mm wide. The sporangia resemble those found in Trimerophyton roskiliensis, but again the mode of branching does suggest a sphenopsid relationship and it is considered by Høeg (1967) to be a primitive sphenophyte.

Hedeia:

This genus is placed by Høeg (1967) in the Hedeiaceae but is considered by other workers (Gensel and Andrews 1984) to be a questionable Rhyniophyte. H. corymbosa was found by Cookson (1935) in Lower Devonian localities from Victoria, Australia. She found fragments with sporangia 5 to 9mm long and 1 to 2 mm wide. Another species Hedeia parvula was found by Jurina (1969) from Kazakhstan, which had similar clusters of erect terminal sporangia terminating dichotomising axes. These have been considered by Hueber (1983) to have trimerophyte affinities and that a further species Yarravia oblonga (Lang and Cookson 1935) represents a poorly preserved specimen of Hedeia. The sporangia are considerably larger than those found on Fair Isle, although Chaloner (1972) did report sporangia of various sizes with a variety of modes of attachments. The morphology of the vegetative axes of Hedeia is unknown; this and the difference in sporangial size separates Hedeia from the specimens found on Fair Isle.

Introduction.

Specimens assignable to Svalbardia scotica were first identified by Chaloner from the North Gavel Beds of Bu-Ness, Fair Isle, Shetland. Additional collections were made by Allen and Marshall (1986) and from new localities on Mainland Shetland and Bressay.

The genus was established by Høeg (1942) on the basis of specimens from a Upper Middle Devonian locality on Spitsbergen. Authors differ on the most appropriate systematics of the genus. Its similarities with Archeaopteris are accepted but because of lack of anatomical information Svalbardia is here regarded as a seperate genus within in the Archeaopteridales on the basis of similar morphology only. Beck (1971) stated that "several genera, eg., Svalbardia (Høeg 1942) and Actinoxylon (Matten 1968) have been considered to strongly resemble Archaeopteris but for one reason or another have been separated from it, however I can no longer accept Svalbardia as a valid genus" (p777).

Chaloner considers Svalbardia to differ significantly from Archaeopteris in having ultimate branches and leaves borne spirally on the axis, but he admits that its reproductive structures are almost identical. Andrews et al (1970) also emphasises this three-dimensional branching as a significant point of difference, but the demonstration by Carluccio et al (1966) that the vascular supply to leaves of Archeaopteris macilenta indicating their spiral insertion

reduces the differences between the two genera.

Svalbardia is place by Andrews et al (1970) in the Svalbardiaceae among the Filicophyta incertae sedis, while Archaeopteris is placed in the Progymnospermopsida. Other workers (Chaloner 1972) preferred the veiw of Banks (1968) and Carluccio et al (1966) that the similarity between the genera should be recognised by placing the genus with Archaeopteris in the Pityales but following Andrews et al (1970) assignment at the family level. Since the early seventies two comprehensive review papers by Bonamo (1975) and Beck (1976) recognise that Svalbardia should be include in the same order, the Archeaopteridales. The Pityales having been discarded since Pitys had been identified as a Pteridosperm. Recent work (Scheckler 1978) suggests that Svalbardia represents a developmental stage within Archaeopteris. This view has however been challenged by Matten (1981) who prefers to consider Svalbardia as a precursor of Archeaopteris. Allen and Marshall (1986) considered that since spirally arranged flattened flabelliform leaves have been found together with typical fertile specimens that "there was no reason to retain the name Svalbardia". They however retained the name Svalbardia until a thorough review had been carried out.

Fertile and vegetative axes were collected by the author from previously described localities and a new locality at Skersund, Shetland. This included well preserved permineralised specimens. Type specimens of other species of Svalbardia were also examined for comparisons to be made. These included S. avelinsiana from the Stockmans collection

at the Institute Royal des Sciences Naturelles de Belgique, as well as Svalbardia polymorpha from the Høeg collection in the Oslo Museum. Specimens of Archaeopteris hibernica were also examined from the British Museum.

Svalbardia scotica Chaloner 1972.

Mainland Shetland: Lebotton.

Vegetetative morphology: Fragments of fronds assignable to Svalbardia scotica were found from the same lithology as specimens of Thursophyton milleri. The striated axes (Plate 5 fig 3) were seen to have spirally attached leaves (Plate 5 fig 1) which were either laminate and flabelliform (Plate 5 fig 1), deeply divided and web like (Plate 5 fig 2), or filiform (Plate 5 fig 5). A few specimens resembling Corduroy material were also found in associated lithologies (Plate 5 fig 4). One terminal portion of fertile frond was also found (Plate 5 figs 6-8) showing lateral branches with numerous erect fusiform sporangia.

The distance between the emergence of the leaves was difficult to measure because points of insertion were obscured due to the spiral nature of their insertion, but it was estimated to be between 8 and 14mm (x=10mm n=11). The majority of leaves were incomplete, however one well preserved specimen (Plate 5 fig 2) was at least 38mm long and 3.1mm wide at the base. It was deeply divided showing dichotomous divisions of the tips. The filiform leaves were incomplete but at least 37mm long and 1.3mm wide at the

base. The flabelliform leaves were at least 16.6mm long and 1mm wide at the base. The width of the frond axes varied from 4.6 to 7.5mm (x=6.3mm n=7). The largest specimen (Plate 5 fig 1) being 67mm long and 4mm wide.

The corduroy material from this locality was poorly preserved but striations could be distinguished (Plate 5 fig 4) these were on average 1.5mm apart. No permineralised specimens were obtained from this locality and transfers failed to reveal any cuticle.

Fertile morphology: One specimen (Plate 5 fig 6) after uncovering was found to have sporangia situated on lateral branches (possibly modified leaves), which terminated in dichotomising tips. The mode of attachment could not be seen as the points of insertion were obscured (Plate 5 fig 6). The erect sporangia were situated on the upper surface of the lateral branches and were concentrated towards the main axis. Pairing of the sporangia or other modes of attachment to the lateral branch could not be seen. The sporangia were however between 2 to 3mm (x=3.5mm n= 7) long and 0.4 to 0.7mm (x=0.5mm n=7) wide. The sporangia ended in a triangular tip (Plate 5 fig 8) but there was no indication of surface detail or a dehiscence line (Plate 5 fig 7). The distance between sporangial insertion could not be measured because of the distorted nature of the specimen. Transfers were carried out on a fragment of the counterpart but it did not reveal spores.

Skersund.

Vegetative morphology: Rare fragmented portions of fronds (Plate 6 fig 9) were found together with numerous axes presumed to be root material (Plate 6 fig 10, Plate 17 fig 1,2) of Svalbardia scotica, some presumed to be growing in situ. A typical specimen of corduroy material was also found (Plate 17 fig 3) and numerous isolated, unbranching, pyrite permineralisations of frond material. Too few specimens of frond were collected for measurements to be taken.

The root material showed lateral branches (Plate Plate 17 fig 1) which gave rise to further laterals at regular intervals and appeared similar in appearance to roots of extant plants. In extant plants roots develop endogenously from inner layers of relatively mature tissue. In gymnosperms the lateral roots are commonly initiated in the pericycle and pass through the cortex of the parent plant to the exterior (Stover 1951). The emergence of what appears to be a lateral root is shown in Plate 6 (fig 10) where the central branch of the lateral seems to burst through the outer layers of the axis. The angle of emergence of the laterals from the main axis was between 45 to 100' (x=72' n=14). This gave rise to a ramifying network of axes. The lateral branches themselves had laterals emerging at regular intervals between 4.6 and 6.6mm (x=5.9mm n=8) apart. The emergence of the lateral branches did not appear to be in a spiral as in the aerial portions of S. scotica, but opposite forming a two dimensional network. One specimen (Plate 6 fig

6) was interpreted as being a portion of axis with filiform leaves which dichotomised at least once. Transfers were carried out but no cuticular remains were found.

Anatomy: Well preserved pyrite permineralisations of frond, were common. These unbranched axes were sectioned transversely (Plate 17 figs 4-9) polished and etched in HNO3 as described in the techniques chapter (Plate 17 figs 4-9, Plate 18 figs 1-6). These axes were photographed under reflected and, after metallurgical polishing, with incident light (Plate 18 fig 7, Plate 19 figs 1-5, Plate 21 figs 1-5). SEM observations were carried out after shallow and deep etching (Plates 20, 22). Longitudinal sections were also made (Plate 23) and viewed under the SEM after shallow and deep etching.

A few fusainised specimens; SF1, SF2, SF3, SF4, (Plate 24 figs 1,2,3,5) presumed to be of frond were also found. One was sectioned transversely but this technique failed to reveal any detailed information. The remainder were degaged or dissolved from the rock in HF, these were mounted on SEM stubs and veiwed with no further treatment (Plate 24 figs 6-8, Plate 25, Plate 26). Fractured secondary tracheids were observed in transverse and longitudinal section.

The permineralised specimens; S21, S22, S23, S26, S51, measured between 3.2 and 6.4mm in diameter, and were assumed to be terminal portions of frond. In specimens S42 S51, secondary tracheids were seen (Plate 4-9) to surround an area of primary tissue (Plate 18 figs 1-7) this was seen to be endarch in maturation with smaller protoxylem elements

situated in the centre,and these appeared to have collapsed. The larger metaxylem elements were present towards the periphery (Plate 18 figs 2-7). The assumption that these portions of axis were aerial fronds is supported by this, since Achaeopteris a close relative has mesarch anatomy in its primary bundles from the stem (Beck 1976), while the root has exarch primary xylem, as in extant spermatophytes (Beck 1953). This graduated into secondary xylem in some cases (Plate 1,2) with no transition zone, while in other sections (Plate 18 figs 3-7) a definite boundry was seen between primary and secondary tissues. In no cases were an inner cortex, phloem or cambium visible. In one specimen S42 (Plate 18 figs 3-7) an outer cortex of small thick walled circular cells were visible. In another specimen, S22 (Plate 18 fig 1) possible growth rings were seen, they were however discontinuous and interpreted as zones of tracheids which had collapsed after deposition. Measurements of intact metaxylem gave a diameter of between 27.0um and 74.3um (x= 49.6um n=20), their outline was distorted but generally circular to polyhedral.

The secondary tracheids were uniform brick like cells, radially elongated in transverse section, and present in radial rows (Plate 22 figs 5,7). They ranged from 54.9 to 84.9um (x=70.7um n=20) in length and between 15.4 and 24.7um (x=22.3um n=20) in width. The secondary wall of the tracheids could be seen to be perforated by intervascular pits and sclariform pitting, occurring on all walls of the tracheid (Plate 20 fig 9, Plate 22 fig 4). The secondary tissue generally surrounded the primary forming a circular

axis in cross-section (Plate 18 figs 1,2). Specimen S42 (Plate 18 figs 3-6, Plate 20 figs 5,6) illustrates a second stem morphology where the seondary tissue is present in two arms radiating from the primary tissue in a hour glass shape termed clepsydropsid. This specimen also showed two separate primary bundles possibly representive of a branch or leaf trace (Plate 18 figs 3-6). Specimens S42 and S51 were examined under the SEM and showed elliptical bordered pits present on all walls of the tracheids (Plate 22 figs 6-8, Plate 20 fig 8). These were on average 6.8um in diameter measured across the border and present in horizontal rows (Plate 20 fig 8, Plate 23 figs 5-8), termed opposite pitting and in diagonal rows (Plate 21 fig 8) termed alternate pitting (Fahn 1982). The tracheid wall was widest at the corners (Plate 19 fig 4,5, Plate 20 fig 3,4, Plate 21 fig 4,5) and thinnest in the middle. The width of the wall was therefore measured across the thinnest part of adjacent cells and varied from 4.5 to 7.0um (x=5.3um n= 20).

Specimens S26 and S42 were sectioned longitudinally (Plate 23) and the length of the secondary tracheids were between 102.2 and 156.2um (x=125.7um n=20). The intervascular pits (Plate 23 fig 1,2) were present on all walls of the tracheids. A variety of pitting types were seen in specimen S42 (Plate 23 figs 3-8) including sclariform (Plate 23 fig 3,4) to elliptical and circular bordered pitting (Plate 23 figs 5-8) present in diagonal rows.

The fusainised specimens showed longitudinally and transversely fractured tracheids (Plates 24-25). In specimen SF1 a fracture line passed across a row of pits

confirming the intervascular nature of the circular bordered pits (Plate 25 figs 3,4). This specimen also showed elliptical bordered pits (Plate 25 figs 5-8). Specimen SF2 confirmed the range of pitting types and across a small number of tracheids the pitting changed from sclariform (Plate 26 fig 2,6) to circular bordered pits (Plate 26 figs 4,5) and an intermediate type with elongated pits (Plate 26 fig 3). Some of the bordered pits had been fractured across the adjacent secondary wall but retaining the pit (Plate 26 fig 3). Specimen SF3 showed transversly fractured tracheids (Plate 26 fig 7) with predominately circular bordered pits (Plate 26 fig 8).

Bressay

Vegetative Morpology: A large amount of well preserved specimens assignable to fronds of Svalbardia scotica were found from localities on Bressay. Fragments of main axis (rachis) were recovered (Plate 27 fig 1, Plate 28 figs 1,1a) together with lateral branches (pinnae). Both the main axis and the base of the laterals were covered by spirally arranged leaves (pinnules) these were planated, filiform, dichotomising up to three times (Plate 27 fig 2, Plate 28 figs 1,1a). The filform leaves were gradually replaced along the laterals by laminate leaves which were highly divided dichotomously (Plate 28 figs 3,3a). These became flabelliform and often appeared planated, but their insertion remained spiral (Plate 27 fig 1,2, Plate 28 fig 1,2).

The distance between emergence of the leaves was consistant varying from 2.9 to 12.8mm (x=8.2mm n=14). The exact distance being difficult to measure in the spirally inserted leaves. Their angle of emergence being between 42 and 48' (x=45' n=8). The majority of leaves were incomplete, the largest was flabelliform and well preserved being at least 42mm long and 26.3mm wide at the margin. This margin was divided dichotomously and faint striations were seen running along the lamina. A few complete filiform leaves (Plate 27 fig 6) were found, these being between 20 and 25mm long and upto 0.75mm at the base. These leaves divided dichotomously up to three times. The intermediate laminate leaves, dividing dichotomously upto four times, the largest being 17.5mm long and 1.25mm wide. The width of the main axis varied from 3.2 to 7.5mm (x=4.2 n=7) and the width of the laterals varied from 2.1 to 5.7mm (x=3.0 n=11) and these emerged at an angle 30'. The largest specimen (Plate 27 fig2) was 105.5mm long and showed a main axis 3.3mm wide and lateral branches 1.7mm wide.

Plates 33-34 show a range of material found from associated lithologies assignable to Svalbardia or the Corduroy plant. These include pith casts (Plate 34 fig 5, Plate 33 fig 2) one of which came from Seli Geo found amoungst Svabardia scotica fronds. The corduroy plant from Ullins geo yeilded tracheids with elliptical bordered pits on all walls (Plate 35 figs 5-9).

Fertile Morphology: Numerous fertile portions of frond were found from the major localities on Bressay. Large

erect sporangia were observed on the upper surface of dichotomising lateral branches (sporophylls). The sporangia were present along the upper surface of the sporophylls, being absent only from the tips which dichotomised and turned upwards (Plate 28 figs 3,3a, Plate 29 figs 1-8). The sporophylls dichotomised occas ionally (Plate 29 figs 2,2a,3,3a), while the leaves below the fertile region (Plate 29 fig1) were highly divided and laminate. The insertion of the fertile branches was interpreted as being spiral (Plate 29 figs 3,3a). From a transfer to reveal the insertion points of the sporangia (Plate 29 figs 4-6) and camera lucida drawings (Plate 29 figs 2a,3a), it was determined that the sporangia were inserted on short peg like structures (Plate 28 fig 7). Pairing of the sporangia was not seen although their attachment in small clusters was (Plate 28 figs 4-6), but this was not considered to be a significant feature. The sporangia were between 1.6 and 4.8mm (x=3.6mm n=20) long and between 0.8 and 1.6mm (x=0.9mm n=20) wide. The variation in size was not considered great enough to sugest the presence of mega and microsporangia. The sporangia often ended in sharp tips (Plate 29 fig 2a) but no dehiscence line was visible, only a faint longitudinal striation (Plate 29 figs 7,8). The distance between sporangial insertion was from 0.1 to 5mm (x=0.8 n=15)in many cases they were too close for accurate measurement.

Transfers were caried out but no spores were revealed. One specimen (Plate 29 figs 7,8) did show black circular objects within the sporangia but cellulose acetate peel

failed to show spores. Branching of the frond axis in the fertile region was not seen and the distance between sporophylls was between 0.4 and 1.8m (x=0.9 n=10).

Anatomy: A few main axes were found to be poorly preserved in limonite. These were embedded and sectioned as described in the techniques chapter. Transverse and longitudinal sections were prepared for light and SEM microscopy (Plates 30, 31). Demineralisation of the longitudinal sections in HCL caused the cell walls to collapse and only a few isolated areas showed detailed information (Plate 31, Plate 32 figs 4-9).

In transverse section (Plate 32 fig 1,3) a single area of primary tissue can be seen, this is apparently endarch in maturation and surrounded by radial rows of secondary tissue (Plate 32 figs 1,2,4). No pith, outer cortex, phloem, cambium or ray tracheids were distinguished. Measurements of the circular to polyhedral metaxylem gave a diameter of between 14.1 and 25.4um (x=19.8um n=15). The secondary tracheids were uniform brick like cells between 18.6 and 59.5um (x=34.1um n=20) along the radial walls and between 18.5 and 24.2um (x=21.2um n=20) along the tangential walls. The tracheid secondary walls were covered in pits determined to be sclariform (Plate 32 figs 5,6), elliptical bordered or circular bordered (Plate 32 figs 7,9). These pits were interpreted as intervascular and alternate, occurring in diagonal rows. As in the previous material the primary wall was not preserved, and the thickness of the secondary wall was measured across adjacent cells, at the thinnest point

(Plate 32 fig 5) and varied between 1.8 and 5.6um (x=4.9um n=20). The wall thickness increased towards the corners of the cell (Plate 32 figs 5,8).

The longitudinally sectioned specimens were poorly preserved but seen to be elongated between 22.6 and 90.4um (x=56.5um n=20) long (Plate 30 figs 3-6). The demineralised tracheids had circular to elliptical bordered pits (Plate 31 figs 1,2,4-8), or sclariform pitting. The bordered pits were alternate in arrangement and present on all walls of the tracheids (Plate 31 figs 1,4,8). The diameter of the bordered pits, measured across the border, was between 5.9 and 8.5um (x=7.1um n=20).

