

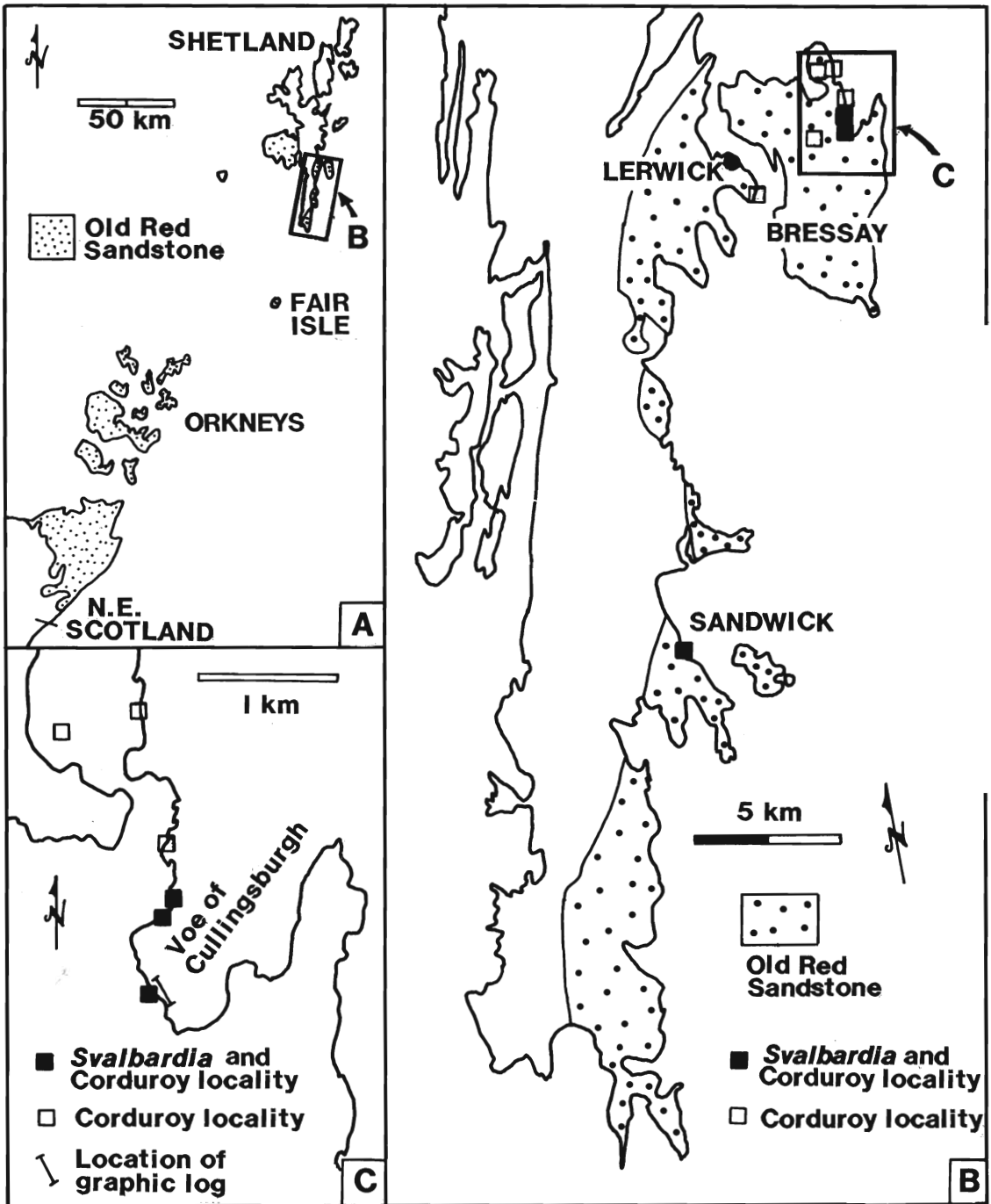
# SVALBARDIA AND THE 'CORDUROY' PLANT FROM THE DEVONIAN OF THE SHETLAND ISLANDS, SCOTLAND

by K. C. ALLEN *and* J. E. A. MARSHALL

ABSTRACT. Occurrences of *Svalbardia scotica* Chaloner 1972 from the Devonian of Fair Isle and Shetland are described. Most sites occur in fluvial and lake margin sediments. The 'Corduroy' plants, which are ribbed stems, occur largely in sandstones and are of unknown origin. Sterile material of *S. scotica* shows a wide range of leaf morphology. Fertile material is similar to that of *Archaeopteris*. The detailed morphology of the 'Corduroy' plant is described and the rib pattern is interpreted as being derived from tangentially arranged strips of fibres surrounding a central pith. The 'Corduroy' stems occur in a wide variety of preservation but most are believed to represent a single taxon. The 'Corduroy' plant is associated with *Svalbardia*, shows some features in common, and is believed to represent its stem. The palaeoecology of the *in situ* miospores (*Geminospora*) of *Svalbardia* are discussed in the context of hypotheses suggesting an inverse distribution relationship with the miospores *Rhabdosporites langii* and *Ancyrospora* spp. The common occurrence of *Geminospora* with *Svalbardia* in a proximal facies in the Shetland Islands shows that the primary control on its occurrence is stratigraphical and not ecological.

