EARLY DEVONIAN PLANT FOSSILS FROM A SOUTHERN ENGLAND BOREHOLE

by W. G. CHALONER, A. HILL, *and* E. C. W. ROGERSON

ABSTRACT. Vegetative specimens of the psilopsid *Sawdonia ornata* and sporangia of *Dawsonites arcuatus* are described from borehole cores of Emsian age from Oxfordshire. The material has been investigated by hydrofluoric acid maceration, examination by SEM of plant surfaces and latex replicas, and light microscopy of oxidized cuticles and polished rock surfaces. The spines of *Sawdonia* have become flattened in a vertical plane as a result of compression phenomena; the stomata were sunken. The processes of compression and collapse of plant tissue are evidently a function of the scale of the organs concerned, and so operate differently in axes, spines, and stomata of *Sawdonia*. The *Dawsonites* sporangia are in pairs with opposed longitudinal dehiscence slits and spiralized mechanical tissue in the wall. Spores found adhering to sporangial fragments are of *Apiculiretusispora* type.

THE plant fossils described here were obtained from cores from the Institute of Geological Sciences borehole at Apley Barn, Witney, in Oxfordshire. Some of the plants were observed directly on the fractured core surfaces, while others were extracted from the matrix by bulk maceration with hydrofluoric acid. The plant-bearing shales and sandstones lie between 1290 m and 1420 m below O.D. in the borehole; they underlie beds containing a late Devonian fauna and are associated with a spore assemblage dated as Emsian (see Poole 1969, who gave a detailed log of the borehole; also Chaloner 1963; Richardson 1967; Chaloner and Richardson (1977). In the account of the stratigraphy of the borehole, Poole (1969, p. 25) records the identification by one of us (W. G. C.) of '*Psilophyton*' and *Hostimella*, as seen on the cleaved core surfaces; although palynological preparations were made from small samples of rock matrix, no further investigation of the plant macrofossils was attempted at that time. However, the recent work of Zdebska (1972, 1975) drew our attention to the potential of subjecting this type of borehole material to bulk maceration with hydrofluoric acid. This and other methods of investigation are described below. In the following account, no formal revision of the plant taxa is attempted, but significant new features revealed by SEM and other means are briefly reviewed.

MATERIAL AND METHODS

The plants occur largely as coalified compression fossils in grey mudstones, shales, and sandstones. Locally, parts of the internal structures are preserved in pyrites. The compressed coalified plant material was extracted from the matrix by halving promising cores with a vertical cut on a rock saw, disaggregating the matrix with 30% hydrofluoric acid, washing, decanting, and sieving off the plant fragments from the residue. The vertical cut faces of cores were photographed under alcohol immersion (Pl. 76, figs. 7, 8). Latex was poured on to patches of pyritized tissue, as exposed on a fractured surface, and a mould of the pyritized tissue surface obtained (cf. Chaloner and Gay 1973). These replicas, and the dried fragments obtained by HF maceration, were mounted on stubs, coated with gold in a Polaron sputter-coater, and examined under a Cambridge S600 SEM. It was found that certain features of the plants could be demonstrated most convincingly in the form of stereo-pairs of photographs, which can be viewed to give a three-dimensional image of the fossil (Pl. 74, figs. 1–4). Such stereo-pairs illustrate features of topography of the stem surface,

[Palaeontology, Vol. 21, Part 3, 1978, pp. 693–707, pls. 74–76.]

the spines, and sporangia which could not be satisfactorily shown in any other way. The stereo-pairs were generally taken with the stub viewed at a tilt angle of 45°, by rotating it through 7–10° between the two photographs. These rotational pairs (Pl. 74) show the plant material on the stub surface sloping towards the observer. SEM study of the plant surface was supplemented by macerating fragments with Schulze's solution followed by alkali, and examining the cuticle preparation obtained by transmitted light microscopy.

All the Witney specimens described and figured here are deposited in the Institute of Geological Sciences, London (I.G.S.).

THE PLANT FOSSILS

Three types of determinable fragments of plants were obtained on sieving the maceration residues. These were *Sawdonia ornata* (Dawson) Hueber, *Dawsonites arcuatus* Halle, and *Pachytheca* Hooker sp. In addition some small fragments of cuticle, some apparently of arthropods and others resembling *Nematothallus* Lang, were also encountered. Only the *Sawdonia* and *Dawsonites* gave significant new information, and these two alone are dealt with here.

Order ZOSTEROPHYLLALES
Family ZOSTEROPHYLLACEAE
Genus SAWDONIA Hueber, 1971
Sawdonia ornata (Dawson, 1871) Hueber

Plate 74, figs. 3, 4; Plate 75, figs. 1–6; Plate 76, figs. 1–5, 7, 8

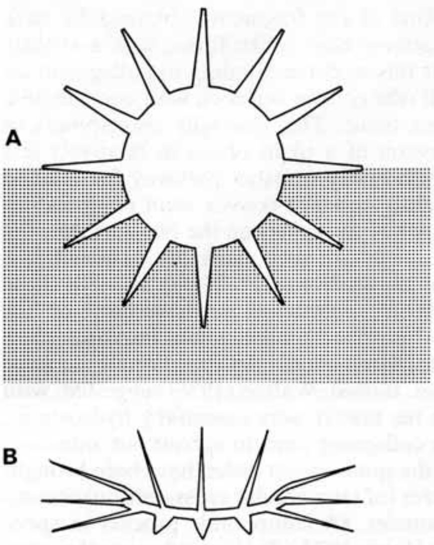
Discussion. Recent revisions of *S. ornata* have been published by Hueber (1971) and Zdebska (1972), and we accept the synonymy suggested by those authors. This species represents part of the old concept of *Psilophyton princeps*, as used by Dawson and many subsequent authors. Hueber outlines the basis for separating *Sawdonia* (with lateral sporangia) from *Psilophyton* (with terminal fusiform sporangia). Zdebska adds to our knowledge of the type species of *Sawdonia* on the basis of material from a Polish borehole. Ananiev and Stepanov (1968) have described and figured axes bearing the globose lateral sporangia in material from Minusinsk (U.S.S.R.), and although they refer it to *Psilophyton* their species appears to conform with *S. ornata* (Dawson) Hueber. A new species of *Sawdonia* has also recently been described from Canada by Gensel *et al.* (1975) which extends our concept of the genus. Banks *et al.* (1975) have also described a new species of *Psilophyton* preserved with internal structure and this confirms the distinction between this genus and *Sawdonia*.