Fair Isle.

Vegetative morphology: This productive locality at Bu-Ness yeilded a large amount of Svalbardia scotica together with the Corduroy plant (Plate 43 figs 1-3) and fertile portions of frond (Plate 42 fig 5, Plate 43 figs 5-7a). The fronds were of reasonable preservation and showed highly divided, planated filiform leaves (Plate 42 figs 1,2,6) attached to the main frond axis (rachis) as well as to the lateral branches (pinnae). The mode of insertion of the leaves was shown to be a possible spiral, while the attachment of the lateral branches was unclear and appeared to be planated. Filiform, highly divided laminate and flabelliform leaves were all seen (Plate 42 figs 3,4,6), but not on the same axis. The flabeliform leaves were incomplete (Plate 42 fig 3) but were at least 14.7mm long

and 8.8mm wide. One highly divided laminate leaf was found and this measured at least 23.5mm long by 3.2mm wide at the base. This leaf showed at least five successive dichotomies. Filiform leaves showed at least three dichotomus divisions (Plate 40 fig 6) but these did not occur in the regular manner seen in the highly divided laminate leaves. The filiform leaves were at least 8.3mm long and 0.5mm at their base.

The angle of leaf emergence varied from 35 to 52' (x=49' n=8) and the distance between emergence was between 2.2 and 5.0mm (x=3.6mm n=7). The angle of lateral branch emergence was from 30 to 50' (x=43' n=10) and the distance between branching of the main axis was between 4.4 and 16mm (x=8.9mm n=9). The main frond axis was also striated in a similar manner to the Corduroy plant (Plate 40 figs 1,2). The width of the main axes varied from 5.5 to 8.3mm (x=6.9mm n=5), while the width of the laterals varied between 1.6 to 2.2mm (x=1.9mm n=8). The largest frond specimen (Plate 42 fig 2) was 128mm long and 66.7mm wide.

Fertile morphology: A limited number of fertle fronds were found, the largest showed a terminal portion of frond with filiform leaves. This axis branched twice to give fertile portions of axis (Plate 43 fig 5).These lateral branches were seen to possess erect fusiform sporangia on the upper surface of sporophylls which dichotomised distally (Plate 43 figs 6,6a,7,7a). Their insertion was obscured, but possibly spiral (Plate 43 fig 6,6a 7,7a). The sporangia were concentrated close to the main axis and absent

distally. The insertion of the sporangia on the sporophyll was not clear but appeared to be on short peg like stalks (Plate 43 fig 7,7a). No pairing of sporangia was seen and they were between 1 and 2.2mm (x=1.7mm n=10) long and between 0.3 and 1.0mm (x=0.8mm n-10) wide. The distance between sporangial insertion being from 0.5 to 0.7mm (x=0.59 n=7). The sporangia ended in triangular often sharp tips, but no indication of a dehiscence line or surface detail could be seen. Transfers for spores and cuticle were also unsuccessful. No anatomy was found from this locality.

COMPARISONS BETWEEN THE LOCALITIES.

The Corduroy plant:

Large striated axes were consistently found in association with fronds of Svalbardia scotica although never in organic connection. The largest specimen came from Fair Isle (Plate 43 fig 2) and was 200mm in diameter, the smallest came from Quarry Bressay (Plate 33 fig 2) and was 12.9mm in diameter. In all cases longitudinal striations were seen, in many localities including Ullins Geo (Plate 34 figs 3,4) and Sillock Geo (Plate 34 fig 3) all that remained were striations, preserved as descreate bands of compression material. These could be seen to occassionally join and separate but they never divided to give new striations (Plate 34 fig 4). These bands of compression material varied from 0.3 to 1.9mm (x=1.1mm n=10) wide. At the locality C2 (Plate 34 figs 1,2) and Ullins Geo (Plate 35

figs 3,4) the striations were seen to consist of carbonised and limonitic permineralisations. These were degaged from the matrix and demineralised for observation with the SEM. In the case of Ullins Geo (Plate 35 figs 5-9) poorly preserved tracheids were found, these were similar to the typical secondary tracheid found in Svalbardia scotica and showed elliptical bordered pits on all walls of the tracheids (Plate 35 figs 5-9). This confirms the assumption by Allen and Marshall (1986) that the striations correspond to vascular bundles. The possiblity that the Corduroy plant represents the main stem of Svalbardia scotica is strengthened. The author considers that Svalbardía had a eustelic main stem similar to Callixylon (Archaeopteris main stem), with a central pith surrounded by numerous primary vascular bundles (upto 36 striations were counted in one specimen Plate 33 fig 6). These gave rise to secondry tissue radiating outwards. The Corduroy material possibly represents the main axis of Svalbardia scotica where the cortical and vascular tissues have been compressed and carbonised leaving ridges corresponding to the vascular bundles. It is suggested that during compression in most of the material the pith was not infilled and so was flattened and not preserved. The lower surface of the stem being flattened against the upper. This forms the confusing arrangement of striations on closely associated layers, found when the material is split. In the case of Sillock Geo where only the striations remain, the author assumes that degradation took place prior to deposition, causing the separation of the vascular bundles and that differential

compression preserved them at a variety of angles in the matrix.

Pith casts form when the pith is infilled prior to deposition. Compression and heating then causes carbonisation of the outer layers, which may be total as in the case of the specimen from Quarry Bressay. The striations representing the internal archetecture. This explanation can be applied to specimens found by Allen and Marshall (1986) from Bressay, where a large pith cast over 300mm long by 110mm wide was found. The outer carbonised layers having been removed leaving an impression of the primary bundles. The author considers that the Corduroy plant represents the main stem of S. scotica. This is supported by the absence of any other plant from the localities on Bressay. A reconstruction of the plant is given by Text Figure 20

Svalbardia scotica.

Vegetative Morphology: A comparision of measured characteristics is give in Table 8.

Table 8. Comparision of Svalbardia scotica from Skersund Bressay Fair Isle and Lebotten.

	L	S	B	FI
LI.	s	-	s	s
LT.	fLF	-	fLF	fLF
Al.'	-	-	45	49

	L	S	B	FI
Ab.'	-	-	30	43
Dl.mm	10	-	8.2	3.6
Db.mm	-	-	-	8.9
St.	ef	-	ef	ef
Sl.mm	3.5	-	3.6	1.7
Sw.mm	0.5	-	0.9	0.8
Si.mm	-	-	0.8	0.6
mx.um	-	49.6	19.8	-
Xr.um	-	70.7	34.1	-
Xt.um	-	22.3	21.2	-
Xl.um	-	125.7	56.5	-
Wt.um	-	5.3	4.7	-
Pt.	-	s,b	s,b	-

L=Lebotton, S=Skersund, B=Bressay, FI=FairIsle. LI=leaf insertion, LT=leaf type, Al'=angle of emergence of leaf, Ab'=angle of emergence of lateral branch, DL=distance between emergence of leaves, Db=distance between emergence of lateral branches, St=sporangial type, Sl=sporangial length, Sw=sporangial width, Si=distance between sporangial insertion, mx=metaxylem diameter, Xr=length of radial wall of secondary tracheid, Xt=length of tangential wall of secondary tracheid, Xl=length of secondary tracheid, Wt=wall thickness, Pt=pitting type. s=spiral insertion, f=filliform, L=laminate highly divided, F=flabelliform. ef=erect fusiform.

The four major localities all show general ag reement on

the arrangement of the fronds. These consist of a main axis (rachis) which branches frequently giving lateral branches (pinnae). Both main axis and lateral branches are covered with leaves (pinnules). This terminology was prefered instead of using, rachis, pinnae, and pinnules because these terms imply a fern like stem anatomy with leaf and branch traces not seen from this locality. Table 8 summarises the the measurements taken, Skersund is the only locality which shows questionable morphology, and the compression specimens from this locality were interpreted as root material. While the anatomy was interpreted as portions of frond. Three distinct leaf types came from all of the localities, except for Skersund with only the filiform type being present.

Dichotomising filiform leaves were present on the main axis as well at the base of the lateral branches and fertile portions of frond. The second leaf type occurred in an intermediate position, and was of intermediate morphology between filiform and flabelliform. These laminate leaves were highly divided dichotomously (Plate 5 fig 3, Plate 28 fig 3, Plate 42 fig 4). The laminate leaves from Bressay (Plate 28 fig 2,2a) are planated but those from Fair Isle were spirally inserted around the axis (Plate 42 fig 3).

The angle of emergence of the leaves varied from 35 to 52' (x=44') and was consistent at all the localities except for Lebotton , which could not be measured. Specimens from Skersund which, were determined to be root material branched regularly, having an angle of emergence of 72'. In the frond main axis the angle of branching varied between 30 and 50' (x=36.5') and in specimens from Bressay and Fair Isle it

was considered to be similar. The distance of emergence between the leaves was difficult to measure because of their spiral insertion on the axis. It was however measured approximately and shows general agreement at the localities were it could be measured, varing between 2.2 and 14mm (x=7.3mm). The large range of measurments was assumed to have resulted from obscuring of leaf insertion rather than any significant ontogenetic difference. The distance between emergence of the lateral branches could only be measured from Fair Isle and was on average 8.9mm between branches.

Fertile Morphology: Fertile specimens were found from Lebotton, Bressay and Fair Isle and all showed the same arrangement of the sporangia. The sporangia being present on lateral filiform branches presumed to be modified leaves (sporophylls), which occassionally dichotomised along its length and always branched at the tip. The sporangia were present on the upper surface and appeared to be inserted in one row only, occassional grouping did occur but this was never consistent.

The sporophylls were seen to be spirally inserted at all three localities and were similar in appearance to the filiform leaves. They formed a structure which can be interpreted as a primitive cone like organ (pannicle) with the tips of the sporophylls turning up to give some protection to the sporangia. The sporangia were all erect and fusiform with an apical tip and some showed a short peg like insertion on to the sporophyll. The sporangial length

from Lebotton and Bressay was similar (x=3.5mm), however the value from Fair Isle (x=1.7mm) indicated that the sporangia were smaller. The width of the sporangia however was consistent at all three localities varying from 0.3 to 1.6mm (x=0.7mm). The variation in sporangial size was considered to be the result of preservational differences, rather than any significant variation in the species. The distance between sporangial insertion could only be measured from Bressay and Fair Isle but showed general agreement varing from 0.1 to 5mm (x=0.7mm). The sporangia became less frequent along the sporophyll being absent distally. A reconstruction of Svalbardia scotica is given in text figure 19.

Anatomy: Only Skersund and Bressay showed anatomical details of Svalbardia, and from the Corduroy plant at Bressay. These two localities showed almost identical arrangement of the tissues in the frond. In progymnosperms generally the arrangement of lateral appendages tends to reflect the morphology of the stele (Beck and Schmid 1982), such that branches and ultimate appendages (leaves) are decussate on axes with four ribbed steles and helical on axes with three ribbed steles. In Svalbardia the stele appeared terete and so the interpretation of the morphological arrangement of the leaves as a spiral can not be confirmed by the anatomy. In the Archaeopteridales and in particular in Archaeopteris the primary vascular system is interpreted as a eustele (Scheckler 1978) on the basis of the distribution of the protoxylem strands, which may

surround a pith (see text fig.20), although these can be connected by metaxylem in more basal and more apical regions. In the eustele each rib of the stele contains a protoxylem strand (Beck 1971, Carluccio et al 1966, Scheckler 1978). The degree of medullation increases from the base towards the mid region of the axis and diminishes from this region to the tip (Scheckler 1978). The sections from Bressay and Skersund show a non-medullated solid terete stele. This may be interpreted as a reduced eustele (Schmid 1982).

If we assume that Svalbardia like Archeopteris is most conspicuously eustelic in the mid regions of penultimate axes, the lack of a typical eustele in Svalbardia, should not prevent assignment to the Archaeopteridales, but it does prevent assignment to the genus Archaeopteris since a eustele is considered to be a distinguishing feature of the genus (Beck 1975, Bonamo 1975).

The genotype Svalbardia is therefore retained until a conspicuous eustele has been found within the genus. The solid, terete and endarch primary xylem is seen from both localities and like the mesarch Arceopteridales (Beck and Schmid 1982) it is surrounded by radial rows of secondary tracheids. An exception to this is seen in a number of specimens found from Skersund (Plate 17 fig 8, Plate 18 figs 3-7), which showed radial rows of secondary tracheids in two arms (clepsydrodsid). This was considered to be an ontogenetic variation, the specimen coming from a more terminal portion of ultimate axis. No ray tracheids were found and this may be significant since some authors

(Leclercq and Bonamo 1971, Scheckler 1975a) indicate that secondary tissue without ray tracheids may in fact be modified rows of metaxylem. Since doubt persists as to the origns of the secondary tissue in Svalbardia, it provides another justification for retaining the Svalbardia separate from Archeopteris since this genus has been shown to possess well developed ray tracheids (Beck 1970b).

The metaxylem tracheids of Svalbardia from both localities were circular to polyhedral in cross-section, the diameter of which ranged from 14 to 74um (x=34.7um). The diameter of the primary tracheids from Skersund was twice as long, and the secondary tracheids were also larger. This was considered to have been caused by ontogenetic or environmental variation, and consequently not a significant difference between the localities. In transverse section the secondary tracheids from both localities appeared "brick" shaped being radially elongated, varing from 18.6 to 84.9um (x=52um) along the radial wall and between 15.4 and 24.7um (x=21.7um) along the tangential wall. In longitudinal section the tracheids were between 22.6 and 156.2um (x=90.8) long. The wall thickness measured across the thinnest part of adjacent cells was between 4.9 and 5.3um (x=5.1um) and was similar from both localities. The walls of the secondary tracheids were thickened towards the corners of the cell and this was a consistent characteristic seen at both localities (Plate 22 fig 8, Plate 32 fig 5).

When veiwed under the SEM the secondary tracheids showed pitting on all walls. Beirhorst's (1960) terminology was used to describe the secondary tracheids. Two general types

of which were seen, with intermediate variations. The first formed primary wall was not preserved in tracheids from either locality, being represented by a gap between adjacent secondary (presumably lignified) walls (Plate 20 fig 8, Plate 22 figs 7,8). In many cases (Plate 21 figs 7,8) the large amount of thickening present in the secondary wall filled the space left by the primary wall. In fossil material the presence of a first formed primary wall capable of stretching cannot be demonstrated and Beirhorst (1960) states that "lignification must be regarded as an incidental secondary modification". Thus the area between the walls is regarded as a presumed primary wall and the tracheids as presumed secondary tracheids.

Beirhorst (1960) also noted that pits are usually circular bordered in the narrow elements of the Lycopodiaceae and elongate in the wider elements. The elements with transversely elongate or sclariform pits following ontogenetically those with circular bordered pits. This explanatiion may be applied to the variation in pitting seen from both localities, which varies from circular and elliptical bordered to sclariform. Well developed pit pairs were seen from Bressay and Skersund (Plate 22 fig 8, Plate 25 figs 3,4, Plate 32 figs 7,9) and are termed intervascular pits (Fahn 1982). Using Beirhorst's terminology when a pit is transversely elongated it is termed sclariform (Plate 26 fig 6 Plate 31 fig 3, Plate 32 fig 3) and was seen from both localities as were elliptical bordered pits, with there distinct circular border and slit like aperture. Circular bordered pits were present (Plate 25 figs 3,4, Plate 31 fig

6, Plate 32 fig 9) although these were less frequent. The bordered pits were arranged in horizontal rows (Plate 25 fig 7), termed opposite pitting (Fahn 1982) or in diagonal rows (Plate 26 fig 5, Plate 31 figs 4,5,8, Plate 32 fig 9) termed alternate pitting (Fahn 1982). The bordered pits measured from 5.9 to 8.5um (x=7.4um) in diameter measured across the border, and was similar for both localities.

Generally the anatomy from Skersund and Bressay confirmed the similarites between the localities seen from the vegetative and fertile morphology, and supporting the assumption that the plant fossils found from these localities are indeed Svalbardia scotica.

Diagnosis.

Genus: Svalbardia Hoeg 1942 emend.

Derivation: After Svalbard (the area in which Spitsbergen is found) Hoeg's type locality. Main axis (rachis) at least one metre bearing primary branches (pinnae) which in turn bear pinnule like organs which were filiform, or laminate and several times divided, or flabelliform. The fertile branchlets (sporophylls) are also divided and bear up to a twelve sporangia in their middle region. The sporangia are generally erect pear shaped, fusiform, or cylindrical with rounded or sharp tips 1.5 to 4mm long and 0.5 to 0.7mm wide.

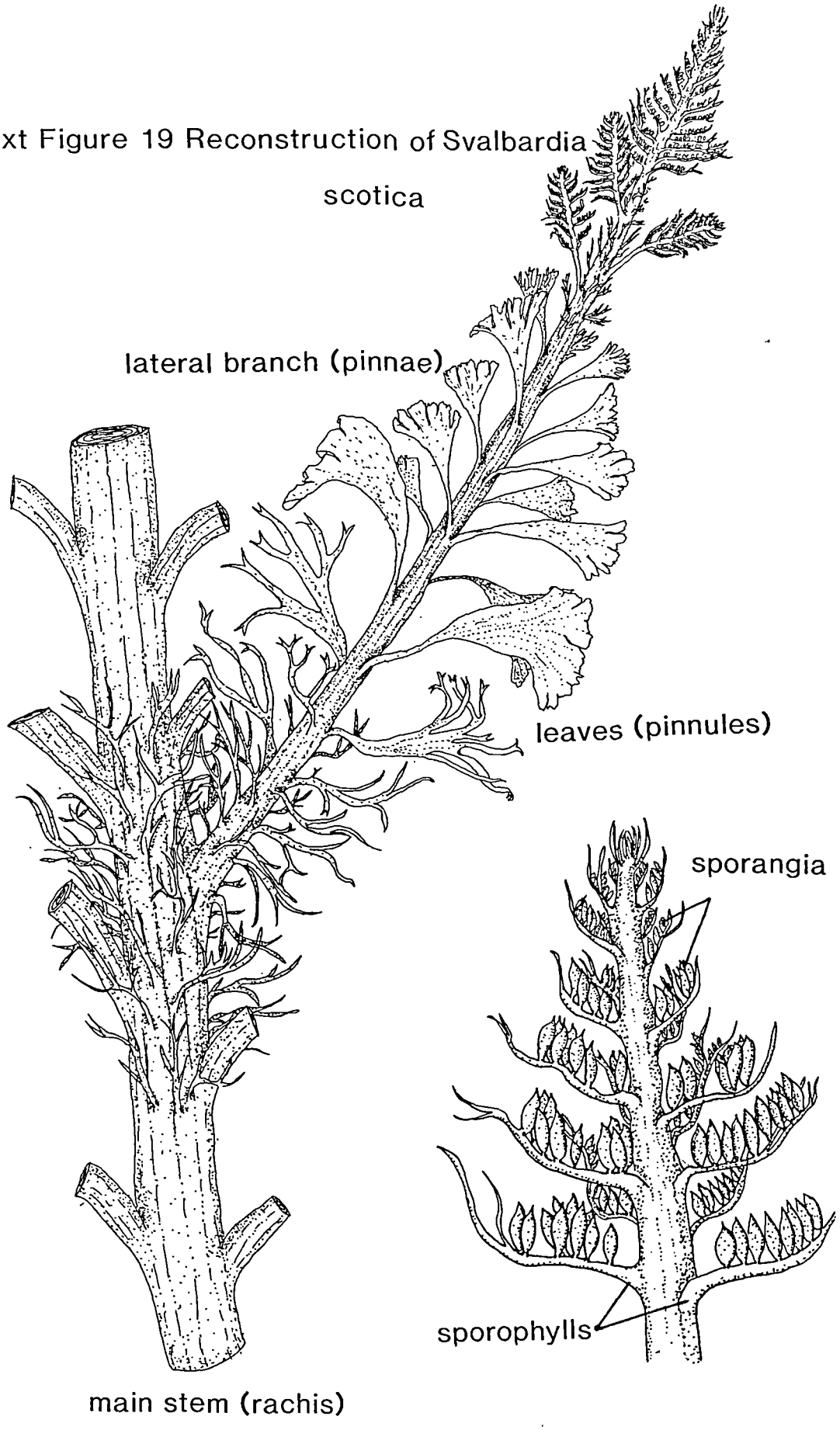
Species: Svalbardia scotica Chaloner 1972, emend.