IN the Devonian successions of northern Scotland significant developments of Middle Old Red Sandstone occur in the Shetland Islands some 150 km north of the Scottish mainland (text-fig. 1). Both macro-fossil plants and miospores (e.g. Chaloner 1972; Marshall and Allen 1982) have been recorded from these successions, but little attempt has been made at any systematic palaeobotanical collecting since the work of Lang (unpublished). This account documents further occurrences of the progymnosperm *Svalbardia scotica* Chaloner 1972 including the first fertile material to be recorded for this species. Occurring in the Shetland successions with *Svalbardia* is the enigmatic plant stem known as the 'Corduroy' plant. These are large stems (up to 1.5 m in length) which are found mostly in the sandstone lithologies, and are characterized by uninterrupted longitudinal striations running the length of the stem giving the appearance of the fabric known as corduroy. The earliest record is that of Fleming (1811) who commented on their occurrence with fronds (presumably *Svalbardia*). Further occurrences have been noted by later authors, especially Hooker (1853), Peach (1878), Geikie (1879), and Mykura (1976). The stem was attributed to *Calamites* by some of these early workers but since at least 1926 it has become informally known as the 'Corduroy' plant of unspecified assignment (Finlay 1926). Other records of a similar plant exist for the older Devonian successions of the Scottish mainland (e.g. Geikie 1878; Peach 1879; C. J. Cleal, pers. comm.) which may in part be related. However, some of these records come from strata attributed to the early Devonian (Murchison 1859; House *et al.* 1977) and are certainly not the same taxon. These records of a 'Corduroy' type organization indicate the difficulties in studying poorly preserved isolated stem material where different plants may become similar during fossilization.

The palaeoecology of *Svalbardia*, and particularly its known *in situ* miospore *Geminospora* (Balme) Playford 1983, is of significance since the control on the occurrence of this distinctive miospore has been regarded by some authors as geological age and by others as sedimentary facies (compare McGregor and Camfield 1982 with Richardson 1969). In view of the possible significance (Playford 1983) of *G. lemurata* as a biostratigraphical marker akin to *Retispora lepidophyta* (Kedo) Playford 1976, it is important that the nature of the control should be resolved.

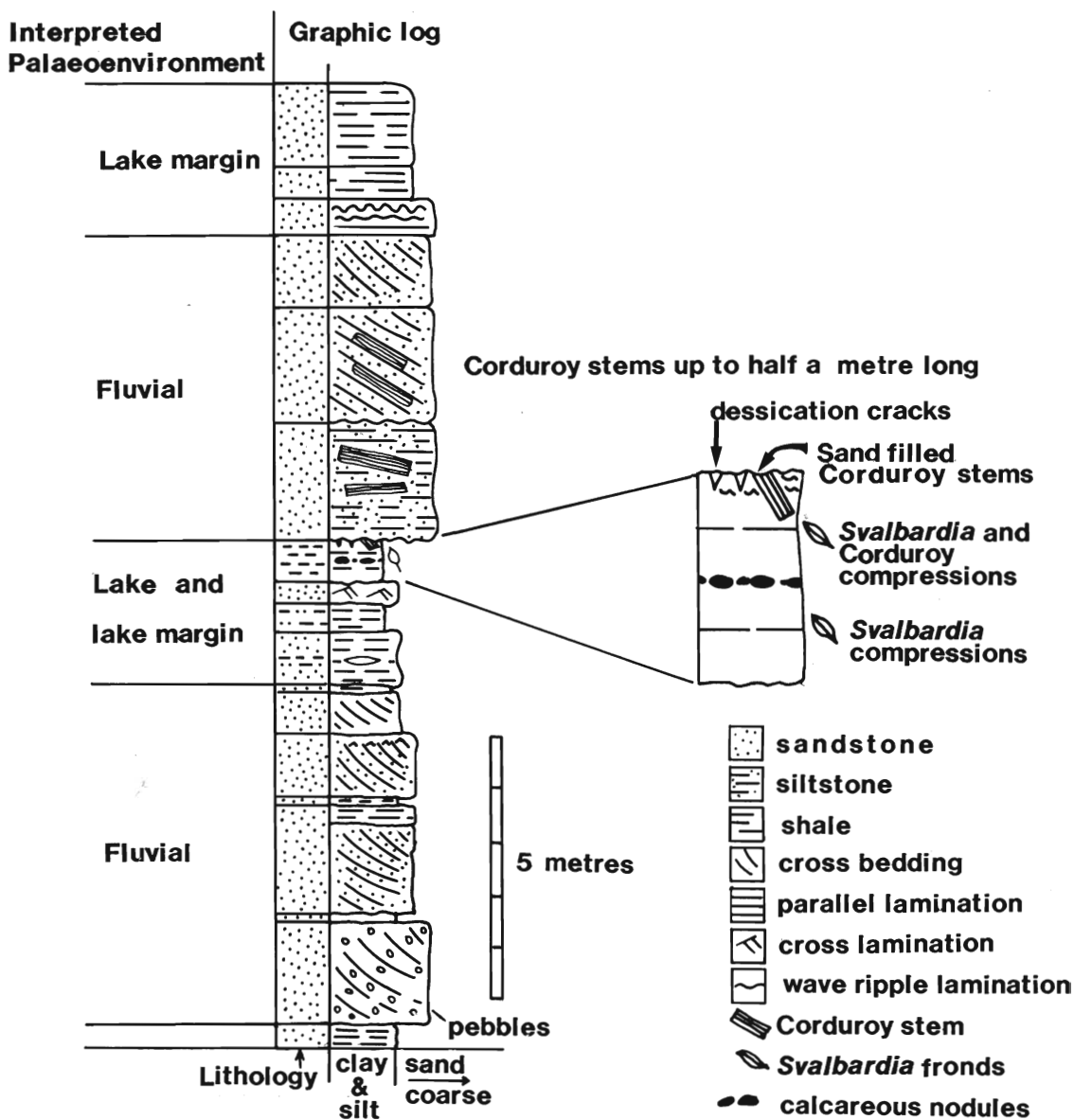


TEXT-FIG. 1. A, Old Red Sandstone outcrop in north-east Scotland (Caithness, Orkney, and Shetland). B, south-east Shetland. C, north-east Bressay.

MATERIAL

*Fair Isle*

Numerous specimens of *S. scotica* were collected from the locality described by Chaloner (1972) and are late Givetian in age (Marshall and Allen 1982). The most productive site is illustrated in Mykura (1972, pl. IIB) where the plants occur in the first shale unit from the right. In addition to sterile and fertile branch systems, a large three dimensional 'Corduroy'-type axis (Pl. 3, fig. 6) was recovered in close association with *S. scotica*. Recent sedimentary facies interpretations (T. Astin, pers. comm. 1983) in these North Gavel Beds have shown the shale units to have been deposited in a lacustrine environment, whilst the intervening sandstones represent a lake margin beach. The beach sands contain abundant and large stems of the 'Corduroy' plant. *S. scotica* and



TEXT-FIG. 2. Sedimentary facies log, Sillock Geo, Bressay (text-fig. 1c)

'Corduroy' plants occur on Fair Isle only in this unit (North Gavel Beds), the lower parts of the succession having different assemblages (Chaloner 1972). However these lower units, which also contain lacustrine beds, have similar palynofloras to the North Gavel Beds and are all dominated by *Geminospora lemurata* (Balme) Playford 1983 and *Rhabdosporites langii* (Eisenack) Marshall and Allen 1982. *Contagisporites optivus* (Chibrikova) Owens 1971 is found only in the North Gavel Beds and then rarely.

#### *South-east Shetland*

*Svalbardia* was collected at two main sites in south-east Shetland. The Leebotten (Sandwick, text-fig. 1B) site (HU 4343 2496) is on the cliff top in front of XYZ cottage, adjacent to the sewer pipe running down the rock exposure. Only sterile axes were collected from this locality.

The other *Svalbardia* localities (text-fig. 1C) are grouped around the Voe of Cullingsburgh (HU 512 425) on the Island of Bressay. An interpreted sedimentary facies log (text-fig. 2) is shown for one of these localities (text-fig. 1C) which is notable for yielding two sandstone-filled three-dimensional casts of 'Corduroy' plants (Pl. 3, figs. 4-6, illustrates one of these) in addition to a 'Corduroy' plant compression (Pl. 3, fig. 3) in the same horizon as *Svalbardia* fertile and sterile branch systems. The sandstone-filled casts occur as two sub-parallel inclined stems in a shale unit truncated by an overlying sandstone. The palaeoenvironment for this part of the sequence is interpreted as a lake margin with fluvial input. Sedimentary facies present include lake margin sandy beaches, lacustrine shales, and fluvial channel sands with deltaic margins into a lake.

'Corduroy' plant stems are numerous in the fluvialite and lake margin sandstones of these localities. Other sites where 'Corduroy' plants are abundant in south-east Shetland include the disused quarries on the west of Bressay (HU 504 419) and on the Knab, Lerwick (HU 483 406; Pl. 3, fig. 8). At both these localities the sedimentary facies is fluvialite.

Figured specimens are housed in the Bristol University Palaeobotanical Collection, BUPC.

#### *Preservation*

The macrofossil plant material from both south-east Shetland and Fair Isle, whilst appearing in good condition, has in fact been subject to significant carbonization through a local heating event. It is estimated that temperatures rose to about 200 °C (Marshall *et al.*, 1986) and this caused significant damage to the organic material. Sheets of cuticle and woody material are homogenized and show the development of close set orthogonal shrinkage cracks. Attempts to identify these materials have produced few results. Miospores, although heavily carbonized, have not suffered to the same extent and this probably results from their being smaller and isolated in the sediment. Palaeobotanical studies are thus limited to the external features of the plant fossils.

## SYSTEMATIC PALAEONTOLOGY

### *Svalbardia scotica* Chaloner 1972, emend.

Plate 1, figs. 1-6; Plate 2, figs. 1-5; text-fig. 3A, B

*Emended Diagnosis.* Striated axial systems, with main axes up to 2 cm diameter, bearing (spirally arranged?) subsidiary axes. Leaves, up to 3 cm long, apparently spirally arranged on main and subsidiary axes. Leaves variable in shape, but dominantly dichotomously divided and wedge-shaped; some on subsidiary axes flabelliform. Fertile axes striated, up to 5 cm long, 2.5 mm wide, with up to 9 sporophylls, each with 8-12 erect axial fusiform sporangia.

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#### EXPLANATION OF PLATE 1

Figs. 1-6. *Svalbardia scotica*. 1 and 2, part and counterpart of a fertile branch system, showing sporophylls and position of sporangia,  $\times 2$ . Voe of Cullingsburgh, Bressay, BUPC CI-001. 3, dichotomizing sterile branch systems characteristic of this species, together with isolated sporophylls and sporangia,  $\times 2$ . Bu Ness, Fair Isle, BUPC BU-002. 4, fertile branch system with striated axis. In the process of sedimentation the sporangia have either been lost or bent out of their original position,  $\times 2$ . Voe of Cullingsburgh, Bressay, BUPC CI-002. 5 and 6, isolated more flabelliform leaves, not attached to the typical branch system, but similar to poorly preserved specimens which have attachment. Voe of Cullingsburgh; 5,  $\times 1$ , CI-003; 6,  $\times 2$ , CI-004.



ALLEN and MARSHALL, *Svalbardia scotica*

*Description of sterile material.* The largest axes, having typical *S. scotica* ultimate branches attached, are up to 20 cm in length (text-fig. 3A) and narrow only slightly towards the apex. The maximum diameter of such axes is 2 cm, and they are frequently strongly ribbed, which may indicate vascular strands, or a ribbing of the outer surface. Smaller striated axes arise pseudomonopodially from these larger axes, at an acute angle, usually between 12–20° to the main axes, though they may bend out at up to 80° after the initial acute branching. This may, however, be a result of sedimentation. From these ultimate branch systems arise the leaves. Preservation is poor and the specimens very flattened, and it is impossible to say whether they arise spirally along the axis. The leaves are very variable in shape and clearly striated. On the major axes (and some of the minor axes), they are up to 3 cm long, dichotomize up to four times, and are the more typical leaves (text-fig. 3A; Pl. 1, fig. 3; Pl. 2, figs. 3 and 4) illustrated by Chaloner (1972). Some leaves on subsidiary axes are more flabelliform, dichotomizing from one to three times. The first dichotomy ranges from half-way along the leaf to near its distal end (Pl. 1, fig. 6; Pl. 2, fig. 5).