Derivation: Named after its first recorded locality in Scotland. Generic description as above. Main axis up to three metres high bearing numerous fronds up to one metre long. Both main axis and frond axis striated. Lateral branches of uncertain arrangement, possibly planated and emerging at an angle of 38.5'. Leaves of varying morphology, those along the main axis filliform and dichotomously divided at least three times. Those at the base of the lateral branch becoming laminated but highly divided up to five times. These are replaced distally by flabelliform leaves up to 40mm long, with a dichotomously divided margin. All leaves spirally inserted, emerging at a mean angle of 44', with 7.3mm between leaf emergence. Flabelliform leaves may be planated.

Fertile branchlets terminal on axes forming a loose pannicle of dichotomising spirally arranged sporophylls. Abundant erect fusiform sporangia inserted on short peg like structures on the upper surface of the sporophyll. Sporangia, 0.7mm apart, and between 1.7 and 3.5mm long and on average 0.7mm wide, being absent only from the distal ends of the sporophylls which dichotomise and turn upwards.

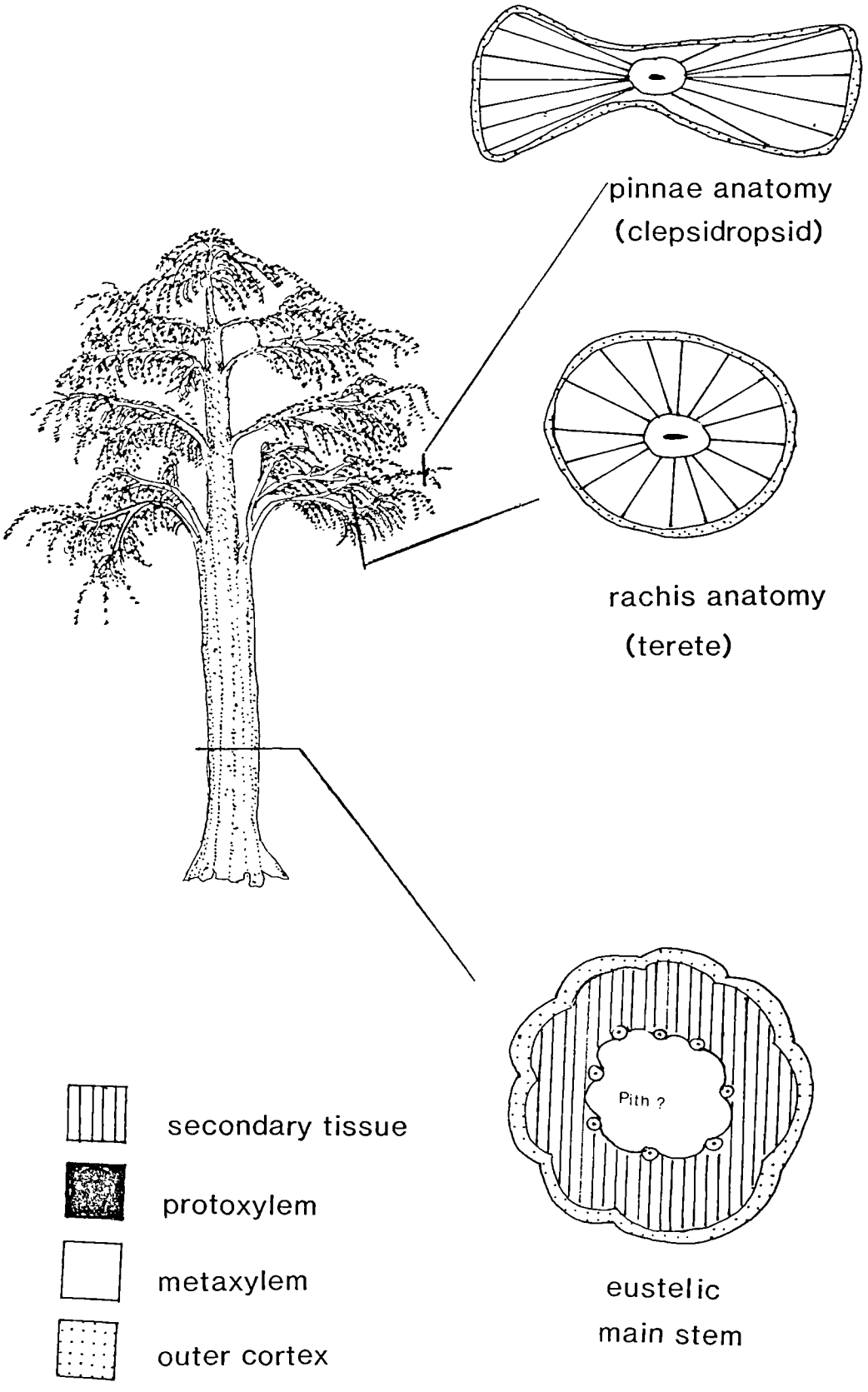
Anatomy consisting of a possible eustelic main stem. Tracheids with circular or elliptical bordered pits or sclariform thickening, the pits present on all walls of the tracheid opposite or alternately arranged. Frond anatomy consisting of a possible reduced eustele with a large centrally located solid, terete, endarch primary bundle, surrounded by radially elongated secondary tracheids in radial rows. Ray tracheids not present.

Text Figure 19 Reconstruction of Svalbardia scotica

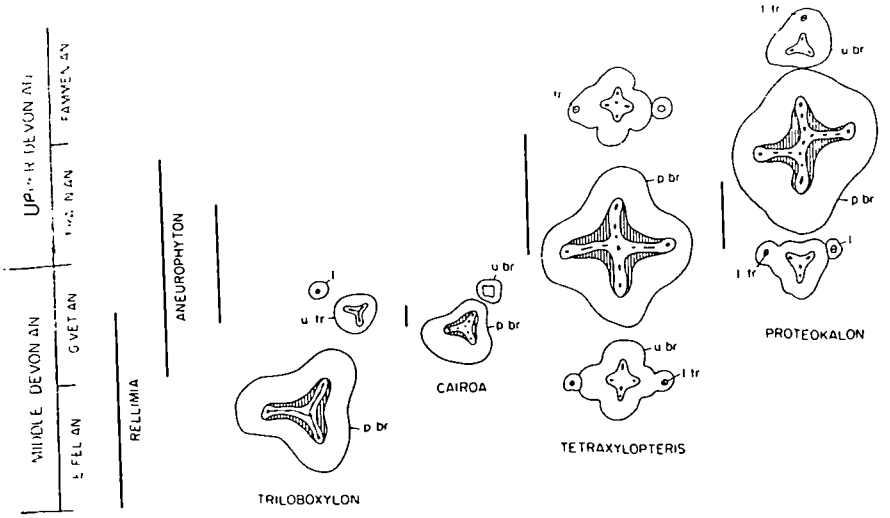


Text Figure 20

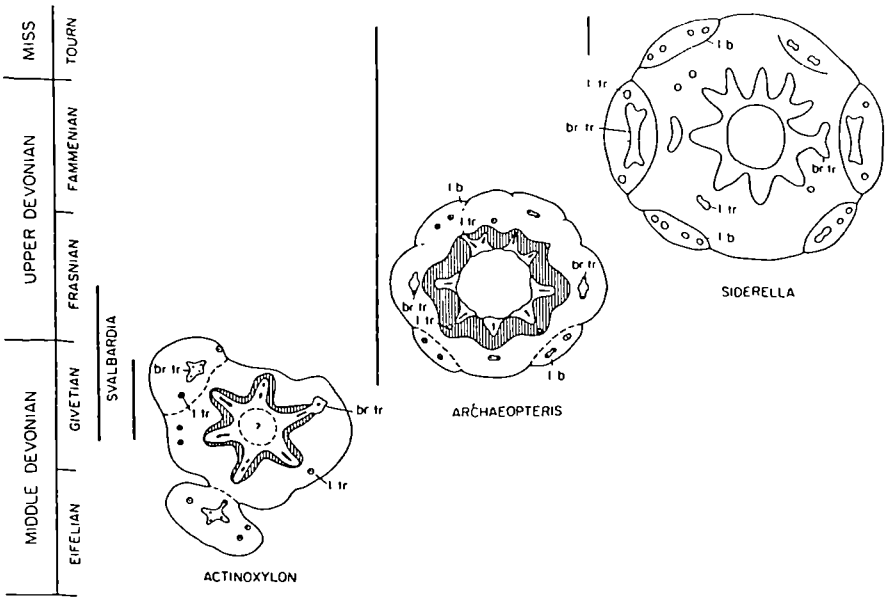
Reconstruction of the anatomy of Svalbardia scotica



Text Figure 21 Anatomy of some of the Progymnosperms



Geologic ranges (heavy lines to left of names and diagrams) and morphologic features of some members of the Aneurophytales. Some aspects of the primary and secondary xylem, branching patterns, and phyllotaxy are shown. Lined secondary xylem encloses unshaded metaxylem that contains black protoxylem strands. The smallest appendages containing traces, terete in sectional view, are considered to be the basal parts of leaves. Genera are arranged from left to right in order of increasing levels of morphologic specialization. *l* = leaf; *l.tr.* = leaf trace; *p.br.* = penultimate branch; *u.br.* = ultimate branch.



Geologic ranges (heavy lines to left of names and diagrams) and morphologic features of some members of the Archaeopteridales. Some aspects of the primary and secondary xylem, branching patterns, and phyllotaxy are shown. Lined secondary xylem encloses unshaded metaxylem that contains black protoxylem strands. The smallest appendages containing one or more traces, terete in sectional view, are the basal parts of simple leaves. Note that the leaf bases of *Archaeopteris* and *Siderella* are decurrent on the axes that bore them. Genera are arranged from left to right in order of increasing levels of morphologic specialization. *br.tr.* = branch trace; *l.b.* = leaf base; *l.tr.* = leaf trace.

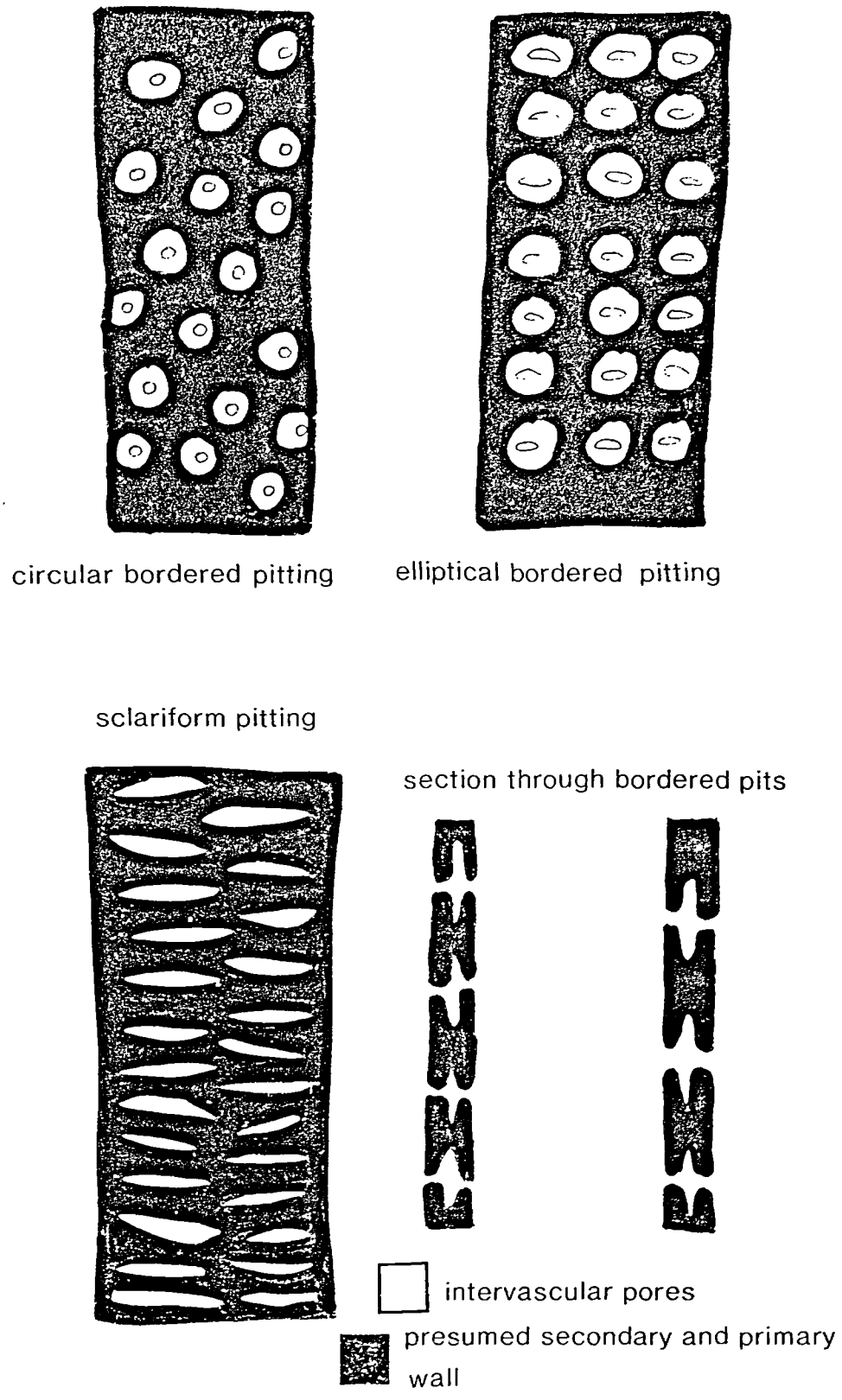


Figure 22 Diagramatic representation of pitting found in Svalbardia scotica

COMPARISONS WITH OTHER SPECIES.

Progymnospermopsida:

The progymnospermopsida (Beck 1960) consists of plants with a pteridophytic free sporing type of reproduction combined with gymnospermic stem anatomy, showing secondary xylem. Svalbardia scotica meets these requirements, and morphologically and anatomically is closest to the Archaeopteridales and in particular Archaeopteris.

Aneurophytales.

Aneurophyton germanicum:

The fronds of this plant were described by Kräusel and Weyland (1923) and was associated with the presumed main stem described as Eospermatopteris (Goldring 1924) by Serlin and Banks (1978). It was found from the Upper Devonian of New York State. The branching arrangement is spiral, the ultimate appendages are one to three times dichotomised but are unlaminated and three dimensional as opposed to the planated, or laminate leaves found in Svalbardia scotica. The lyre shaped fertile cluster also shows differences being terminal on lateral branches and containing up to 48 sporangia. The stelar anatomy is also different being triangular in cross-section, with four protoxylem strands, one in each arm and one centrally located, in a mesarch position. Similarities do exist and include elliptical bordered pitting of the secondary tracheids, but in

Aneurophyton they occur only on the radial walls. This plant is therefore similar to Svalbardia scotica in having progymnosperm morphology and anatomy but significant differences are seen in the vegetative and fertile morphology, as well as in the anatomy.

Aneurophyton olnense:

Stockmans (1948), first reported compressions and impression material of this plant. Schweitzer and Matten (1982) however considered that it was not a species of Aneurophyton. The vegetative and fertile morphology is quite distinct from that of Svalbardia and in particular the sporangial aggregates borne on short side branches separate the two species.

Aneurophytom hallii:

This species found initially by Dawson, was described by Arnold (1940) from the Middle Devonian of New York State and consists of fragments of axis 2cm in diameter showing triangular primary tissue surrounded by secondary tissue consisting or radial rows of secondary tracheids. In general arrangement the anatomy is reminiscent of Svalbardia scotica but the triangular primary bundle with its mesarch protoxylem points is quite different from the terete primary bundle of S. scotica.

Tetraxylopteris schmiditii:

Petrified specimens were described by Beck (1957) from the Upper Devonian of New York State and assigned to this

species. The main axis bears a three dimensional branching system in a dense spiral, possibly equivalent to the rachis, pinnae and pinnules of Svalbardia scotica but distinct from it. The primary xylem is a cruciform protostele with protoxylem points at the ends of the arms and a further point centrally located, which differs from the single centrally located protoxylem point in S. scotica. Secondary xylem is present in stem and rachis with circular bordered pits on all walls, but there is no indication of sclariform or elliptical pits as in S. scotica. The sporangia are dense clusters on ultimate branchlets of a pinnately branched sporangial complex, unlike the erect fusiform sporangia present on the upper surface of sporophylls, as in S. scotica. Thus this plant is again similar on the basis of its progymnosperm morphology and anatomy but does show differences.

Triloboxylon aschlandicum:

Matten and Banks (1966) initially described this plant from pyritised axes from the Lower Frasnian of New York State. The anatomy of the main axis immediately separates it from Svalbardia scotica. It has a three armed primary xylem with protoxylem points in each arm and two to four centrally located groups. Like S. scotica it has strong development of the secondary xylem, consisting of tracheids with multiserate bordered pits on all walls. The arrangement of primary tissues however is significantly different, as is the morphology of spirally arranged planated three times divided ultimate appendages.

Proteokalon petryi:

This plant was found by Scheckler and Banks (1971) from the Upper Devonian of New York State. The stele is four ribbed in the first order branches and three ribbed in the second order branches. The protoxylem bundles occur at the ends of each rib and others occur in a central position. This provides a significant difference to Svalbardia scotica in which there is a single centrally located protoxylem point.

Cairoa lamenekii:

This genus, similar to Proteokalon, was found by Matten (1973) from the Givetian of New York State, and shows a three ribbed stele in the main axis and a four ribbed stele in the lateral branches. The protoxylem strands are mesarch occurring at the ends of the arms and in a central position. This plant therefore is quite distinct on the basis of its primary xylem alone, and like the Aneurophtyales in general it represents a plant with relatively primitive ultimate appendages, and fertile structures when compared to Svalbardia scotica. The only similar character being the presence of secondary xylem.

Protopitayles.

Protopitys:

This class is represented only by one genus, with two species P. buchina (Goeppert 1850) from the Upper Devonian

of Silesia and P. scotica (Walton 1957) from the Lower Carboniferous of Scotland. The genus has a main stem with an oval pith consisting of parenchyma with a band of primary xylem around the periphery. At either end of the oval pith are two protoxylem strands which are all slightly mesarch. The leaves were distichously arranged with sclariform metaxylem. This organisation of primary tissues separates this genus from Svalbardia scotica. The secondary tracheids are however similar with elongate bordered pits, but the fertile morphology with its terminal fusiform sporangia on dichotomising branches is qutie different from that seen in S. scotica. This plant also shows similarities in its progymnosperm morphology and anatomy but the specific arrangement of the plant is significantly different.

Archaeopteridales.

Actinopodium nathorstii:

Høeg (1942) described this species from specimens collected by Nathorst from the Middle Devonian of Spitsbergen. It consists of a leafless axis of broad parenchymatous cortex and a star shaped stele, composed of a mixed pith with irregular metaxylem which is probably mesarch and it also has outer zone of secondary xylem. Although poorly known, the structue appears to be identical to the main axes of the lateral branch system of Archaeopteris and has been compared with this genus by Beck (1975). Carluccio et al (1966) suggests that Actinopodium represents the main axis of Svalbardia polymorpha, and

indeed it was found in the same horizon from which Svalbardia was recovered. If this is true it supports the veiw of Beck (1971, 1975) that Svalbardia and Archaeopteris are cogeneric. The fact that the stele is terete in Svalbardia scotica however does not give support to this veiw.

Actinoxylon banksii:

Matten (1968) reported this plant from petrifactions found in the Givetian of New York State. It shows a main axis with spirally arranged ultimate branches. These bear leaves, which dichotomise three to four times and are inserted in a sub-opposite and decussate arrangement. The primary xylem is a six pointed actinostele with one protoxylem point at the tip of each arm and another just within the radius. These features separate the plant from Svalbardia scotica. Limited development of secondary tissue is also a distinguishing feature.

Eddya sullivenensis:

This plant described by Beck (1967) from the lower Upper Devonian of New York State has a stele consisting of four or five primary bundles arranged around a parenchymatous pith. The bundles are mesarch and are in contact with the secondary xylem, which consists of tracheids and ray tracheids. Pitting is bordered and grouped on the radial walls of the tracheid in a similar way to those of Archaeopteris. The leaves are similar to Archaeopteris obtusa and arranged alternately on the stem. The plant can

be separated from Svalbardia scotica by its small size (50cm) and its Archaeopteris like anatomy. It does however show similarities in leaf morphology and in its progymnospermous anatomy.

Archaeopteris hibernica:

This plant found from the Upper Devonian of Ireland, originally found by Forbes (1858). It was redescribed by Dawson (1871) and is the type species. The fronds are planated and bi-pinnate reaching a length of up to 1.5m (Andrews et al 1970). The ovoid leaves occur in two ranks having a serrate margin and a striated lamina. The main axis is also striated, as in Svalbardia scotica. The fertile sporophylls are simi lar to those of Svalbardia in that they occur in zones on an otherwise sterile frond, but they are however not terminal, occurring in a median position on the pinnae. Like the sterile leaves they occur in two ranks, but as in Svalbardia the erect fusiform sporangia occur on the upper surface of the sporophyll. The sporophylls do not dichotomise. In general arrangement the morphology of A. hibernica is very similar to that of Svalbardia scotica but significant differences do occur in the positioning of the sporophylls and in the arrangement and morphology of the leaves.

Archaeopteris macilenta:

This is one of the better known of the eight species of Archaeopteris and was described by Carluccio et al (1966) from the Lower Frasnian of New York State. The axes were

refered to as compound fronds, consisting of a main axis or rachis, two rows of pinnae or primary branches, which in turn bore the pinnules. The spirally arranged flabelliform leaves were also found on the main axis and were strongly dissected ending in delicate tips. While those on the primary branches were mixed with fertile leaves. The fertile leaves were found to be non-laminate and dichotomise several times. In general appearance the vegetative morphology is suggestive of Svalbardia scotica with its spirally arranged leaves borne on lateral branches which may occur in two rows. The fertile morphology is however quite different, the sporangia occurring in terminal aggregates considered to be loose pannicles which are wholly fertile.

The anatomy of A. macilenta was investigated by Carluccio et al (1966) and Beck (1971), who showed that the rachis and pinnae contained a eustele conforming to the typical stem anatomy seen in Callixylon (Beck 1960). In the rachis two kinds of vascular strand depart from the lobes of the primary bundles, all in the same ontogenetic spiral; small ones which supply leaves, and larger ones that become four lobed and supply the primary branches The author considers that the presence of a eustele is an important distinguishing feature of this genus which is not proven in Svalbardia scotica, from the material so far examined. Secondary xylem occurs in both genera. Those of A. macilenta show grouping of bordered pits on the radial walls only. This, and the presence of ray tracheids also provide significant differences between the genera.

Archaeopteris halliana:

This species first described as Archaeopteris by Dawson (1871) was found together with A. macilenta from New York State. The sterile leaves are broadly fan-shaped and close to those seen in Svalbardia scotica, but are entire or have only slightly serrate margins as opposed to the variety of leaf types seen in S. scotica; the flabelliform leaves of which show a dichotomously divided margin. The primary branches of this Archaeopteris species show erect fusiform sporangia of a similar size and shape and with the typical peg like insertion into the upper surface of the sporophylls. The sporangia however have a longitudinal dehiscence line and are present in groups of only three or four and as such cannot be confused with those of S. scotica.

Archaeopteris latifolia:

Arnold (1939) found this species from the Upper Devonian of New York State. It closely resembles A. hibernica having leaves 1-2cm long which are rounded or ovate, with a serrate margin and therefore shows very different vegetative morphology from that seen in Svalbardia scotica. The fertile leaves also possess micro. and megasporangia containing micro. and megaspores.

Archaeopteris jacksoni:

This represents another species within this genus that has been demonstrated to be heterosporous. It was initially found by Dawson (1871) and later described by Pettitt (1965)

from the Upper Devonian deposits of Quebec. The vegetative morphology is also quite different from Svalbardia scotica in having (like all the species of Archaeopteris) only one leaf form. This type is however different, being flabelliform but without the characteristic dichotomously divided margin seen in S. scotica.

Archaeopteris obtusa:

Both Archaeopteris obtusa and A. fissilis (below), were described by Nathorst (1904) from the Upper Devonian of Ellesmere Island. They were later examined by Andrews et al (1965). A. obtusa has only sterile wedge shaped leaves, up to 7cm long, similar to the flabelliform leaves of Svalbardia scotica but with an almost entire margin. These are present on lateral branches, which emerge from a rachis in two rows, and in general the plant is a much larger than S. scotica. One specimen being 233mm long and the rachis 6mm wide.

Archaeopteris fissilis:

This plant has filamentous leaves which dichotomise one to three times and appears similar to the filiform leaves of Svalbardia scotica. Matten (1981) considers that this plant should be assigned to Svalbardia on the basis of its morphology. The primary branch of A. fissilis bears a mixture of, planated fertile and sterile leaves, the fertile leaves occurring in a usually median position along the pinnae. Andrews et al (1965) suggested the possibility of heterospory after describing sporangia of two sizes. A

section of petrified root was also found, not in connection but in associated lithologies, and this displayed the typical grouped bordered pits on the radial walls of the secondary tracheids as seen in Callixylon (Arnold 1930). They also found stem impressions presumed to be the main stems of Archaeopteris. The possible presence of anatomy typical to the genus separates this species from Svalbardia scotica as does the occurrence of only one leaf morphology although this was similar to that seen in S. scotica.

Archaeopteris fimbriata:

Nathorst (1902) described this little known species from the Upper Devonian of Bear Island, It shows the typical arrangement of rachis, pinnae and pinnules seen in the genus. The main stem and the lateral branches are covered in delicate highly divided fimbricate leaves, different from anything seen in Svalbardia scotica.

Svalbardia polymorpha:

This genus was established by Høeg (1942) on the basis of specimens from the Givetian of Spitsbergen, with the specific name S. polymorpha. The leaves are filiform, up to 2.5cm long and similar to those seen on S. scotica on the main axis and at the base of the lateral branches. The occurrence of other leaf types seen in S. scotica did not occur in S. polymorpha.

Svalbardia avelinesiana:

Stockmans (1968) described this plant from the Middle

Devonian of Belgium and it differs from S. scotica in having only filiform leaves. Although flabelliform leaves were found in associated lithologies and named Sphenopteris barantica and Ginkophytopsis belgica. The author has examined these specimens and considers that they may belong to the Svalbardia/Archaeopteris leaf complex. Fertile material of S. avelinesiana is also very similar to that found in S. scotica showing filiform dichotomising sporophylls possibly spirally arranged. The clusters of sporangia occur close to the main axis, and this provides the main difference between the fertile material of the species.

Svalbardia boyi:

This species found by Kräusel and Weyland (1960) is considered by Carluccio et al (1966) to be a species of Archaeopteris. It has laminate deeply divided leaves which bifurcate up to three times which are similar to some of those seen in S. scotica. The sporophylls are however quite distinct, showing clusters of sporangia possibly in two rows with the sterile distal portions of the sporophyll being much longer in relation to the fertile portion.

Svalbardia osmanica:

Pe trosian and Radezenko (1960) described this species from the Devonian of Russia. It has spirally arranged decurrent leaves, which are laminate and striated. The fertile sporophylls occur in associations described as a strobilus, with fusiform sporangia in two rows. The

similarities in vegetative and fertile morphology illustrate the close relationship ofthis species but the lack of the variety of leaf types and the differences in fertile morphology separate it from S. scotica.

Svalbardia banksii:

This species found by Matten (1981) from the Frasnian of New York State shows spirally arranged leaves being cuneiform (fan-shaped) and un-webbed forming a three dimensional pattern which is significantly different from S. scotica.

CHAPTER 6.

DISCUSSION

Introduction.

Banks (1980) discussed some of the inadequacies of palaeobotanical data in relation to biostratigraphy, as mentioned earlier (see chapter 1). Previous authors have been hampered by a lack of detailed anatomical and morphological information as well as inacurate age determination caued by a lack of stratigraphic control for the fossil localities. In this thesis the author has attempted to describe the fossils as acurately and as fully as possible, within the limits imposed by the material and the time available. Detailed anatomical and morphological information is essential to taxonomy and classification. The floristic zonation of Banks (1980) favoured in this thesis, is broadly based on a phylogenetic classification, so changes in the interpretation of phylogenetically relevant characters will effect the taxonomy, which in turn alters the biostratigraphy, biogeography and evolutionary interpretations.

PALAEOECOLOGY.

The depositional environments in which Svalbardia scotica and Thursophyton milleri occur are lake shore, lake deposit and the more proximal environments of river channels. In the case of Bressay and Fair isle Svalbardia scotica and Trimerophyton roskiliensis represent the only plants found,

occur exclusively in those deposits where they were found. Similarly Thursophyton milleri is the only plant found in on Foula, Shetland, Navity, Eathie and Kinkell. Svalbardia and Thursophyton are present in the same lithology only in the south east Shetland deposits of Lebotton and Skersund. This immediately suggests a stratigraphical age based separation, or environmental separation, or both. The low diversity flora has parallels in the Upper Devonian of the Catskills, U.S.A. (Beck 1964) where marginal lacustrine sediments are dominated by numerous specimens of the Archaeopteris main stem Callixylon.

Identifying the environments in which these plants grew is more difficult than identifying the deposits in which they were preserved, but by association it does give some indication as to their prefered environment. In the case of Svalbardia the specimens found were relatively unbroken with delicate leaves remaining in connection and, we can therefore assume a limited transport prior to deposition. If a fairly local source is assumed then it is reasonable to suggest the plant grew in lake margins and high sinuosity braided streams. These represent the finer sedimentary facies in the Shetlands and considering the domination of these fluvial and lake-shore sedimentary processes it is hardly surprising that one plant assemblage dominates. More surprising is that this consists of only one plant species. The occurrence of other plants should be expected even if they were transported and not present as an understorey vegetation.

Rootlets have been observed in silted up channels of

braided streams (Allen and Marshall 1981) from south east Shetland, and at Skersund they are considered to be roots of Svalbardia. Thus we can imply that the channels became colonised after abandonment, and would then be removed and deposited when a fluvial regime was re-imposed. This can be seen to have occurred in a similar way on Fair Isle where the fine sandstone deposits containing Svalbardia are rhythmically deposited with massive sandstone units, which have been interpreted by Austin (in Allen and Marshall 1986) as being representative of rivers meandering across an alluvial plain. The shale units being deposited during periods of lacustrine dominance and the sandstones as lake margin beach deposits.

The low diversity or monospecific nature of the flora may be explained by some, as yet unknown niche restriction. Svalbardia may therefore have grown on the fringe of lakes and rivers, but not on an alluvial fan environment. Thursophyton appears similarly to have grown in monotypic stands. On Foula the plants appear fragmented, the delicate dichotomising branches being stripped from the large unbroken psuedomonopodial axes. This may suggest a moderate amount of transport prior to deposition. The plants occur in fine grained deposits which have been interpreted as overbank deposits of silts and muds from rivers meandering across a wide sandy alluvial plain (Marshall pers. comm. 1987). Thus we can assume that Thursophyton may have grown close to river banks on the flood plain, being washed away during flood conditions, in the silts and muds, and transported only moderate distances before deposition.

At Skersund, amongst the sandstone deposits of braided streams, occassional alluvial deposits infill abandoned channels. In one these deposits plants have been found assigned to both Svalbardia scotica and Thursophyton milleri. This may indicate that both plants grew together, but the fragmentary nature of the material suggests considerable transport prior to deposition. It may therefore be the case that both plants were deposited after flood events, which also filled the abandoned channel. The infilled channel then became colonised by Svalbardia, the roots of which were preserved by further flood events, some of them being found in situ. The author envisages Thursophyton growing on the banks of wide rivers, flowing across sandy plains into deltaic environments on the margin of lakes. This type of area is dominated by Svalbardia. The niche separation that prevented these plants from growing together may be the competition for space or light, a competition in which the tall Svalbardia would be dominant. Svalbardia scotica may have been unable to colonise other areas, since the author considers that a large progymnosperm with its relatively simple vascular system would require a constant supply of water. Thus Svalbardia might dominate only in the wet environments of a lake margin and the banks of braided streams. Thursophyton milleri. a smaller plant, may have been a relatively xerophytic or mesophytic plant, able to survive on drier flood plains, but still close to a water supply.

The south east Shetland Basin has been dated as being from the Middle to Upper Givetian close to the boundary with the

Frasnian and consequently younger than the Early Givetian (post Achanarras) deposits of Foula. The dominace of Thursophyton in the Early Givetian may result from the absence of Svalbardia allowing Thursophyton to dominate. During the Givetian the influx of Svalbardia would result in competition and possible niche separation between the species allowing Svalbardia to dominate in the lake margin and braided stream environment. Since this is the major deposit in the Shetland basin it is hardly surprising that Thursophyton is found from only a few deposits, being deposited with Svalbardia scotica only when extensive transport occurs.

No in situ miospores have been recovered from Svalbardia scotica by this or other authors (Allen and Marshall 1986). They have however been recorded in many Archaeoteridales (Allen 1980), including S. polymorpha (Hoeg 1942, Vigran 1964), where they are similar to the dispered spore Geminospora lemurata. Those deposits lying to the east of the Melby Fault (Fig. 5) differ from those lying to the west by containing G. lemurata together with other characterisic Givetian forms (Marshall 1988). Indeed, G. lemurata is the most abundant miospore in south east Shetland and Fair Isle deposits (Allen and Marshall 1986, Marshall and Allen 1982). Ecological control on the distribution of Geminospora sp. has been proposed by several authors (Streel 1967, Richardson 1965, 1967, 1969) and is thought to have grown on and around flood plains and marginal marine areas. The percentage of Geminospora sp. from Fair Isle fluctuate between 39% to 2% in a non-marine, internal basin facies

(Marshall and Allen 1982). The percentage of Geminospora varies from high in the fine grained alluvial deposits containing Svalbardia to low in the sandstones without Svalbardia. This supports the assumption that Svalbardia contains the insitu spore Geminospora, and that it grows in an ecologically restricted environment on the edges of lakes and streams.

Richardson (1965, 1967, 1969) noted the absence of Geminospora from the lacustrine and fluvial deposits of the Orcadian Basin. These deposits were dominated by Rhabdosporities and Ancyrospora. Since Shetland was in fluvial connection with the Orcadian Basin, and proximal to it (Allen and Marshall 1986), it might be expected that the Ancyrospora/Rhabdosporities complex of spores would dominate in the lacustrine deposits. However J.E.A. Marshall (pers. comm. 1989) has found Geminospora lemurata and other Givetian elements in the Orcadian Basin sediments of the Eday Group and John O'Groats Sandstone of Caithness. This discovery discounts the possibility of a palaeogeographical or palaeoecological separation within the deposits, but rather a stratigraphical age-based separation.