*Comparisons.* Some of the more typical leaves (Pl. 2, fig. 3) are very similar to *S. avelinesiana* (Stockmans 1968, pl. 2, fig. 2). *S. polymorpha* (Høeg 1942) also exhibits variable leaf form, but the dominant filiform leaves of this species do not occur in *S. scotica*. In *S. banksii* Matten 1981 the leaves are non-planated, and show no evidence of venation. Some flabelliform leaves are attached to typical *S. scotica* axes, whilst others are found isolated in the rock. Some are clearly similar to *Ginkgophytopsis belgica* Stockmans 1968 (pl. 5, fig. 1), *Sphenopteris brabantica* Stockmans 1968 (pl. 5, fig. 6), and *Platyphyllum peachii* Høeg 1942 (p. 101, text-fig. 23). It is possible therefore that many of the Middle Devonian flabelliform leaves are in fact part of the *Archeopteris-Svalbardia* complex. Indeed, Beck (1967) described the flabelliform leaved *Eddyia* as being a progymnosperm. With more flattened flabelliform leaves reported here in *S. scotica* it seems that this, the only remaining reason for separating *Svalbardia* from *Archeopteris*, no longer exists. However, we retain the name *Svalbardia* at present until there has been a thorough review of all species.

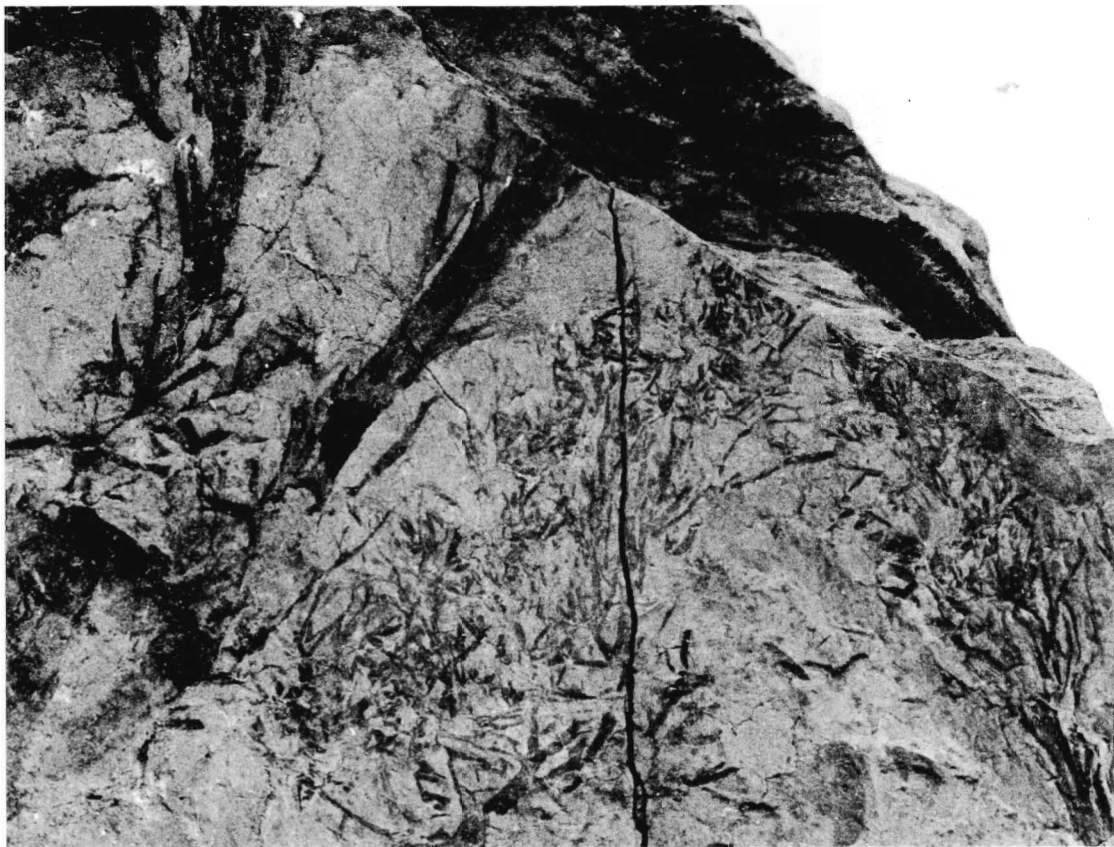
*Description of fertile material.* In association with the sterile branch systems on both Fair Isle and Bressay, but rarely found attached, were ultimate fertile branches (strobili of Beck 1981), fertile leaves (sporophylls of Beck 1981), and abundant isolated sporangia. The ultimate fertile branches (Pl. 1, figs. 1, 2, 4) are up to 5 cm long, though incomplete at both ends, and 1.0–2.5 mm wide. Like the sterile axes, they are often strongly striated with up to five major striations (Pl. 1, fig. 4) and numerous minor ones. These axes bear spirally arranged sporophylls, of which nine are seen in the best specimen (Pl. 1, figs. 1 and 2). The sporophylls bear 8–12 erect, fusiform sporangia on their adaxial surface. The sporangia, which appear to be in two ranks, are 2–4 mm high, and are situated on the proximal two-thirds of the sporophyll. They narrow towards the base, but are not obviously stalked. The dehiscence line is vertical, but numerous macerations failed to show any *in situ* spores. The sporophylls are 1–2 mm wide, and at least some are dichotomously branched distal to the sporangia.

*Comparisons.* The fertile parts of species included within both *Archeopteris* and *Svalbardia* are remarkably similar. Criteria upon which species are based include: *a*, length of sporophyll; *b*, whether the sporophyll is branched, and if so, is the branching proximal or distal to the sporangia?; *c*, are the sporangia in one or more rows on the sporophyll?; *d*, the number and shape of the sporangia; *e*, does the fertile ultimate branch form a loose panicle, or is it more rigid?; and *f*, are there sterile leaves on the fertile branch systems? However, even within species there is some variation, so significant differences between *S. scotica* and other species are difficult to quantify. The sporangia of *S. avelinesiana* are more globose, and fewer (4–6) occur on each sporophyll (Stockmans 1968). In *S. polymorpha* the fertile branches form a loose panicle, though Høeg (1942) illustrated one specimen as *Svalbardia* sp.