G. lemurata occurs in large numbers from the Early Givetian (see McGregor and Camfield 1982) and forms a stratigraphically distinct event. This influx is identical to its appearance from the rest of the Old Red Continent from the lateset Eifelian of the Eifel region in West Germany (Streel et al 1987), the Early Givetian of the Russian Platform (Kedo and Obukhovskya 1981), the Givetian of Germany (Riegel 1982), Spitsbergen (Allen 1967), and

Arctic Canada (McGregor and Camfield 1982). A possible explanation (Marshall and Allen 1982) is that the time difference between Orcadian deposits and Fair Isle deposits allows migration of Geminospora. Initially from from the Eifel region of Germany, where it occurs in the latest Eifelian, to the Russian Platform, where it occurs from the Early Givetian and on to Shetland where it occurs in the Late Givetian. This influx is mirrored by that of Svalbardia found in Givetian deposits of Shetland and the surrounding areas. Thus Svalbardia is considered like its in situ spore type to have migrated from Germany via the Russian platform during the Early Givetian.

The major miospore types from the deposits in which Thursopyton milleri dominate on Foula are characterised by the absence of Geminospora and the presence of Rhabdosporities langii and Ancyrospora sp. among other Early Givetian indicators (Donovan 1978). A large increase in Ancyrospora has been seen by J.E.A. Marshall (pers. comm. 1987) at the top of the Foula succession in the Noup Sandstone Formation from which Thursophyton was found. This may be significant indicating a possible spore type for Thursophyton but no in situ spore has been found for this species, by this or previous authors. Thus it is difficult to make assumptions on the ecological significance of Thursophyton with regard to the dispersed spore record, or on the possible in situ spore type of Thursophyton milleri.

The Ancyrospora/Rhabdosporities spore complex is however more abundant in Early Givetian upper flood plain and possibly lacustrine environments (Streel 1964, 1967,

Richardson 1965, 1967, 1969). This also seen in deposits from Foula as is the absence of Geminospora the in situ spore type of Svalbardia. Thus suggesting its absence from the Early Givetian of Shetland and supporting the assumption that Thursophyton milleri could dominated similar environments to Svalbardia before its influx into the Shetlands.

The Svalbardia/Archaeopteris complex.

Beck (1969, 1970, 1976) has summarised the problem of interpreting various genera within the Archaeopteridales as either a proliferation phenomenon due to incomplete information, as representing ontogenetic variation within a smaller number of taxa, or as representing evolutionary change through time. The nature of the fossil record is such that incomplete information due to disarticulation and preservational state of the plant will always prove a hinderance to a clear understanding of the systematics of these fossils.

Some parameters of variation within the fossil assemblage can be quantified, when a large collection from a single locality is studied. Such sites and collections generally represent a single sequence of events leading to preservation, and varying from catastrophic floods to slow continuous accumulation of sediment and plant parts of a relatively short period of time, such as a few thousand years. Measurements will, in this instance, reflect variation of individuals within a population or community

which had relatively little chance for much evolutionary change.

Specimens from supposedly one genus or species, collected from widely spaced separate localities where stratigraphic and chronological levels might be separated by millions of years, may no longer represent biological variation of a single biological genus or species. This palaeontological genus or species will represent, at best, the equivalent of a biological species and, at worst, a mixture of species that may or may not be related. The distinguishing biological features and isolating mechanisms, such as, morphology, cytology, physiology, genetic, and ecological are not apparent to the palaeobotanist.

Convergent and parallel evolution within an environmental regime may create many morphologically similar plants, and distortion of these plants through compression and permineralisation might lead to the kinds of variation seen within the Archaeopteridales. The differences between Svalbardia and Archaeopteris may represent differences between biological families in some instances and biological genera and species or individuals in other instances. The time interval between the stratigraphic occurrences of the major Svalbardia and Archaeopteris localities tends to support their distinction as major species, either as subgenera of a single comprehensive genus or as two genera. The separation of Svalbardia from Archaeopteris was made easy by the restriction of Svalbardia to the Givetian, and the absence of flabelliform leaves in the genus. Matten's (1981) description of Svalbardia banksii, with filiform

leaves in the Frasnian, and the discovery of flabelliform leaves from Svalbardia scotica in the Givetian (Allen and Marshall 1986) weakens the assumption that they are two stratigraphically separated genera.

Scheckler (1978) indicates that Actinopodium is indistinguishable from Archaeopteris and should be synonymous. However this may be the case of incomplete information, and Matten (1981) suggests that information on leaf trace departure to leaves or branches, secondary xylem, or extended morphology is needed in Actinopodium to warrant its inclusion within Archaeopteris. Recent workers (Carluccio et al 1966, Beck 1976, Scheckler 1978, Matten 1968) agree that Actinopodium represents the anatomy of Svalbardia polymorpha. This study of Svalbardia scotica clearly shows that by the absence of a eustele its anatomy is distinct from Archaeopteris and Actinopodium, although the terete haplostele surrounded by Secondary tissue can be formed from a reduced eustele (Beck et al 1982).

While not disproving the synonymy of Actinopodium and/or Archaeopteris with Svalbardia it does show the best evidence so far, to suggest that there are some differences. In the case of Svalbardia scotica the morphology indicates a close relationship, but the anatomy separates Svalbardia from Actinopodium and Archaeopteris.

Thus at the present Svalbardia should be considered as a separate genus anatomically different from the eustelic Archeaopteris/Actinopodium/Actinoxylon complex which possibly evolved from an early form of Svalbardia type within the Givetian. Whether or not the genera can be

retained in the Frasnian depends upon the discovery of anatomy in Svalbardia banksii and in the Archaeopteris species which morphologically resemble Svalbardia.

The evolution of the leaf and Svalbardia.

In most Lower Devonian groups, evolution of the megaphylluos leaf is regarded as occurring at a very early stage. Considered by Gensel (1984) to be manifested as variability in branching pattern of stem like axes in these Lower Devonian plants. The first plants with undoubted megaphyllous leaves occur in the Givetian (Allen and Marshall 1986) and the Upper Devonian (Chaloner 1970, Galtier 1981), although rare occurrences of incompletely preserved laminate, and apparently megaphyllous leaves (Platyphyllum) of uncertain affinities have been reported from the Emsian (Chaloner 1970, Chaloner and Sheerin 1979). It has been postulated (Banks 1975, Gensel 1977), that the trimerophytes exhibit early transitions of branch systems to megaphyllous leaves, from Psilophyton with variation in dichotomous to pseudomonopodial branching through to Pertica and Trimerophyton, with the development of distinct robust major axis and sudordinate lateral branches, and in the latter two genera a tendancy to pseudomonopodially divided lateral branches.

Where anatomy is known, no major changes in vascular shape occur in the various orders of branching, except for a slight difference in strand shape departing of the fertile branches in Psilophyton dawsonii (Banks 1975), and in a as

yet unamed plant from the Lower Devonian of Gaspe Canada. This was found by Gensel (1984) and demonstrates a pronounced anatomical change from the lobed xylem of the main axis to an elliptically shaped, first order lateral branch trace. Comparable changes occur in younger fossils. This plant might then be regarded as a trimerophyte derivative leading towards these later plant groups such as the Aneurophytales, Archaeopteridales or Iridopteridales.

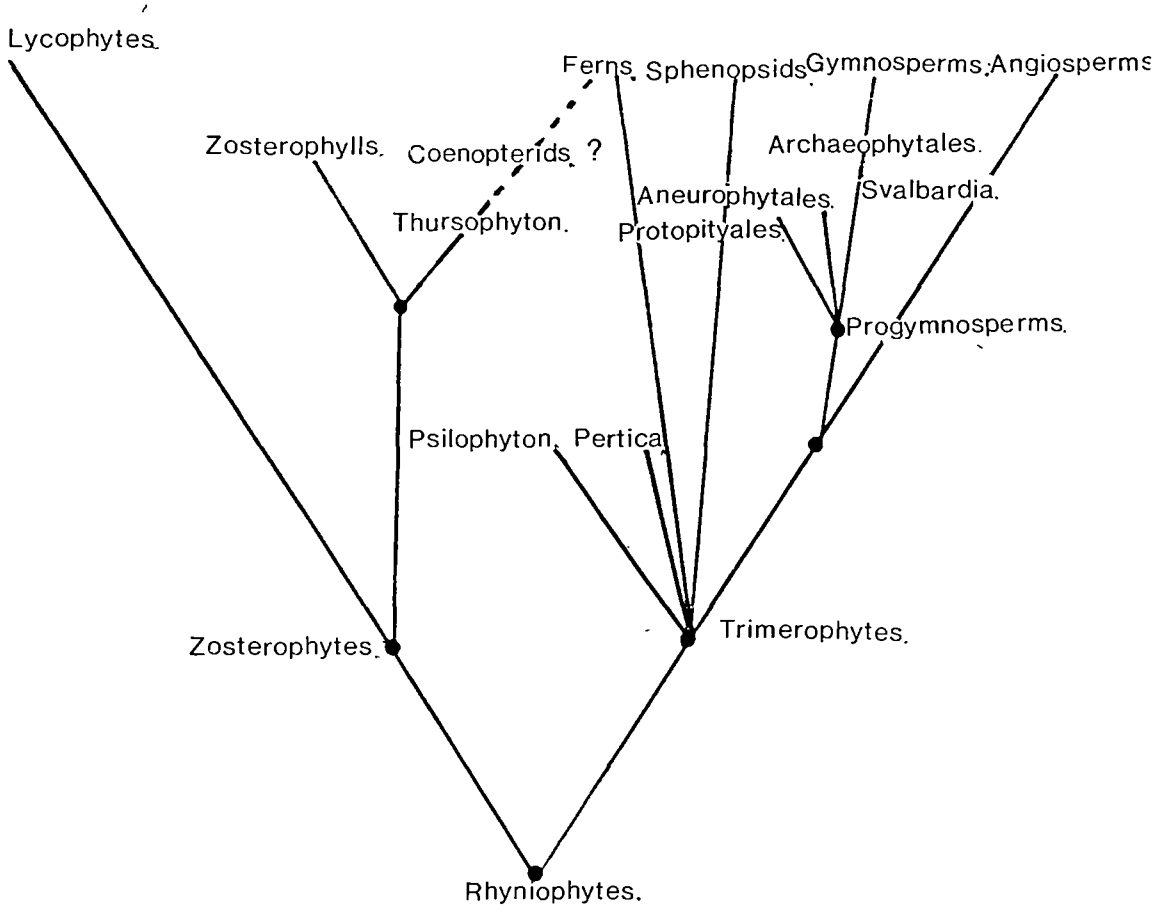
The presence of leaf traces in Svalbardia scotica has not been proved, but the plant can be assumed to possess megaphylls similar to those in Archaeopteris. In Svarbardia scotica there is an ontogenetic variation in leaf type ranging, from filiform to laminate and highly dividedand finally to flabelliform. This may be a feature under environmental control, however the variation along the stem may be regarded as illustrating the probable stepsin the evolution of a megaphyll. Firstly by planation of the filiform leaves and then webbing to form a laminate structure which ultimately becomes flabelliform. Thus Svalbardia may represent a plant that links a Pertica/Trimerophyton precursor to the Flabelliform leaves of the Archaeopteridales. It is proposed that precursors of Svalbardia possessed filiform appendages which became megaphyllous and laminate by planation and webbing, culminating in the highly developed forms seen in Svalbardia and Archaeopteris.

Evolution and Thursophyton milleri.

The anatomy of most vascular plants from the Lower Devonian consists of a solid terete or elliptical cylinder of tracheids with centrach or exarch primary xylem maturation, except in lycopods or lycopod precursors, with vascularised microphyllous leaves and a lobed xylem. These early plants possess variety of sporangial structures, shapes and modes of attachment, from terminal to lateral, and some possess unvascularised usually multicellular emergences. In contrast Middle Devonian plants show the first appearance of more complex stelar patterns, some morphological and anatomical distinction between stems and megaphyllous leaves, secondary tracheids, arboresence, and heterospory. The major plant groups can be distinguished and linked at least indirectly to modern groups.

Thursophyton milleri from the Givetian not only shows an increase in complexity of branching but also shows a change in vascular strand shape during branching, from elliptical in the main axis to terete in the psuedomonopodial branches. The anatomy is otherwise typical of the Lower Devonian genera, Gosslingia and Zosterophyllum, but no Lower Devonian plant exhibits the particular combination of complex pseudomonopodial and trichotomous branching together with a change in vascular strand shape on branching. The closest relatives of the genus are Margophyton golgschmiditi from the Lower Devonian of Norway together with Euthursophyton hamperbacence and Thursophyton elberfeldense from the Middle Devonian. These genera together with Thursophyton form a natural grouping of plants that show predominately psuedomonopodial branching (trimerophyte like) together with

Text Figure. 23. Simplified summary of the evolutionary relaionships of the major plant groups including Svalbardia and Thursophyton.



zosterophyll characteristics. Thursophyton milleri described here might be regarded as a zosterophyll derivative initiated possibly in the Lower Devonian which may lead on to other younger plant groups such as the Cladoxylales and Coenopteridales. The transition from an elliptical exarch xylem strand, typical of the zosterophylls to a lobed, mesarch xylem as seen in several Middle-Upper Devonian plants of various affinities is here considered possible by variable development of the metaxylem to give a lobed xylem with sunken mesarch protoxylem areas in the lobes. This type of stele may then develop into the complex steles seen in the protopteridales. At the very least the presence of complex branching morphology in an Upper Givetian zosterophyll does suggest that the class did not become extinct in the Frasnian.

Biostratigraphy.

The age of the Shetland Middle Devonian plant assemblages were dated where possible by dispersed spores (Allen and Marshall 1981, Marshall 1981, Marshall and Allen 1982) and fish fossils (Loffter pers. comm.) and found to range from Early Givetian to Late Givetian, close to the boundry with the Frasnian. This makes the assemblage comparable with the Assemblage Zone V, the Svalbardia Zone, of Banks (1980). A notable feature that occurs in this zone is the abundance and widespread geographic range of genera that had already appeared in Zone IV. Banks placed the zone somewhere above the Eifelian/Givetian boundary, because of the difficulty in

distinguishing the boundary at many localities, which may have hampered the assignment of a particular assemblage to this zone. This zone sees the start of the proliferation of the advanced progymnosperms consisting of Actinoxylon, Svalbardia, and Actinopodium, which are Archaeopteridalean and considered by this author to be the precursors of the genus Archaeopteris. This genus is the index plant for Zone VI and it becomes widespread in that zone. Actinoxylon is the first genus of the group to appear, near the base of the Givetian. Svalbardia and Actinopodium being younger.

The localities at which the Svalbardia Assemblage zone occurs were listed by Banks and includes Bohemia (Obrhel 1962,1968), Germany (Schweitzer 1966, 1972, 1973), Belgium (Leclercq 1940, Stockmans 1948), eastern New York State (Bonamo 1977, Grierson 1976), USSR, Siberia (Iurina 1969, Petrosian 1968), Spitsbergen (Hoeg 1942). The south east Shetland Basin can now be included on the basis of the presence of Svalbardia scotica. The new morphological characteristics that appear during this zone are considered by Banks to include Arborescent habit, ligule, abundant secondary xylem, primary xylem with numerous protoxylem strands secondary phloem and periderm. The occurrence of secondary xylem, arborescent habit and the possiblity of a eustele, with its numerous protoxylem strands, from Shetland all support its inclusion in this zone. Banks considered the zone to be less precise than the corresponding Triangulatus zone (Richardson 1974) based on spores. The author suggests that the occurrence of Svalbardia and the parallel influx of Geminospora sp. should be used as the

boundary for Zone V since it is a widespread and stratigraphically distinct event from the Old Red Continent.

Taphonomy.

It is here suggested by the author that in fossil plants preserved in pyirite/limonite selective decay occurs after death and before the permineralisation process has been completed. Transport from the site of growth to the place of burial, perhaps over a considerable distance, would have been accompanied by aerobic decay. During transport and initial burial decay would therefore be swift due to autolysis and aerobic bacterial attack (Jørgensen 1983). In vascular tissue there is a selective decay of the cell wall, the cellulose being removed preferentially relative to the lignin (Spike and Hatcher 1987, Stout et al 1981). the resistance of lignin is due to its complex structure and in extant plants its breakdown is one third that of cellulose (Stout et al 1981). The amount of aerobic decay in Svalbardia and Thursophyton can not be determined but we can suggest that the process would have been slower because of the lower concentrations of oxygen in the Devonian atmosphere (Holland 1984). The presence of basidiomycetes one of the organisms responsible for aerobic decay has been demonstrated from the Upper Devonian in Callixylon wood (Stubblefield et al 1985).

As sediment acculated and the aerobic organisms mopped up the remaining oxygen anaerobic conditions would be imposed. Further decay of cellulose would now involve hydrolysis.

This process is seen in many extant bacteria (Jorgensen 1983) and the complete decay of cellulose involves a chain of bacteria. The sulphate reducers, central to sedimentary pyrite formation are one of these groups feeding on the breakdown products of cellulose (Widdel and Pfennig 1977). Under anaerobic conditions lignin is the most decay resistant consitituent of the plant cell (Varossieau and Breger 1951) and would have remained relatively intact during anaerobic decay. The sulphate reducing bacteria use sulphate present in the ground water as an electron acceptor and reduce it to hydrogen sulphide (Love et al 1983). The energy source for this is provided by the breakdown products of cellulose. After the production of hydrogen sulphide the process is essentially inorganic.

The hydrogen sulphide reacting with iron ions present in the sediments to form iron monosulphide (Love et al 1983). The formation of pyrite occurs as minute framboids, which can be distinguished from sections of Thursophyton milleri (Plate 15 fig 2,3), when elemental sulphur reacts with the iron monosulphide (Love et al 1983). In Thursophyton and Svalbardia pyrite is present as an amorphous material within the inter and intra-cellular spaces and the spaces occupied by decomposed cellulose cell wall. Undecomposed lignified walls and cellulose cell walls are preserved and have become coalified during diagenisis. In the region between the tracheids and the peripheral tissues was presumed to have been parenchymatous. This has been completely decomposed, and may have provided a source of hydrogen sulphide diffusing into the relatively cellulose-poor tracheids,

completing the pyritation process.

The presence of coalified walls in Thursophyton and Svalbardia will therefore reflect their original lignified composition. The coalified wall seen in Svalbardia and Thursophyton may however represent the primary and secondary wall and that the wall pyrite fills spaces between the tracheids and forces them apart. In this case the perforate connecting wall may represent the primary wall. This is however very unlikely and the author prefers the interpretation in relation to decay. The perforate pores in the secondary wall are considered to be simple pits. It has however been proposed that these pores are formed by the growth of pyrite through the wall (Hartman 1981). The circular nature of these pores however does not suggest that they were punctured by sharp framboidal crystals of pyrite, also the presence of wall pyrite does suggest that decomposition has occured close to the perforate wall and if this was the primary wall then it would not have been preserved. Additionally perforations of this type are present in tracheids preserved in totally different ways in involving pyrite formation (see Table 7.).

REFERENCES.