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EXPLANATION OF PLATE 2

Figs. 1–5. *Svalbardia scotica*. fertile and sterile branch systems. The fertile branch system on the right is attached to a typical sterile branch, × 2. Bu Ness, Fair Isle, BUPC BU-003. 2, flabelliform leaf attached to a striated axis, × 2. Voe of Cullingsburgh, Bressay, BUPC CI-005. 3 and 4, characteristic dichotomizing sterile branch systems. 3, × 2, Voe of Cullingsburgh, Bressay, BUPC CI-006; 4, × 1, Bu Ness, Fair Isle, BUPC BU-004. 5, isolated flabelliform leaf, × 2. Voe of Cullingsburgh, Bressay, BUPC CI-007.



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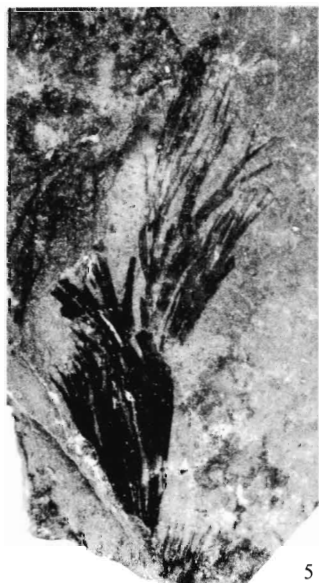
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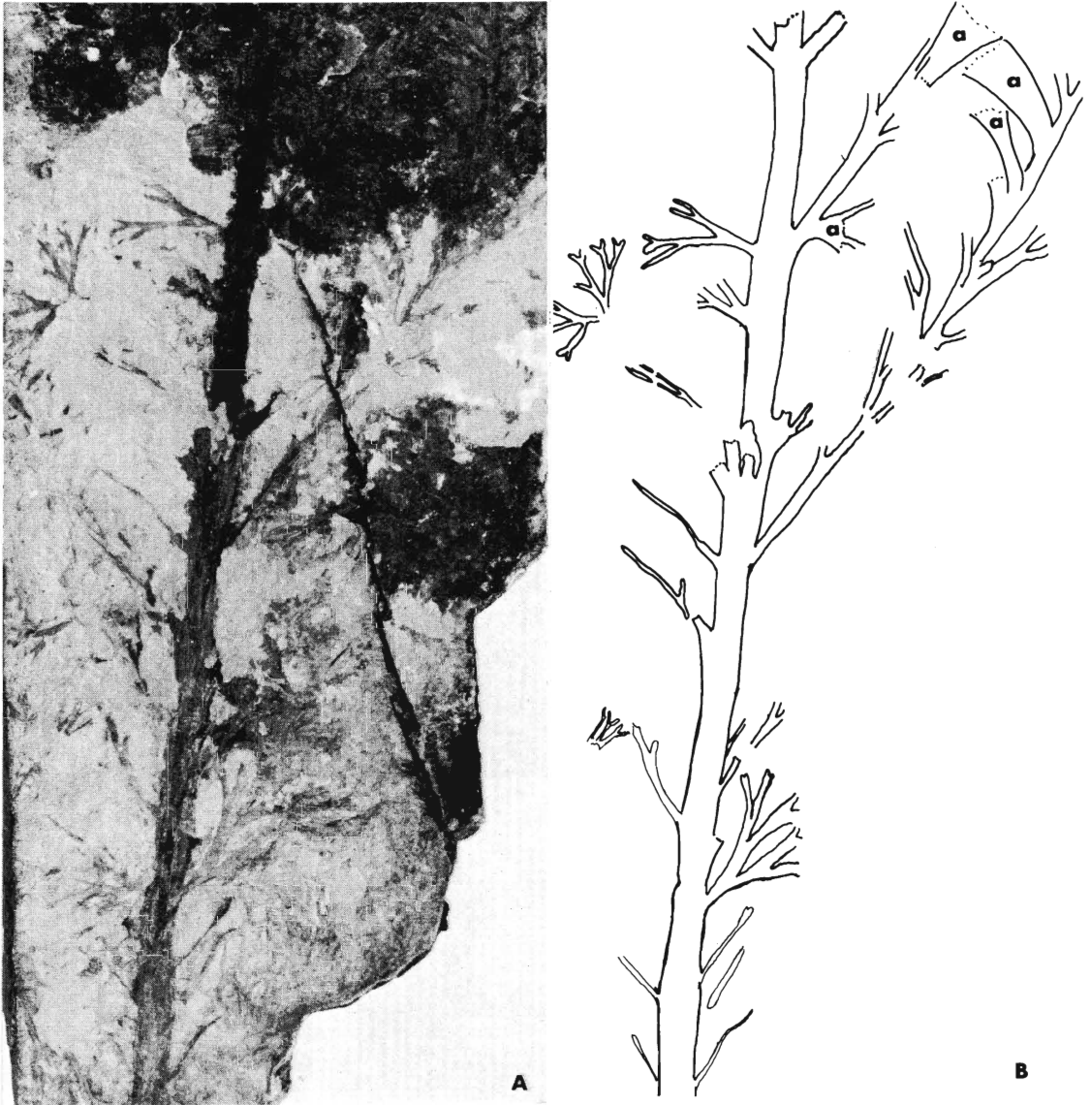
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TEXT-FIG. 3. *Svalbardia scotica*, sterile axes. A, Bu Ness, Fair Isle, BUPC BU-001,  $\times 0.75$ . B, drawing for comparison with A (ferruginous staining and poor impression-preservation make details difficult to resolve in a photograph). At a, the ultimate branch systems (?leaves) appear to be flabelliform but this could be the result of overlap of a number of branches whose edges are not clear. The striations on the axes are not shown.

which is similar to *S. scotica*. In *S. boyi*, the sporangia-free distal portion of the sporophyll is much longer in proportion to sporophyll length (Kräusel and Weyland, 1960). On the basis of the sterile branch system Carluccio *et al.* (1966) indicated that this last species should be transferred to *Archaeopteris*. The fertile portion of *S. osmancia* has fertile and sterile leaves on alternate branches (Petrosjan and Radzenko in Lepjehina *et al.* 1962). *S. banksii* is known only from sterile specimens (Matten 1981).



## 'CORDUROY' PLANTS

Plate 3, figs. 2-9

A typical 'Corduroy' stem (Pl. 3, fig. 5) occurs as an impression or coalified compression in sandstone, and shows a series of uninterrupted longitudinal ribs running the length of the stem. Incomplete stems are up to 1.5 m in length and from 0.6 to over 15.0 cm in width. Branching is only known in one example and it is pseudomonopodial. The stem preservation in sandstones is very variable with forms showing well-developed ribs (Pl. 3, fig. 7) to those in which the ribbing is less obvious, irregularly developed, and absent on parts of the stem. Stem width and preservation is dependent on clastic grain size. The larger, less well-preserved specimens occur in coarser sediments which additionally may have received more abraded plant debris by virtue of their depositional regime. Fortunately, some 'Corduroy' plants occur atypically preserved in fine lithologies and these provide critical evidence for the interpretation of the original stem structure.

Specimens of 'Corduroy' plants from some of the finer sandstones show an interesting arrangement of the ribs (Pl. 3, fig. 2). Here, although the ribs are well preserved and show a thin coaly layer of the original plant tissue, they are sub-parallel and of variable width through lying at a variety of angles to the bedding planes. It is believed that these ribs were originally arranged tangentially in a plant stem and were internal and not a surface feature, since they have distinct edges and act as discrete elements. These ribs were disrupted on differential compaction of the 'corduroy' stem.

A unique occurrence of the 'Corduroy' stem is as a compression fossil (Pl. 3, fig. 3) in a lacustrine shale from the Voe of Cuppa, on the western side of the Voe of Cullingsburgh, south-east Shetland (text-fig. 2) where it was associated with *Svalbardia* fronds. The 'Corduroy' pattern on the stem is very regular and of constant width across the stem (over 15 cm). The central core (3 mm thick) of the specimen is filled with siltstone which has two organic layers external to it on both top and bottom of the fossil. The outer of these layers is a striated sheet of carbonaceous material and the inner one is similar except that it bears the rib pattern of the 'Corduroy' stem. This specimen is interpreted as a 'Corduroy' stem which underwent slow compression in the shale and was in the form of a hollow cylinder filled with some sand before, during, and after collapse. The striated organic layer represents the plant surface and the ribbed layer reflects the internal 'Corduroy' ribbing. This occurrence of an internal ribbing with an outer striated layer is also seen in a much less well-preserved specimen from Fair Isle (Pl. 3, figs. 7 and 9) which also occurs with *Svalbardia* fronds which are up to 20 cm in length.

The Voe of Cuppa locality provided another critical 'Corduroy' stem (Pl. 3, figs. 4-6) which is in the form of a three-dimensional sandstone-filled cast with regular surface 'Corduroy' ribbing. Two of these stems occurred in a shale unit, truncated by an overlying sandstone, and were sub-parallel but inclined at about 30° to the bedding. It proved possible to extract one which is elliptical transversely (Pl. 3, fig. 4) and shows an interesting history of infilling. An alternation of coarse and fine material indicates a sequential infill over a period of time. Large plant stems preserved as external casts do occur in the Coal Measures but these in detail are quite different. They usually occur as trunks surrounded by sandstone which was rapidly deposited, and then on rotting of the plant tissue, the mould produced was infilled with sediment but without the laminations seen in the Shetland 'Corduroy' stems. These laminations run uninterrupted for the length of the specimen (36 cm) showing little sign of disturbance. The external surface to the specimen is not well preserved but in places shows a regular 'Corduroy' pattern with some carbonaceous material present. The cast infill must have been deposited in a void to account for the continuous uninterrupted laminae, the stem lying on the surface of the substrate. The shale matrix surrounding the specimens shows no sign of early rigidity (i.e. calcretization) sufficient to support a thin-walled cylinder during an infill over a period of time. The sandstone cast is interpreted as a 'pith-cavity' of an original stem, which was then supported by other external layers which are no longer present, and indicate that the 'Corduroy' ribbing was probably internal. This interpretation of the 'Corduroy' plant shows its stem to have an internal 'pith', and outer layers (cortex, wood) with a striated surface. The origin of the ribbing is

unclear, but a possibility includes tangentially arranged strands of fibres. Secondary wood is not comparable, but was certainly present in some of the stems which show a thick (8 mm) layer of carbonaceous material.

Whether all of these 'Corduroy' stems belong to a single taxon is difficult to prove as the morphology could simply reflect a general progymnosperm organization, and be referable to different progymnosperm groups based on their fronds. However, a certain amount of evidence can be assembled based on macrofossil plant evidence and dispersed miospores.

The Shetland plant assemblages appear to be impoverished, with *Svalbardia* being the sole compression fossil recorded from most localities. Additionally, the miospore floras are dominated by *Rhabdosporites langii* and *Geminospora* spp. which are found *in situ* (Allen, 1980) in the progymnosperm orders Aneurophytales and Archaeopteridales. In the Shetland microfloras these are not discrete taxa but morphologically intergrade (Marshall and Allen 1982), indicating a possible single origin for these two genera. This is supported by our understanding of the origin of the Archaeopteridales in the Givetian from an aneurophytalian precursor. The Shetland miospores reflect this transition from an aneurophytalian/*R. langii* dominated macro/microflora to an archaeopteridalian/*Geminospora* dominated macro/microflora. This low diversity flora has parallels in the late Devonian of the Catskills, USA (Beck 1964) where marginal sediments are dominated by numerous specimens of the *Archaeopteris* wood *Callixylon*.