AGASSIZ, L., 1834. On the fossil fish of Scotland. Rep. Br. Ass. Advamt. Sci., 4th Meeting. Edinburgh, Transactions of Sections: 646-649.

ALEXANDER-MARRACK, P.D. and FRIEND, P.F., 1976. Devonian sediments of east Greenland. 3. The eastern sequence, Vilddal Supergroup, and part of the Kap Kolthoff Supergroup. Meddelelser om Gronland, 206(3): 1-121.

ALLEN, J.R.L., 1965. A review of the origin and characteristics of recent alluvial sediments. Sedimentology, 5: 89-191.

ALLEN, K.C., 1965. Lower and Middle Devonian spores of central Vestspitsbergen. Palaentology, 8: 687-748.

ALLEN, K.C., 1967. Spore assemblages and their stratigraphical applications in the Lower and Middle Devonian of north and central Vestspitsbergen. Palaentology, 10(2): 280-297.

ALLEN, K.C., 1972. Devonian megaspores from east Greenland: their bearing on the development of certain trends. Rev. Palaeobot. Palynol. 14: 7-17.

ALLEN, K.C., 1980. A review of *in situ* Late Silurian and Early Devonian spores. Rev. Palaebot. Palynol. 29: 253-270.

ALLEN, K.C. and DINELEY, D.L., 1988. Mid-Devonian to Mid-Permian flora and fauna regions and provinces. In Harris, A.L. and Fettes, D.J. (eds), 1988, The Caledonian Appalachian Orogen. Geographical Society Special Publication No. 38 pp.531-548.

ALLEN, K.C. and MARSHALL, J.E.A., 1986. Svalbardia and the "Corduroy Plant" form the Devonian of the Shetland Islands, Scotland. Spec. Pap. Palaeontology 35: 7-20.

ALLEN, P.A. and MARSHALL, J.E.A., 1981. Depositional Environments and Palynology of the Devonian south-east Shetland Basin. Scott. J. Geol.17,(4): 257-273.

ALVIN, K.L., DALBY, D.H. and OLADELA, F.A., 1982. Numerical analysis of Cuticular Characters in Cupressacae. In: D.F. Cutler, K.L. Alvin and C.E. Price, eds. The plant cuticle. Academic Press, London, pp 179-196.

ANANIEV, A.R., 1957. New plant fossils from the Lower Devonian of Torgachino in south eastern part of western Siberia. Bot. J. SSSR. 42: 691-702.

ANANIEV, A.R., 1959. Vajneichie mestonakhojdeniia devonskikh flor v Saiano-Altaiskoi gornoi oblasti. pp 1-99. Moskova.

ANANIEV, A.R. and STEPANOV, S.A., 1968. Finds of sporiferous organs in Psilophyton princeps Dawson emend. Halle in the Lower Devonian of the southern Minusinsk trough western Siberia. In: New materials on the stratigraphy and palaeotology of the Lower and Middle Paleozoic western Siberia. Tumsk. State Univ. Trudy, 202: 30-46.

ANDREWS, H.N., PHILIPS, T.L. and RADFORTH, N.W., 1965. Paleobotanical studies in Artic Canada. 1. Archaeopteris from Ellesmere Island. Can J. Bot 43: 545-556.

ANDREWS, H.N., KASPER, A.E. and MENCHER, J., 1968. Psilophyton forbesii, a new Devonian plant from northern Maine. Bull. Torrey Bot. Club, 95(1): 1-11.

ANDREWS, H.N., ARNOLD, C.A., BOUREAU, E., DOUBLINGER, J. and LECLERCQ, S., 1970. Filicophyta. In: Boureau, E. (ed), Traite de paleobotanique. 4. Masson, Paris.

ANDREWS, H.N., GENSEL, P.G. and KASPER, A., 1975. A new fossil of probably intermediate affinities (Trimerophyte-Progymnosperm). Can. J. Bot. 53: 1719-1728.

ARBER, N.E.A., 1921. Devonian Floras. Cambridge University Press 1921.

ARNOLD, C.A., 1939. Observations on fossil plants from the Devonian of eastern north America. 4. Plant remains from the Catskill delta deposits of north Pennsylvania and new York. Contrib. from the Mus. of palaeontol. Univ. of Michigan Vol 4, 10: 271-314.

ARNOLD, C.A., 1940. Structure and relationships of some Middle Devonian plants from western New York. Am. J. Bot. 27: 57-63.

BANKS, H.P., 1966. Devonian flora of New York state. Empire State geogram, 4: 10-24.

BANKS, H.P., 1968. The Early History of land plants In: E.T.Drake (ed) Evolution and Environment. Yale University Press, New Haven Conn. pp.73-103.

BANKS, H.P., 1975(a). Reclassification of Psilophyta. Taxon. 24(4): 401-413.

BANKS, H.P., 1975(b). The oldest vascular plants: a note of caution. Rev. Palaeobot. Palynol, 20: 13-25.

BANKS, H.P., 1980. Floral assemblages in the Siluro-Devonian. In: Dilcher, D.L. and Taylor, T.N., (eds). Biostratigraphy of fossil plants. pp 1-24, Dowden, Hutchinson and Ross.

BANKS, H.P., BONAMO, P.M. and GRIERSON, J.D., 1972. Leclerqia complexa gen et sp. nov. a new lycopod fron the late Devonian of eastern New York. Rev. Palaeobot, palynol. 14: 19-20.

BANKS, H.P., LECLERCQ, S. and HUEBER, F.M., 1975. Anatomy and morphology of Psilophyton dawsonii spec. nov. from Late Lower Devonian of Quebec (Gaspe) and Ontario Canada. Palaeontographica Americana, 8: 75-127.

BARNARD, P.D. and LONG, A.G., 1975. Triradioxylon a new genus of lower Carboniferous petrified stems and petioles together with a review of the early pteridophytina. Trans. R. Soc. Edin. 69: 231-249.

BARGHOORN, E.S. and DARRAH, W.C., 1938. Horneophyton, a necessary change of name for Hornea. Bot. Mus. leaflets Harvard Univ. 6: 142-44.

BECK, C.B., 1957. Tetraxylopteris schmidtii gen. et. sp. nov. a probable pteridosperm precurser from the Devonian of New York. Am. J. Bot. 44: 350-367.

BECK, C.B., 1960(a). The connection between Archaeopteris and Callixylon. Science, 131(3412): 1524-1525.

BECK, C.B., 1960(b). The identity of Archaeopteris and Callixylon. Brittonia, 12: 364-368.

BECK, C.B., 1962. Reconstruction of Archaeopteris and further consideration of its phylogenetic position. Am. J. Bot. 49(4): 373-382.

BECK, C.B., 1967. Eddya sullivanensis gen. et. sp. nov. A plant of Gymnospermic morphology in the Upper Devonian of New York. Palaentographica B. 121: 1-22.

BECK, C.B., 1970. Problems of generic delimitation in Paleobotany. Proc. North Am. Paleontol. Conv. 1969, (Chicago), C, pp. 173-193.

BECK, C.B., 1970(b). The appearance of gymnospermous structure. Bio. Rev. 45: 379-400.

BECK, C.B., 1971. On the anatomy and morphology of lateral branch systems of Archaeopteris. Am. J. Bot. 58: 758-784.

BECK, C.B., 1975. The current status of the Progymnospermopsida. Rev. Palaeobot. Palynol. 21: 5-23.

BECK, C.B., SCHMID, R. and ROTHWELL, G.W., 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48: 691-815.

BERRY, W.B.N., 1973. Silurian-Early Devonian graptolites. In: Hallam, A. (ed), Atlas of Palaeobiogeography. Elsevier, Amsterdam, pp. 81-88.

BIERHORST, D.W., 1960. Observations on tracheary elments. Phytomorphology, 10: 249-305.

BIERHORST, D.W., 1971. Morphology of vascular plants. MacMillan: New York.

BOLD, H.C., ALEXOPOULOS, C.J. and DELEVORYAS, T. 1980. Morphology plants and fungi. 4th ed. Harper and Row, New York, pp. 819.

BONAMO, P. M., 1975. The progymnospermopsida: building a concept. Taxon 24(516): 569-579.

BOTT, M.N.P. and WATTS, A.B., 1970. The Great Glen fault in the Shetland area: reply to D Flinn. Nature 227: 268-269.

BOUCOT, A.J., 1974. Silurian and Devonian biogeography. In: C.A. Ross (ed), Palaeogeographic provinces and proviciality. Soc. Econ. Palaeontol. Mineral., Spec. publ., 21: 165-176.

BRAUER, B.F., 1980. Barinophyton citruliforme (Barinophytales Incertae Sedis Barinophytaceae) from the Upper Devonian of Pennsylvania. Am. J. Bot. 67: 1186-1206.

BRYHNI, I., 1963. Relasjonen mellum senkaledonsk tektonikk og sedimentasjon ved Hornelens og Hasteinens Devon. Norges. Geol. Undersokelse, 223: 10-25.

BRYHNI, I., 1964(a). Migrating basins on the Old Red Continent. Nature. 202: 384-385.

BRYHNI, I., 1964(b). Sedimentary structures in the Hornelen series. Norsk Geol. Tidsskr. 44: 486-488.

CARROLL, P.L., BELT, E.S., DINELEY,D.L., BAIRD, D. and McGREGOR, D.C., 1972. Vertebrate Palaeontology of Eastern Canada, Exursion A59. Guidebook, 24th International Geographical Congress, Montreal. 113pp.

CARLUCCIO, L.M., HUBER, F.M. and BANKS, H.P., 1966. Archeaopteris macilenta, anatomy and morphology of its frond. Am. J. Bot. 53: 719-730.

CHALONER, W.G., 1970. The Rise of the first Land Plants. Biol. Rev. 45: 353-377.

CHALONER, W.G., 1972. Devonian plants from Fair Isle, Scotland. Rev. Palaeobot. Palynol. 14: 49-61.

CHALONER, W.G. and SHEARIN, A., 1979. Devonian macrofloras. In: M.R. House, C.T. Scrutton and M.G. Bassett (eds). The Devonian System. Spec. Pap. Palaeontol, 23: 145-161.

CICHAN, M.A. and TAYLOR, T.N., 1982. Vascular cambium Development in Spenophyllum: A Carboniferous Arthrophyte. I.A.W.A. Bull. 3: 155-160.

CRAMPTON, C.B. and CARRUTHERS R.G., 1914. The Geology of Caithness. Mem. Geol. Surv. Gt. Br.

CRANE, P.R., 1989. Patterns of Evolution and extinction in vascular plants. In. Allen, K.C. and Briggs, D.E.G., Evolution and the fossil record. Belhaven press London.

COOKSON, I.C., 1935. On plant remains from the Silurian of Victoria, Australia, that expanded and connect floras hitherto described. Phil. Trans. R. Soc. London, 225B: 127-148.

DAWSON, J.W., 1859. On the fossil plants from the Devonian rocks of Canada. Q. J. Geol. Soc. London, 15: 477-483.

DAWSON, J.W., 1862. On the flora of the Devonian period in north eastern America. Q. J. Geol. Soc. London, 18: 296-330.

DAWSON, J.W., 1870. The primative vegatation of the earth. Nature, 2: 85-88.

DAWSON, J.W., 1871. Fossil plants of the Devonian and Upper Silurian formations of Canada. Geol. Surv. of Canada (Montreal): 1-92.

DILCHER, D.L., 1979. Early Angiosperm reproduction: An introductory report. Rev. Palaeobot. Palynol. 27: 291-328.

DONOVAN, R.N., 1980. Lacustrine cycles, fish ecology and stratigraphic zonation in the Middle Devonian of Caithness. Scott. J. Geol. 16: 35-50.

DONOVON, R.N., FOSTER, R.J., and WESTOLL, T.S., 1974. A stratigraphical revision of the Old Red Sandstone of N.E. Caithness. Trans. R. Soc. Edinb. 69: 167-201.

DONOVON, R.N., ARCHER, R., TURNER, P. and TARLING, D.H., 1976. Devonian palaeogeography of the Orcadian Basin and the Great Glen Fault. Nature 259: 550-551.

DONOVON, R.N., COLLINS, A., ROWLANDS, M.A. and ARCHER, R., 1978. The age of the sediments on Foula, Shetland. Scott. J. Geol. 14: 87-88.

DORAN, J.B., 1980. A new species of Psilophyton from the Lower devonian of northern New Brunswick, Canada. Can. J. Bot. 58: 2241-2262.

EDWARDS, D., 1969. Zosterophyllum from the Lower Old Red Sandstone of South Wales. New Phytol. 68: 923-931.

EDWARDS, D., 1973. Devonian floras. In: Hallam, A. (ed) Atlas of palaeobiogeography, Elsevier, Amsterdam.

EDWARDS, D., 1975. Some observations on the fertile parts of Zosterophyllum myretonianum Penhallow from the Lower Old Red Sandstone of Scotland. Trans. R. Soc. Edin. 69: 251-265.

EDWARDS, D., 1980. Early land floras. Systematics Association, Specical Vol. 15: 55-85.

EDWARDS, D. 1981. Studies on Lower Devonian petrifactions from Britain. 2. Sennicaulis, a new form genus for sterile axes based on pyrite and limonite petrifactions from the Senni Beds. Rev. Palaeobot. Palynol. 32: 207-226

EDWARDS, D. and EDWARDS, D.S., 1986. A reconsideration of the Rhyniophytina Banks: 199-221. In: Spicer, R.A., and Thomas, B.A. (eds), Systematics and Taxonomic approaches in Palaeobotany, Vol 31. Oxford, England: The Systematics Association.

EDWARDS, D.S., 1986. Algaphyton major, a non vascular land plant from the Devonian Rhynie Chert. Bot. Journ. Linn. Soc. 93: 173-204.

FAHN, A., 1982. Plant Anatomy. Pergaman Press Oxford.

FAIRON-DEMARET, M., 1969. Dixopodoxylon goense gen. et. sp. nov. a new form of genus from the Middle Devonian of Belgium. Acad. Bull. Cl. Sci. 55(4): 372-386.

FAIRON-DEMERET, M., 1974. Nouveaux Specimans du genre Lerclergia Banks, H.P., Bonamo, P.M. et Grierson, J.P., 1972, du Givetian (?) du Queensland (Australia). Bull. Inst. R. Sci. Nat. Belg. 50: 1-4.

FAIRON-DEMERET, M., 1980. A propos des specimans determines Protolepidodendron scharianium par Krausel et Weyland, 1932. Rev. Palaeobot. Palynol. 29: 201-20.

FAIRON-DEMERET, M., 1981. Le genre Leclergia Banks, H.P., Bonamo, P.M. et Grierson, J.D., 1972 Dons le Devonian Moyen de Belgique. Bull. Inst. R. Sci. Nat. Belg. 31(XII): 1-10.

FAIRON-DEMERET, M., 1985. Les Plantes fossiles de l'Emsian du Sart Tilman, Belgique. I. Stockmansella Langii (stockmans) comb. nov. Rev. Palaeobot. Palynol. 44: 243-260.

FANNIN, N.G.T., 1970. The sedimentary environment of the Old Red Sandstone of Western Orkney. Ph. D. thesis, University of Reading (unpublished).

FINLAY, T.M., 1926. The Old Red Sandstone of Shetland. Part I. South-eastern area. Trans. R. Soc. Edin. 54: 553-72.

FINLAY, T.M., 1930. The Old Red Sandstone of Shetland. Part II: North-western area. Trans. R. Soc. Edin. 54: 671-694.

FLEMING, J., 1811. Mineralogical account of Papa Stour, one of the Zetland Islands. Men. Wernerian. Hat. Hist. Soc. Edin. 1: 162-75.

FLETCHER, A., 1975. Devonian Spores from the Melby Fish Beds. (abs). Comm. Int. Microflora Paliozoiqum, Newsletter 10: 3.

FLETCHER, A., 1976. Investigations of Devonian Megapores. PhD thesis Univ. of Bristol.

FLETT, J.S., 1898. The Old Red Sandstone of the Orkneys. Trans. R. Soc. Edin. 46: 313-319.

FLINN, D., 1961. Continuation of the Great Glen Fault beyond the Moray Firth. Nature, 191: 589-591.

FLINN, D., 1967. The metamorphic rocks of the sothern part of the mainland of Shetland. Geol. J. 5: 251-290.

FRAKES, L.A., 1979. Climates throughout geologic time. Elsvier, Amsterdam. pp 107-110.

FRIEND, P.F., ALEXANDER-MARRACK, P.D.,NICHOLSON, J. and YEATS, A.K., 1976. Devonian sediments of east Greenland. 2. Sedimentary structures and fossils. Meddelelser om Gronland, 206(2): 1-91.

FRENGVELLI, J., 1954. Plantas Devonicas de la Quebrada de la Charnela en la Precordillera de San Juan. Notas Mus. la Plata, 17: 359-376.

FRIEND, P.F. and WILLIAMS, B.P.J., 1978. A field guide to selected outcrop areas of the Devonian of Scotland the Welsh Borderland and South Wales. International symposium on the Devonian system (P.A.D.S. 78). Palaeontological Association (1978).

FRIEND, P.F., ALEXANDER-MARRACK, P.D., ALLEN, K.C., NICHOLSON, J. and YEATS, A.K., 1983. Devonian sediments of east Greenland, 6. Review of results. Meddelelser on Gronland, 206: 1-96.

GARRET, M.J., 1978. New evidence for a Silurian (Ludlow) age for Baragwanathia flora. Alcheringa, 2: 217-224.

GARRET, M.J., 1984. Graptolite biostratigraphy of early land plants from Victoria, Australia. Proc. York. Geol. Soc. 44: 377-384.

GARRET, M.J., TIMS, J.D., RICKARDS, R.B., CHAMBERS, T.C., DOUGLAS, J.G., 1984. The appearance of Baragwanathia (Lycophytina) in the Silurian. Bot. Jour. Linn. Soc. 89: 355-358.

GEIKIE, A., 1879. On the Old Red Sandstone of western Europe. Trans. R. Soc. Edin. 28: 345-452.

GENSEL, P.G., 1976. Renalia hueberi, a new plant from the Lower Devonian of Gaspe. Rev. Palaeobot. Palynol. 22(1): 19-37.

GENSEL, P.G., 1977. Morphological and taxonomic relationships of the psiloaceae relative to evolutionary lines in early land vascular plants. Brittonia 29(1): 14-29.

GENSEL, P.G., 1979. Two Psilophyton species from the Lower Devonian of eastern Canada with a discussion of morphological variation within the genus. Palaeontographica, 168B: 81-99.

GENSEL, P.G., 1980. Devonian In Situ spores: A survey and discussion. Rev. Palaeobot. Palynol. 30: 101-102.

GENSEL, P.G., 1982(a). A new species of Zosterophyllum from the Early Devonian of New Brunswick. Am. J. Bot. 69: 651-669.

GENSEL, P.G., 1982(b). Orcilla, a new genus referable to the Zosterophyllophytes from Late Early Devonian of northern New Brunswick. Rev. Palaeobot. Palynol. 37: 345-359.

GENSEL, P.G., 1984. A Lower Devonian plant and the early evolution of leaves. Nature 309: 785-787.

GENSEL, P.G., ANDREWS, H.N. and FORBES W.H., 1975. A new species of Sawdonia with notes on the origin of microphylls and lateral sporangia. Bot. Gaz. 136: 50-62.

GENSEL, P.G. and ANDREWS, H.N., 1984. Plant life in the Devonian. Praeger Publishers, 1984. New York, U.S.A.

GIBSON, G.A., 1877. The Old red Sandstone of Shetland. Edingurgh: Williams and Norgate.

GOEPPERT, H.R., 1850. Monographie der fossilen Coniferen. Hollandsche, Maat. Wetensch. Matuurk, 6: 1-286.

GOLDRING, W., 1924. The upper Devonian forests of seed ferns in E. N.Y. Bull. N.Y. state Mus. 251: 50-92.

GOLDSCHMIDT, V.M.,1913. Das Devongebiet am Roragen bei Roros mit eiem Palaebotanischen Bietrag. Die Pflanzenreste der Roragen-Ablagerung, von Nathorst, A.G., Skr. Videnskapsselskapet i Kristiania, 2.

GRANOFF, J.A., GENSEL, P.G. and ANDREWS, H.N., 1976. A new species of Pertica from the Devonian of eastern Canada. Palaeontographica, 155B: 119-128.

GRIERSON, J.D. and BANKS, H.P., 1963. Lycopods of the Devonian of New York State. Palaeobot. Amer. 4: 220-295.

HALLE, T.G., 1916(a). A fossil sporangium from the Lower Devonian of Norway. Bot. Notiser, pp 78-81.

HALLE, T.G., 1916(b). Some Devonian plants from Roragen in Norway. Kgl. Svenska, Vetensk. Acad. Handl. 57: 1-46.

HARRIS, T.M., 1929. Schizopodium davidii gen. et sp. nov. A new type of stem from the Devonian rocks of Australia. Phil. Trans. R. Soc. Land. 217(B): 395-410.

HARTMAN, C.M. 1981. The effect of pyrite on the tracheid structure of Drepanophycus spinaeformis, a long-ranging Devonian Lycopod. Rev. Palaeobot. Palynol. 32: 239-255.

HEARD, A., 1927. On the Old Red Sandstone plants showing structure from Brecon. Q. J. Geol. Soc. London, 85: 195-209.

HEINTZ, A., 1969. New agnaths from the Rigerike Sandstone. Norske, Vidnsk-Acad. Skr. 26(1): 1-80.

HILL, R.S., 1980. A numerical and Taxonomic approach to the study of Angiosperm leaves. Bot. Gaz. 141: 213-229.

HODSON, F. and RAMSBOTTOM, W.H.C., 1973. The distribution of Carboniferous goniatite faunas in relation to suggested continental reconstructions for the period. Organisms and continents through time. Palaeontological Association, Spec. Pap. in Palaeontology, 12: 321-329.

HØEG, O.A., 1931. Notes on the Devonian flora of western Norway. Kgl. Norske, Vidensk. Selsk. skr. 6: 1-33.

HØEG, O.A., 1935. Further contributions to the Middle Devonian flora of western Norway. Norske, Geol. Tidsskr. 15: 1-17.

HØEG, O.A., 1936. Norges fossile flora. Naturen, 60: 53-96.

HØEG, O.A., 1942. The Downtonian and Devonian flora of Spitsbergen. Norges, Svalbard-og Ishavs-Underskelser, 83: 1-228.

HØEG, O.A., 1945. Contributions to the Devonian flora of western Norway, 3. Norske, Geol. Tidsskr. 25: 183-192.

HØEG, O.A., 1967. Psilophyta: In Boureau, E. (ed). Traite de Paleobotanique, vol 2. Masson et Cie, Paris. pp. 193-433.

HOLLAND, H.D., 1984. The chemical evolution of the atmoshpere and oceans. Princeton University Press.

HOOKER, J.D., 1953. Notes on the fossil plants from the Shetlands. Q. J. Geol. Soc. London, 9: 49-50.

HOPPING, C.A., 1956. On the specimen of "Psilophyton robustinus" Dawson, from the Lower Devonian of Canada. Proc. R. Soc. Edin. 66: 1-28.

HOUSE, M.R., 1975. Facies and time in tropical areas. Proc. York. Geol. Soc. 40: 233-287.

HUEBER, F.M., 1964. The Psilophytes and their relationships to the origin of the ferns. Mem. Torrey Bot. Club, 21(5): 5-9.

HUEBER, F.M., 1967. Psilophyton: The genus and the concept. In Oswald, D.H. (ed). International Symp. on the Devonian System. Alta. Soc. Pet. Geol. Calgary, Alta, 2: 815-822.

HUEBER, F.M., 1971. Sawdonia ornata: a new name for Psilophyton princeps var ornatum. Taxon. 20: 641-642.

HUEBER, F.M., 1983. A new species of Baragwanathia from the Sextant Formation (Emsian) northern Ontario, Canada. Bot. J. Linn. Soc. 86: 57-79.

HUEBER, F.M. and BANKS, H.P., 1968. Psilophyton princeps: The search for organic connection. Taxon. 16(2): 81-85.

HUEBER, F.M. and BANKS, H.P., 1979. Serrulacaulis forcatus, gen. et sp. nov., a new zostrophyll from Lower Upper Devonian of New York State. Rev. Palaeobot. Palynol. 28: 169-189.

HUEBER, F.M., and GRIERSON, J.D., 1961. The occurrance of Psilophyton princeps in the Early Upper Devonian of New York. Am. J. Bot. 48: 413-479.

JARVIK, E., 1949. On the Middle Devonian crosspptерygians from Hornelen field in western Norway. Univ. i Bergen, Aabok, 1948, Naturvidensk,

JENNINGS, J.R., 1972. A polyvinyl chloride peel technique for iron sulphide pertifactions. J. Palaeontol. 46: 70-71.

JOHNSON, G.A.L., 1981. Geographical evolution from laurasia to Pangaea. Proc. York. Geol. Soc. 43: 221-252.

JØRGENSEN, B.B., 1983. Processes at the sediment-water interface: 477-509. In. Bolin, B. and Cook, R.B., (eds), The major Buogeochemical Cycles and their interactions, (SCOPE; 21). Chichester: John Wiley and Sons.

JOY, K.W., WILLIS, A.J. and LACEY, W.S., 1956. A rapid cellulose peel technique in palaeobotany. Ann. Bot. 20: 635-637.

JURINA, A.L., 1969. Devonian flora of central Kazakhstan. Materials of the Geology of Central Kazakhstan. 8. Moscow State Univ. Moscow, pp143.

KASPER, A.E., ANDREWS, H.N. and FORBES, W.H., 1974. New fertile species of Psilophyton from the Devonian of Maine. Am. J. Bot. 61: 339-359.

KEDO, G.I. and OBUKHOVSKAYA, T.G., 1981. Spore, Middle Devonian of the Baltic region and north east White Russia. In: Sorokin, V.S., Liarskaya, L.A. and Savvaitova, L.S. (eds). Devonian and Carboniferous of the Baltic regions. Riga, Zinatne. p 419-436.

KIAER, J., 1918. Fiskerester fra den devoniske sandsten paa Norges vestkyst. Bergens Mus. Aarbok, Naturvidensk Raekke, 7: 1-17.

KIDSTON, R. and LANG, W.H., 1917. On the Old Red sandstone plants showing structure from the Rhynie Chert Bed, Aberdeenshire. Part 1. Rhynia gwynne-vaughanii, Kidston and Lang. Trans. R. Soc. Edin. 51: 761-784.

KIDSTON, R. and LANG, W.H., 1920(a). On the Old Red Sandstone plants showing structure from the Rhynie Chert Beds, Aberdeenshire. Part 2. Additional notes on Rhynia gwynne-vaughanii, Kidston and Lang; descriptons of Rynia major n. sp. and Hornea lingieri n. g. n. sp. Trans. R. Soc. Edin. 52: 603-627.

KIDSTON, R. and LANG, W.H., 1920(b). On the Old Red Sandstone plants showing structue from the Rhynie Chert Beds Aberdeenshire. Part 3. Asteroxylon mackiei, Kidston and Lang. Trans. R. Soc. Edin. 52: 643-680.

KIDSTON, R. and LANG, W.H., 1921(a). On the Old Red Sandstone plants showing structure from the Rhynie Chert Bed Aberdeenshire. Part 4. Restoration of the vascular cryptograms and discussion of their bearing on the general morphology of pteridophyta and the origin and organisation of land plants. Trans. R. Soc. Edin. 52: 831-854.

KIDSTON, R. and LANG, W.H., 1921(b). On Old Red Sandstone plants showing structure from the rhynie Chert Bed Aberdeenshire. Part 5. The Thallophyta occuring in the plant bed; the succession of the plants throughout a central section of the bed, and the conditions of accumulation and preservation of the deposits. Trans. R. Soc. Edin. 52: 855-902.

KIDSTON, R. and LANG, W.H., 1923. Notes on fossil plants from the Old Red Sandstone of Scotland. 1. Hicklingia edwardii. Trans. R. Soc. Edin. 53: 405-407.

KLITZSCH, E., LEGAL-NICOL, A. and MASSA, D., 1973. Le Siluro-Devonien a Psilophytes et lycophytes du bassin de Mourzouk (Libye). Compte. rendu hebdomadaire des Seances de L'Acadamie des Sciences, Paris. D277: 2465-2467.

KNOLL, A.N., NIKLAS, K.J., GENSEL, P.G. and TIFFANEY, B.H., 1984. Character diversification and patterns of evolution in early vascular plants. Palaeontology, 10(1): 34-37.

KOLDERUP, C.P., 1904. Vestlandets Devonsk lagraekker. Naturen 21: 270-276.

KOLDERUP, C.F., 1915(a). Vestlandets Devonfelter og deres plante-fossiler. Naturen 35: 217-232.

KOLDERUP, C.F., 1915(b). Das Vorkommen der Pffanzenreste. Bergen Mus. Aarbok, 1914-1915, Naturvidensk, Raekke, 9: 1-11.

KOLDERUP, C.F., 1927. Hornelens Devonfelt. Bergen Mus. Aarbok, 1926, Naturvidensk, Raekke, 6: 1-56.

KRAUSEL, R. and WEYLAND, H., 1923. Beitrage zur kenntnis der Devonflora, 1. Senckenbergiana, 5: 154-184.

KRAUSEL, R. and WEYLAND, H., 1926. Beitrage zur Kenntnis der Devonflora, 2. Abh. Senckenb. Naturforsch. Ges. 40: 115-155.

KRAUSEL, R. and WEYLAND, H., 1929. Beitrage zur Kenntnis der Devonflora 3. Abh. Senckenb. Naturforsch. Ges, 41: 315-360.

KRAUSEL, R., and WEYLAND, H., 1930. Die flora des deutschen Unterdevons. Abh. Preuss. Geol. Landesanst. N.F. 131: 1-92.

KRAUSEL, R., 1937. Die Verbreitung des Devonflora. Deuxieme congres pour l'advancement des etudes de stratigraphie et de geologie du Carbonifere. Heerlen: 527-537.

KRAUSEL, R. and WEYLAND, H., 1938. Neue Pflanzenfunde im rheinischen Unterdevon. Palaeontographica, 80B: 171-190.

KRAUSEL, R. and WEYLAND, H., 1948. Pflanzenreste aus dem mit Bemerkungen zu einigen ihrere Arten. Senckbergiana, 29: 77-99.

LANG, W.H., 1925. Conributions to the study of the Old Red Sandstone flora of Scotland. 1. On the plant remains from the fish beds of Cromaty. 2. On a sporagium bearing branch system from the Stromness beds. Trans. R. Soc. Edin. 54(2): 33-279.

LANG, W.H., 1926. Contributions to the study of the Old Red Sandstone flora of Scotland. 3. On Hostimella (Psilophyton) thomsonii, and its inclusion in a new genus, Milleria. 4. On a specimen of Protolepidodendron from the Middle Old Red Sandstone of Caithness. 5. On the identification of the Large "stems" in the Carmyllie Beds of the Lower Old Red Sandstone as Nematophyton. Trans. R. Soc. Edin. 54(2): 785-799.

LANG, W.H., 1927. Contributions to the study of the Old Red Sandstone flora of Scotland. On Zosterophyllum myretonianum, Penh., and some other plant remains from the Carmyllie Beds of the Lower Old Red Sandstone; VII. On a speciman of Pseudosprochnus from the Stromness Beds. Trans. R. Soc. Edin. 55: 443-455.

LANG, W.H., 1932. Contributions to the study of the Old Red Sandstone flora of Scotland. 8. On Arthrostigma, Psilophyton and some associated plant remains from the Strathmore Beds of the Caledonian Lower Old Red Sandstone. Trans. R. Soc. Edin. 57: 491-521.

LANG, W.H., 1937. On the plant remains from the Dowtonian of England and Wales. Phil. Trans. R. Soc. London, B27: 245-291.

LANG, W.H. and COOKSON, I.C., 1930. Some fossil plants of Early Devonian type from the Walhalla series, Victoria, Australia. Phil. Trans. Soc. London, B219: 133-163.

LANG, W.H. and COOKSON. I.C., 1935. On a flora, including vascular land plants, associated with Monograptus, in rocks of Silurian age, from Victoria, Australia. Phil. Trans. R. Soc. London, 224B: 421-449.

LERCLERQ, S., 1939. Premiers resultants oblenus dans l'etude de la flore du Devonien de la Belgique. Ann. Soc. Geol. Belg. 63: 113-120.

LECLERCQ, S., 1940. Contribution a l'etude de la flore du Devonien de Belgique. Acad. Roy. Belg. 12: 1-65.

LECLERCQ, S. 1960. Refendage d'une roche fossilifere et degagment de ses fossiles sous binoculaire. Senckenberiana, Lethaea, 41: 483-487.

LECLERCQ, S. and BANKS, H.P., 1959. Pseudosporochnus is not a psilophyte. Proc. 9th Inter. Bot. Congr. Montreal. 2: 219-220

LECLERCQ, S. and BANKS, H.P., 1962. Pseudosporochnus nodosus sp. nov., a Middle Devonian plant with Cladoxylalean affinities. Palaeontographica B 110: 1-34.

LECLERCQ, S. and BONAMO, P.M., 1971. A study of the fructification of Milleria (Protopteridium) thomsonii Lang 1926 from the Middle Devonian of Belgium. Palaeontographica 136B: 83-114.

LECLERCQ, S. and BONAMO, P.M., 1973. Rellimia thomsonii a new name for Milleria (protopteridium) Lang 1926 Emend. Lerclercq and Bonamo 1971. Taxon, 22: 435-437.

LEPJECHINA, V.G., PETROSIAN, N.M. and RADEZENKO, G.P., 1962. Principal Devonian Plants from the Altai Sayan Mountain District. Tr. Vses. Naushnolszsled. Geol. Inst. Lenigr. 70: 61-188 -in russian-.

LETIQUE STRATOGRAPHIQUE INTERNATIONALE, 1964. Vol. 3 Asie. Fasc. I Rep. pop. chinoize pts 1 and 2.

LIVEMORE, R.A., SMITH, A.G. and BRIDEN J.C., 1985. Palaeomagnetic constraints on the distribution of continents in the late Silurian and Early Devonian. Phil. Trans. R. Soc. London, 309B: 29-56.

LI, XINGXUE, 1981. Preface in Bibliography of Chinese Palaeontology (up to 1980). Institute of Geology and Palaeontology, Academia sinica Wanjing, pp. 1-11.

LOBOZIAK, S. and STREEL, M., 1980. Microspores from Givetian to Lower Frasnian sediments dated with conodants in the Boulonnais (France). Rev. Palaeobot. Palynol. 29: 285-299.

LOVE, L.G., COLEMAN, M.L. and CURTIS, C.D., 1983. Diagenetic pyrite formation and sulphur isotope fractionation associated with a Westphalian marine incursion, northern England. Trans. R. Soc. Edin. Earth siences, 74: 165-182

LYON, A.G., 1984. Probable fertile region of Asteroxylon mackei, Kidston and Lang. Nature, 203(4949): 1082-1083.

MARSHALL, J.E.A., 1980. A method for the successful oxidation and subsequent stabilization of high rank, poorly preserved spore assemblages. Rev. Palaeobot. Palynol. 29: 313-319.

MARSHALL, J.E.A., 1981. Devonian miospores from south east Shetland and Fair Isle. Ph.D. thesis University of Bristol.

MARSHALL, J.E.A., 1988. Devonian microspores from Papa Stour, Shetland. Trans. R. Soc. Edin: Earth Sciences, 79: 13-18.

MARSHALL, J.E.A. and ALLEN, K.C., 1982. Devonian microspores from Fair Isle, Shetland. Palaeontology, 25: 277-312.

MARSHALL, J.E.A., BROWN, J.F. and HINDMARSH, S., 1985. Hydrocarbon source rock potential of the Devonian rocks of the Orcadian Basin. Scott. J. Geol. 21(3): 301-320.

MATTEN, L.C., 1966. Improved technique for preparing iron hyroxide plant petrifactions. J. Palaeontol. 40: 225-226.

MATTEN, L.C., 1968. Actinoxylon banksii gen. et. sp. nov. a Progymnosperm from the Middle Devonian of New York. Am. J. Bot. 55(7): 773-782.

MATTEN, L.C., 1973. The Cairo flora (Givetian) from eastern New York: 1. Reimannia, terete axes, and Cairoa lamanekii gen. t. sp. nov. Am. J. Bot. 60: 619-630.

MATTEN, L.C., 1981. Svalbardia banksii sp. nov. From the Upper Devonian (Frasnian) of New York state. Am. J. Bot. 68(10): 1383-1391.

MATTEN, L.C and BANKS, H.P., 1966. Triloboxylon ashlandicum gen. and sp. nov. from the Upper Devonian of New York. Am. J. Bot. 53: 1020-1028.

MCGREGOR, D.C., 1973. Lower and Middle Devonian spores of eastern Gaspe Canada. 1. Systematics. Palaeontograpgica, 142B: 1-77.