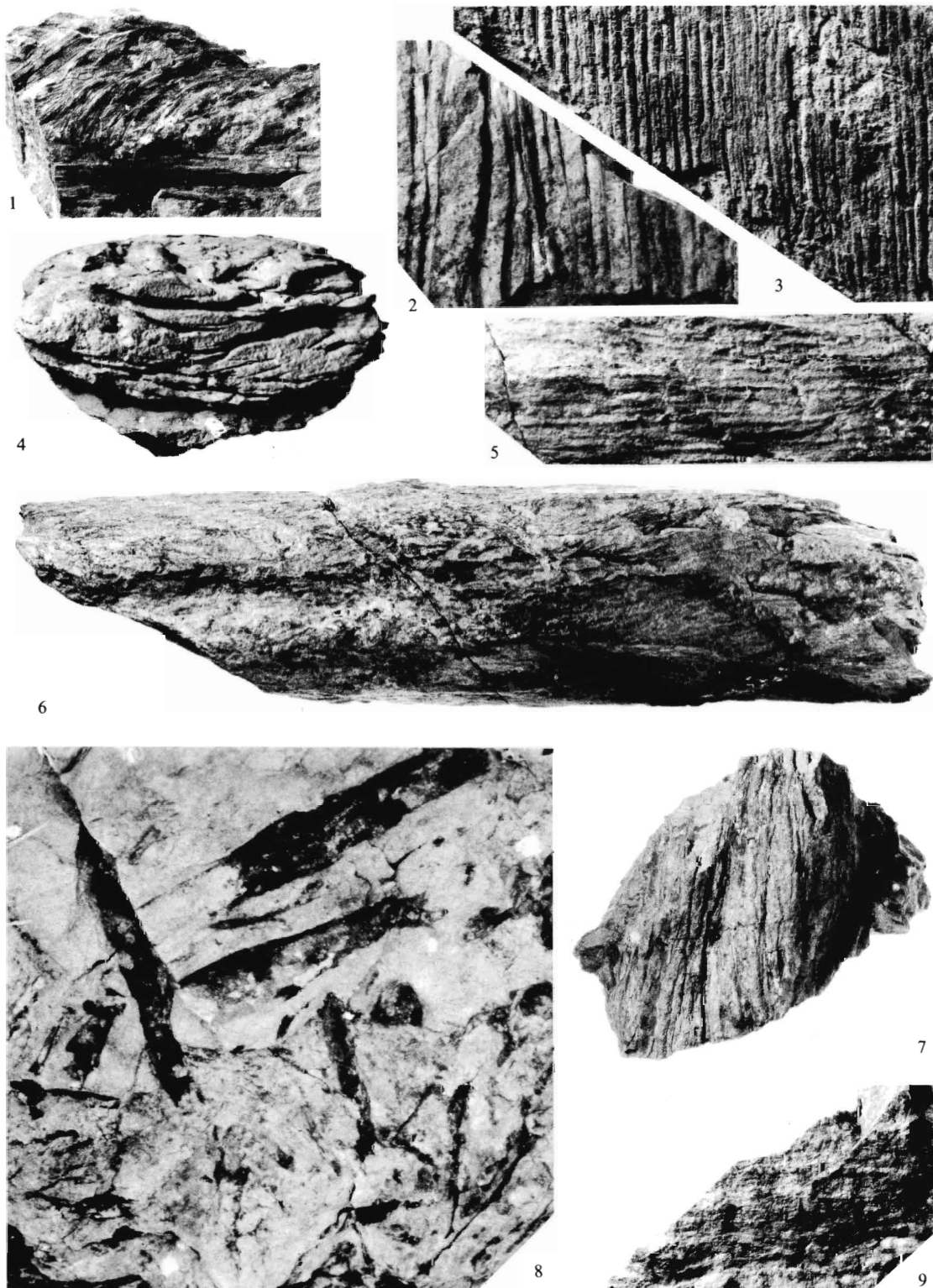
#### *Affinities of the 'Corduroy' Plant*

The Shetland 'Corduroy' plant shows a common association with *S. scotica* but usually occurs in the sandstone lithologies as poorly preserved material, whilst the latter is better preserved in adjacent shales as compression fossils. As noted earlier, they can occur together, with the 'Corduroy' stems as compressions or casts (Pl. 3, fig. 3). Some morphological similarity is apparent, with the presence of an outer striated surface on some well-preserved 'Corduroy' stems (Pl. 3, fig. 9) and on the *Svalbardia* axes (Pl. 3, fig. 1). If *S. scotica* and the 'Corduroy' stems belong to the same plant, then this interpretation must be compatible with accepted views on archaeopteridalian stem anatomy. This is important since recent work (Scheckler 1978 and pers. comm.) suggests that *Svalbardia* probably represents a developmental stage of *Archaeopteris*. This view has been challenged by Matten (1981) who prefers *Svalbardia* as a morphological and evolutionary precursor of *Archaeopteris*. However the two genera are closely related, so our interpretation of the 'Corduroy' stem as the main axis of *Svalbardia*, should be compatible with *Callixylon*, the stem of *Archaeopteris*. Detailed morphological and anatomical descriptions of *Callixylon* are available (e.g. Beck, 1981; Beck *et al.* 1982), and show a main trunk with a central pith surrounded by vascular tissue with an outer cortical layer. This is

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#### EXPLANATION OF PLATE 3

- Fig. 1. *Svalbardia* sterile branch system showing striated main axis,  $\times 1$ ; compare stem striations on 'Corduroy' stem (fig. 9). Bu Ness, Fair Isle, BUPC BU-005.
- Fig. 2. 'Corduroy' stem showing rotation and disturbance of the rib pattern. Sillock Geo, Bressay, BUPC CI-008; field of view 5 cm.
- Fig. 3. Compression of 'Corduroy' stem,  $\times 1$ . Note the regular and fine ribbing. Two layers (one ribbed, one plain) of organic matter are present. Sillock Geo, Bressay, south-east Shetland; position in section on text-fig. 2. BUPC CI-009.
- Figs. 4, 5, 6. Three-dimensional sandstone 'Corduroy' cast. Sillock Geo, Bressay; position in section, on text-fig. 2. BUPC CI-010. 4, transverse view showing coarse and fine laminations indicating slow infill of 'pith cast', width 15 cm. 5, complete stem length 36 cm. 6, close-up of the regular 'Corduroy' ribbing on stem, field of view 11 cm.
- Figs. 7 and 9. 'Corduroy' stem. Bu Ness Fair Isle, BUPC BU-006. 7, poorly preserved stem found with large sterile branch system (text-fig. 3A), height of specimen 12 cm. 9, close-up of outside of stem showing fine striated surface interpreted as external layer analogous to fig. 1, field of view 4 cm.
- Fig. 8. Large 'Corduroy' and unidentifiable stem occurring in coarse pebbly sandstone, The Knab, Lerwick. Field of view 40 cm.



ALLEN and MARSHALL, *Svalbardia*, 'Corduroy' plant

compatible with the 'Corduroy' stem (and many others), except that in *Callixylon* a significant thickness of secondary wood is seen. Some of the poorly preserved 'Corduroy' stems do show a thick layer (up to 8 mm) of coaly material, which may represent vascular tissue. However, in the absence of significant positive evidence, it is difficult to equate these Shetland 'Corduroy' specimens with *Svalbardia* compressions and *Callixylon* permineralizations, and this attribution must be regarded as tentative.

#### PALAEOECOLOGY

The depositional environments in which *S. scotica* and 'Corduroy' plants occur are lake shore sandy beaches, lake deposits, and the more proximal environment of river channels. Identifying the environment(s) in which these plants were growing is more difficult. However, some of these fossils show unbroken branch systems (text-fig. 3A), and probably originated from a fairly local source, considering the dominance of fluvial and lake shore sedimentary processes in the Shetland successions. Plants almost certainly grew in most of the finer sedimentary facies in the Shetlands, which included lake margins, and high sinuosity and braided streams. 'Rootlet' horizons have been observed in silted up channels of braided streams (Allen and Marshall, 1981), which presumably became colonized after abandonment. The low diversity of the Shetland assemblages points to some degree of niche restriction for the vegetation, and a situation can be imagined where *S. scotica* plants fringe the margins of the lakes and rivers up to, but not including, the alluvial fan environment.

Although no *in situ* miospores were recovered from *S. scotica* they have been recorded in *S. polymorpha* (Høeg 1942; Vigran 1964) where they can be compared with the dispersed spore *G. lemurata*. The *in situ* spores of *Archaeopteris* are better known; some of their miospores are similar to the dispersed *G. lemurata*, and their megaspores are most commonly assigned to *Contagisporites* sp. and *Biharisporites* sp. (Allen 1980; see also Medyanik 1981, 1982).

*G. lemurata* (see Playford 1983 for synonymy) is the most abundant miospore in the Shetland sequences, although fluctuating quite widely between adjacent samples (Marshall and Allen 1982, table 2). The palaeoecological distribution of *G. lemurata* has attracted much interest, since the speculations of Streeel (1964, 1967) and Richardson (1965, 1967, 1969) concerning its reciprocal relationship with *Ancyrospora* (Richardson) Richardson 1962 and *R. langii*. The interpretation from their examples is that *Geminospora* tends to be more abundant in marginal marine, distal fluvial and deltaic facies, whilst *Rhabdosporites* and *Ancyrospora* are more abundant in proximal fluvial and lacustrine environments. However, in Shetland, *Geminospora* is the dominant miospore in the latter range of environments. This anomaly is more significant when palaeogeographical reconstructions (Allen and Marshall 1981) are considered, since Shetland is in fluvial connection with the Orcadian Basin but more proximal to it than the area studied by Richardson (1965), which was a major example of his *Ancyrospora/Rhabdosporites* dominated environment. Thus in Shetland *Geminospora* would not have been expected to dominate these environments, but as it clearly does, there is a need to reevaluate this supposed reciprocal distribution of *Geminospora* and *Ancyrospora/Rhabdosporites*. *G. lemurata* seems to appear in large numbers (McGregor and Camfield 1982) in the early Givetian, and as such, forms a distinctive stratigraphical event. The Shetland material, on independent miospore evidence (Allen and Marshall 1981; Marshall and Allen 1982), is younger than any of the Orcadian Basin Middle Devonian, and the presence of *Geminospora* in these proximal sediments is taken to show that the primary control on the occurrence of *Geminospora* is stratigraphical. The Frasnian, New York State example of ecological separation of *Geminospora* from *Rhabdosporites/Ancyrospora* cited by Richardson (1967, 1969) shows evidence for some separation, but the sedimentary facies are not well defined, and the sample localities unspecified in a region which shows well-documented sea level changes. Comparison of the Orcadian Basin with the Escauminac Formation (Canada) lacustrine facies by Richardson (1969) is also interesting, since the former is mostly Eifelian in age, and the latter Frasnian. If the miospores are generally similar, it would seem that this could result from preferential sorting of miospores in the lacustrine environment, with pseudosaccate genera such as *Rhabdosporites* being carried further from the lake margin, similar to

the sorting processes seen in Recent and Jurassic (e.g. Wall 1965) saccate pollen. In our opinion, the transport of *Ancyrospora* could also be affected by its long spinose processes retarding sedimentation, whereas *Geminospora* would probably be deposited more quickly. Thus the ecological controls on these miospores are more subtle than a simple inverse relationship, with separate and independent factors operating. Any significant increase in our understanding of the palaeoecological distribution of miospores will require detailed multidisciplinary studies (e.g. Becker *et al.* 1974; Bridge *et al.* 1980).

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