MCGREGOR, D.C., 1977. Lower and Middle Devonian spores of eastern Gaspe Canada. 2. Biostratigraphy. Palaeontographica, 163B: 111-142.

MCGREGOR, D.C., 1979. Spores in Devonian stratigraphical correlation. In: House, Scrutton and Basset (eds). The Devonian system. Palaeontol. Assoc. Spec. Pap. 23: 164-184.

MCGREGOR, D.C. and CAMFIELD, M., 1976. Upper Silurian to Middle Devonian spores of the Moose River Basin, Ontario. Bull. Geol. Surv. Canada, 263: 1-63.

MCGREGOR, D.C. and CAMFIELD, M., 1982. Middle Devonian miospores from Cape de Bray, Weatherall, and Heda Bay Formations of north-east Melville Island, Canadian Arctic. Bull. Geol. Surv. Canada, 348: 1-105.

MCGREGOR, D.C. and UYENO, T.T., 1972. Devonian spores and conodonts of Melville and Bathurst Islands, District of Franklin. Pap. Geol. Surv. Canada, 71-13: 1-36.

MILES, R.S. and WESTOLL, T.S., 1963. Two new genera of coccosteid Arthrodira from the Middle Old Red Sandstone of Scotland and their stratigraphical distribution. Trans. R. Soc. Edin. 66: 179-210.

MILLER, H., 1841. The Old Red Sandstone. Edinburgh.

MILLER, H., 1849. In the footsteps of the creator. Edinburgh.

MILLER, H., 1857. The testimony of the rocks. Edinburgh.

MURCHISON, R.I., 1853. Note of the age and relative position of the Sandstone containing fossil plants at Lerwick in the Shetland Isles. Q. J. Geol. Soc. London, 9: 50-51.

MURCHISON, R.I., 1859. On the succession of the older rocks in the northern most counties of Scotland: With some observations on the Orkney and Shetland Islands. Q. J. Geol. Soc. London, 15: 353-418.

MUSTAFA, H., 1978. Beitrage zur Devonflora. 3. Argumenta Palaeobotanica 5: 91-132.

MYKURA, W., 1972(a). The Old Red Sandstone sediments of Fair Isle, Shetland Islands. Bull. Geol. Surv. Gt. Br. 41: 1-31.

MYKURA, W., 1972(b). Tuffisitic breccias, tuffisites and associated carbonate-sulphide mineralisation in south east Shetland. Bull. Geol. Surv. Gt. Br. 40: 51-82

MYKURA, W., 1976. British regional geology Orkney and Shetland. I.G.S. Edinburgh.

MYKURA, W., and PHEMISTER, J., 1976. The geology of western Shetland. I.G.S. Edinburgh.

MYKURA, W. and YOUNG, B.R. 1969. Sodic scapolite (Dipyre) in the Shetland Islands. Rep. Inst. Geol. Sci. 69(4): 1-8

NATHORST, A.G., 1884. Redogorelse for den tillsammans med G. de Geor ar geologiska till Spitsbergen. Kgl. Svensk. Vet. Acad. Handl. Bihang. 9(2): 1-78. Stockholm.

NATHORST, A.G., 1902. Zur Oberdevonischen flora der Beren-insel. kgl. Svensk, Vetenskapsakaal. Handlinger 36: 1-60.

NATHORST, A.G., 1904. Die Oberdevonische flora des Ellesmere Landes. Rept Second Norwegian Artic Expedition in the Fram. (1898-1902) 1: 1-22.

NATHORST, A.G., 1913. Die pflanzenrest der Roragen - a ablagerung. In Goldschmidt, V.M., Das Devongebit am Roragen bei Rovos. Skrifter vdg at Videnskabsselśkarabet i Christania, 1: 25-27.

NATHORST, A.G., 1915. Zur Deevonflora des westlichen Norwegens. Bergen Mus. Aarbok, 1914-1915 9(a): 1-34.

NAMBOODRIRI, K.K. and BECK, C.B., 1968. A comparative study of the primary vascular systems of conifers. 3. Stelar evolution in Gymnosperms. Am. J. Bot. 55: 464-472.

NILSEN, T.H., 1973. Devonian sedimentation and tectonics of Norway. In: Pitcher, M.G. (ed), Arctic Geology. Am. Assoc. Pet. Geols. Mem. 19.

OBRHEL, J.V., 1959. Neue Pflanzenfunde in den Srbsko-Schichten (Mitteldevon). Vestrik Ustredniho Ustavu Geologickeho, 34: 384-388.

OBRHEL, J., 1968. Die Silur- und Devonflora des Barrundiums. Palaontol. Abh. 2B: 661-701.

OWENS, B., 1971. Microspores from the Middle and Early Upper Devonian rocks of W. Queen Elizabeth Island Artic Archipeligo. Geol. Surv. Can. Pap. 70: 38-157.

OZOLINA, V., 1963. Spore spectra of the Frasnian stage in Alanda Well. Latv. Acad. Sci. Geologijas un Derigo Izraktenv Instituta Raksti 5: 171-187.

PEACH, C.W., 1879. A list of fossil plants collected in Shetland by Messrs. B.N.Peach and John Horne, of the Geological Survey of 1878. Q. J. Geol. Soc. London, 35: 811.

PEACH, C.W. and HORNE, J., 1879. The Old Red Sandstone of Shetland. Proc. R. Phys. Soc. Edin. 5: 80-87.

PENHALLOW, D.P., 1892. Additional notes on Devonian plants from Scotland. Can. Rec. Sci. 5: 1.

PETTITT, J., 1965. Two hetersporous plants from the Upper Devonian of N. America. Bull. Br. Mus. Nat. His. 10(3): 81-92.

PETROSIAN, N.M., 1968. Stratigraphic importance of the Devonian flora of the U.S.S.R. In: D.M.Oswald, ed., International symposium on the Devonian system, Alberta Soc. Pet. Geol. Calgary, 1: 579-586.

PLAYFORD, G., 1983. The Devonian microspore genus Geminospora Balme 1962: a re-appraisal based on topotypic G. lemurata (type species). Men. Assoc. Australas. Palaeontol. 1: 311-325.

PLUMSTEAD, E.P., 1967. A general view of the Devonian fossil plants in the Cape System of South Africa. Paleontaol. Afr. 10: 1-83.

RAYNER, D.H., 1967. The stratigraphy of the British Isles. Cambridge Univ. Press.

RAYNER, R.J., 1983. New odservations on Sawdonia ornata from Scotland. Trans. R. Soc. Edin: Earth Sciences, 74: 79-93.

READ, C.B., 1936. A Devonian flora from Kentucky. J. Paleont. 10: 215-227.

REMY, W. and REMY, R., 1977. Die Floren des Erdaltertums. Verlag Gluckauf GBMH. Essen.

REMY, W., HASS, H. and SCHULTKA, ST., 1986(a). Anisophyton potonie nov. spec. aus den kulbacher schichten (Emsian) vom steinbruch ufersmuble, Wiehltalsperre. Argumenta Palaeobotanica, 7: 79-107.

REMY, W. SCHULTKA, ST. and HASS, H., 1986(b). Anisophyton gothani nov. gen., nov. spec. Und hinweise zer stratigraphie der sudlichen Willinghauser Scholk. Argumenta Palaobotanica, 7: 79-107.

REUSCH, Y.H., 1914. Norgen bidrag til Hitterens og Smolens geologi. Norges Geol. Undersokelse. 69: 1-50.

RICHARDSON, J.B., 1960. Spores from the Middle Old Red Sandstone of Cromarty, Scotland. Palaeontology 3(1): 45-63.

RICHARDSON, J.B., 1962. Spores with bifurcate processes from the Middle Old Red Sandstone of Scotland. Palaeontology, 5: 171-194.

RICHARDSON, J.B., 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin, North East Scotland. Palaeontology 7: 559-605.

RICHARDSON, J.B., 1967. Some British Lower Devonian spore assemblages and their stratigraphic significance. Rev. Palaeobot. Palynol. 1: 111-129.

RICHARDSON, J.B., 1969. Devonian spores. In: R.H. Tschundy and R.A. Scott (eds). Aspects of Palynology, Wiley. N.Y.: 193-222.

RICHARDSON, J.B., 1974. The stratigraphic utilization of some Silurian and Devonian miorspores in the northern hemisphere: an attempt at a synthesis. Intern. Syup. Belgian Micropaleont. Limits. Publ. (Namur 1974) 9: pp 1-13.

RICHARDSON, J.B. and MCGREGOR, D.C., 1986. Silurian and Devonian spore zones of the Old Red Sandstone region. Geol. Surv. Can. Bull. 364: 1-78.

RICHTER, M., 1958. Die Halbinsel Orland arm Ausgang des Trandheimfjordes. Geologie, 7(3-6): 757-768.

RIEGEL, W., 1982. Palynological aspects or the Lower/Middle Devonian transition in the Eifel region. Cour. Forschinst Senkengerg, 55: 279-292.

SALTER, J.W., 1857. On some remains of Terrestrial Plants in the Old Red Sandstone of Caithness. Quart. Journ. Geol. Soc., 14: 72-73.

SCHECKLER, S.E., 1975. Rhymokalon, a new plant with cladoxylalean anatomy from the Upper Devonian of New York state. Can. J. Bot. 53: 25-38.

SCHECKLER, S.E., 1978. Ontogeny of Progymnsperms. II. Shoots of Upper Devonian Archaeoptericlales. Can. J. Bot. 56: 3136-3170.

SCHECKLER, S.E. and BANKS, H.P., 1971. Proteokalon an new genus of gymnosperms from the Devonian of N.Y. state and its bearing on phytogenetic trends in the group. Am. J. Bot. 58: 874-884.

SCHMID, R., 1982. The terminology and classification of steles: Historical perspective and the outlines of a system. Bot. Rev. 48(4): 817-931.

SCHOPF, J.N., 1935. Modes of fossil preservation. Rev. Palaeobot. Palynol. 20: 27-53.

SCHOPF, J.M., 1964. Middle Devonian fossils from Northern Maine. U.S. Geol. Surv. Prof. Pap. 501(D): 43-49.

SCHWEITZER, H.J., 1968. Pflanzenreste aus dem Devon Nord Westspitsbergens. Palaeotographica, 123B: 43-39.

SCHWEITZER, H.J., 1983. Die Unterdevon flora des Rheinlandes. Palaeontographica, 189B: 1-138.

SCHWEITZER, H.J. and MATTEN, L.C., 1982. Aneurophyton germanicum and Protopteridium thomsonii from the Middle Devonian of Germany. Palaeontographica 184B: 65-106.

SCOTESE, C.R., BAMBACH, R.K., BARTON, C., VAN DER VOO, R.and ZIEGLER, A.M., 1979. Paleozoic Base Maps. J. Geol. 87(3): 217-77.

SCOTESE, C.R., VAN DER VOO, R. and BASSETT, S.F., 1985. Silurian and Devonian base maps. Phil. Trans. Roy. Soc. London. B309: 54-77.

SCOTT, A.C., 1979. The ecology of coal measure floras from northern Britain. Proc. Geol. Assoc. (london) 90: 97-116.

SCOTT, D.H. and JEFFERY, E.C., 1914. Fossil plants from the base of the Waverley Shale Kentucky. Phil. Trans. R. Soc. london,

SERLIN, B.S. and BANKS, H.P., 1978. Morphology and anatomy of Aneurophyton a progynosperm from the late Devonian of N.Y. Palaeont. Amer. 8(51): 343-359.

SENKEWICH, M.A., 1968. Devonian continental deposits of Central Kazatchstan. In: D.H. Oswald, ed, International symposium on the Devonian system. Alberta Pet. Geol. Soc. Calgary, 2: 1117-1127.

SEWARD, A.C. and WALTON, J., 1923. On fossil plants from the Falkland Islands. Q. J. Geol. Soc. London. 79: 313-333.

SMITH, A.G., BRIDEN, J.C. and DREWRY, G.E., 1973. Phanerzoic world maps. In. Hughes, N.F.,: Organisms and continents through time. Spec. Pap. Paleaon. Assoc. 12: 1-42

SOLMS-LAUBACH, H., 1891. Fossil botany (english translation by H.E.F Garnsey, revised by I.B. Balfour). Oxford: Clarenden Press.

SPICER, R.A., 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. U.S. Geol. Surv. Prof. Pap. 1143: 1-77.

SPIKER, E.C. and HATCHER, P.G., 1987. The effects of early diagenesis on the chemical and stable isotopic composition of wood. Geochimica et Cosmochimica Acta, 51: 1385-1391.

STEIN, W.E., WRIGHT, D.C. and BECK, C.B., 1981. Techniques for preparation of pyrite and limonite permineralizations. Rev. Palaeobot. Palynol., 36: 185-196.

STOCKMANS, F., 1940. Vegetaux eodevoniens de la Belgique. Mem. Mus. Roy. Hist. Nat. Belg. 93: 1-90.

STOCKMANS, F., 1968. Vegetaux Mesodevoniens recoltes aux confins du Massif du Brabant (Belgique). Men. Inst. Sci. Nat. Belg. Mem. No 159: 49.

STOUT, J.D., GOH, K.M., and RAFTER, T.A., 1981. Chemistry and turnover of naturally occurring resistant organic compounds in the soil: 1-37. In. Paul, E.A. and Ladd, J.N., (eds), Soil Biochemistry, Vol 5. New York and Bassel: marcel Dekker, Inc.

STOVER, B.L., 1951. An introduction to the anatomy of seed plants. Heath, D.C., Boston.

STREEL, M., 1964. Une association de spores du Givetian inferieur de la vesdre, a Goe (Belgique). Ann. soc. Geol. Belg. 87: 233-262.

STREEL, M., 1987. Associations de spores du Devonian inferieur Belge et leur significantion stratigraphique. Ann. Soc. Geol. Belg. 90: 11-53.

STREEL, M., HIGGS, K., LOBZIAK, S., RIEGEL, W. and STEEMANS, P., 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardennes-Rhenish regions. Rev. Palaeobot. Palynol. 50: 211-229.

STUBBLEFIELD, S.P., TAYLOR, T.N. and BECK, C.B., 1985. Studies of paleozoic wood-decaying fungi in Callixylon newberryi from the Upper Devonian. AM. J. Bot. 72: 1765-1774.

TAYLOR, D.W., 1986. Anatomical and morphological study of a new species of Taeniocrada, a Devonian tracheophyte from New York state. Rev. of Palaeobot. Palynol. 47: 63-87.

TAYLOR, T.N. and SCOTT, A.C., 1983. Interactions between plants and animals during the Carboniferous. Bioscience 33: 488-493.

TEICHERT, C. and SCHOPF, J.M., 1958. A Middle and Lower Devonian psilophyte flora from Central Arizona and its palaegeographical significance. J. Geol. 66: 208-217.

TERMIER, W. and TERMIER, G., 1950. In the Eitelienne de Dechra Ait Abdullah (Maroc central). Bull. Soc. Geol. Fr. 20: 197-224.

TUDOR, J., 1883. The Orkneys and Shetland; Their past and present state. London.

TUFNELL, H., 1853. Notice of the discovery of fossil plants in the Shetland Islands. Q. J. Geol. Soc. London. 9: 49.

TURNER, S.and TARLING, H., 1982. Thelodant and other agnathan distributions as tests of Lower Paleozoic continental reconstructions. Palaeogeog. Palaeclim. Palaeoecol. 39: 295-311.

VAROSSIEAU, W.W. and BREGER, I.A., 1951. Chemical studies on ancient buried wood and the origin of humus. Troisieme congres pour l'advancement des etudes de Stratigraphe et de Geologie du Carbonifere. Heerlen, Vol2 : 637-646. Ernst van Aelst: Maestricht.

VIGRAN, J.O., 1964. Spores from Devonian deposits, Mimerdalen, Spitsbergen. Skr. Nor. Palarinst. 132: 1-32.

VOGT, T., 1929. Undersokelser over den underdevoniske konglomerat-sandstensserie i Ytie Trondelagen. Norges. Geol. Undersokelse. 133: 59-61.

VOGT, T., 1924a. Undersokelser pa kartbladet orlandet. Norges. Geol. Undersokelse. 122: 89-93.

VOGT, T., 1924b. Plantfossiler fra Stofosens devoniske lagraekke. Naturen. 53-56.

WALTON, J., 1957. On Protopitys (Goeppert): with a description of a fertile specimen "Protopitys scotica" sp. nov. from the calcarious sandstone series of Dunbartonshire. Trans. R. Soc. Edinb. 63: 333-340.

WATSON, D.M.S., 1934. Report on fossil fish from Sandness, Shetland. Mem. Geol. Sur. Summ. Prog. for 1933. Pt I: 74-76.

WESTOLL, T.S., 1937. The Old Red Sandstone fishes of the North of Scotland, particularly of Orkney and Shetland. Proc. Geol. Assoc. 48: 13-45.

WESTOLL, T.S., 1951. The vertebrate-bearing strata of Scotland. Rep. 18th Int. Geol. Congr. Pt II, Gt. Br. 1948: 5-21.

WESTOLL, T.S., 1979. Devonian fish biostratigraphy. In: House, M.R., Scrutton, C.T., and Basset, M.G. (eds). The Devonian System. Spec. Pap. Paleont. 23: 341-353.

WIDDEL ,F. and PFENNIG, N., 1977. A new anaaerobic, sporing, acetate oxidising, sulphate reducing bacterium, Desulfotomaculatum (emend) acetoxidans. Archives of Microbiology, 112: 119-122.

WILSON, G.V., 1934. Summary of Progress for 1933. Mem. Geol. Surv. Gt. Br.

WOODROW, D.L., FLETCHER, F.W. and AHRNSBRAK, W.F., 1973. Paleogeographical and Paleoclimate at the deposition site of the Devonian Catskill and Old Red Sandstone facies. Geol. Soc. Am. Bull. 84: 3051-3064.

YEATS, A.K. and FRIEND, P.F., 1977. Devonian sediments of East Greenland IV. The Western sequence, kap kolthoff Supergroup of the Western Areas. Meddeleser. om Gronland. 206(4): 1-112.

ZAKHAROVA, T.V., 1981. On the systematic position of the species Psilopyhton goldschmidtii from the Lower Devonian of Eurasia. Paleontologicheskii Zhurnal 23: 111-118.

ZALESSKY, M.D., 1937. Sur les vegetaux Devoniens du versant oriental de l'Orural et du bassin Kousnetzk. Palaeophytographica. Akad. Nauk. S.S.S.R.: 5-42

ZDEBSKA, D., 1972. Sawdonia ornata (= Psilophyton princeps var. ornatum) from Poland. Acta Palaeobotanica 13: 77-97.