Stem fragments that we attribute to *Sawdonia* occur abundantly in macerated cores from between 1414 and 1417 m. None of the fragments show sporangia in attachment, nor have any sporangia comparable to those of Russian (Ananiev and Stepanov 1968) and Canadian (Gensel *et al.* 1975) material been found associated with them. However, the spiny stems, often with circinately coiled tips show striking agreement with Gaspé (Hueber 1968; Lang 1931) material. In particular they agree in the detail of the fluted spines, with swollen, darkened tips, in the papillate epidermal cells, and in the character of the stomata. On this basis we attribute our plants to *S. ornata*.

While our material is too fragmentary to offer any basis for formal revision of the species, our specimens contribute to knowledge of it in three respects, as dealt with below.

The stem compressions and spine shape. Most of the fragments obtained by bulk maceration show the axis flattened to an almost ribbon-like form, with a slightly concavo-convex cross-section. We interpret this as corresponding to collapse of an originally cylindrical axis into its lower half (the convex surface), with considerable compression (and coalification) of the stem tissue. This generally corresponds to Walton's (1936) representation of compression of a plant organ in relatively less compressible matrix, when there was no pith cavity or other pathway for mud to enter the stem. However, the resulting slightly concavo-convex stem compression shows significant differences in the appearance of the spines on the two surfaces. On the generally concave (upper) surface the spines are very markedly flattened in a (vertical) plane parallel to the axis on which they are borne (Pl. 74, fig. 3), while those on the generally convex (lower) surface are not so flattened but have more or less conical bases (Pl. 75, figs. 2–4). At first sight this spine flattening seems puzzling; there is no theoretical reason why any force in the matrix should act directionally so as to flatten all the spines in parallel vertical planes. Indeed, Walton (1936) suggested, with good reason, that forces of compaction in the matrix were essentially hydrostatic; there was, for example, no force causing a collapsing stem to spread out sideways. We therefore conclude that the flattening of the spines might rather have been brought about by the upper half of the cylinder of stem (of semicircular cross-section) accommodating to a width equal to its own diameter. (A comparable process in spore compression has recently been described by Harris 1974.) This would cause the spine bases in the upper surface to 'close' in relation to the general stem surface (text-fig. 1A, B). The spines on the lower (generally slightly convex) axial surface tend to be less flattened, to have a rather strongly fluted base, and to be generally shorter than those on the upper surface (text-fig. 1B; Pl. 75, figs. 2–4). We believe that this results from two features of the lower surface fossilization environment: *a*, once the spines had lodged in the mud the underside of the axis was cut off from a supply of sediment; the spines therefore underwent compaction together with the surrounding matrix, so becoming considerably shortened (text-fig. 1); *b*, as the internal tissue of the stem became 'macerated' by biological degradation, organic matter would tend to accrue in the pockets of the compressing spines. On the upper surface, in contrast, the spine 'contents' would tend to drop down into the axial cavity as it collapsed. But the spines would continue to stand up as sediment accrued around them. This sediment would undergo some compaction around the spines which became flattened in the vertical plane as the axial surface on which they stood was reduced in width. We believe that this mechanism may explain the different states of the spines on the two surfaces. We see no evidence of dorsiventral (or other bifacial) differentiation of the axes before fossilization; examination of many axes on the matrix (e.g. Pl. 76, fig. 4), showing spines in profile at their margins, suggests a more or less even distribution of comparable spines around the axes.

It is important to note that in such a model of the compression-and-collapse process, not only do the spines on the upper and lower surfaces undergo different degrees of compression, but the spines on the upper surface undergo far less (vertical) compression than the stem itself. Thus the stem, changing from a cylinder to a ribbon of coaly matter, has undergone compaction in a ratio in excess of 20:1 (Pl. 76, fig. 8), while the upright spines on the upper surface can have undergone little vertical compaction as the sediment accumulated around them. They have the same order of length (*c.* 2–3 mm) as spines seen in profile at the flattened axis margin which have presumably not been shortened at all. The spines on the upper and lower surfaces and the axes bearing them have therefore been subjected to three entirely different compression regimes, with resulting differences in character.



TEXT-FIG. 1. A, diagram showing a *Sawdonia* axis in cross-section, its lower surface and spines lodged in mud, before compaction of the matrix. B, the same axis, following compression; continued supply of sediment to the upper surface, accompanying compaction has sustained the spine length, while the spines on the lower surface are much shortened.

It should be acknowledged that spine flattening was suggested by Edwards (1924, fig. 3) on the basis of the shape of the truncated spine base, seen as a slit in the cuticle of *S. ornata* from Gaspé. He described the spines as 'flattened vertically' and said that they 'were very thin'. More recently, in their account of *S. acanthotheca*, Gensel *et al.* (1975) note that the spines on the sporangia of that species are in places 'scale-like' and suggest that this aspect of the spines is 'probably due to flattening during fossilization'.

In our material there is some variation in spine size, even allowing that many apices are broken off; this variability is seen even in the young, still circinately coiled tips of the axes (Pl. 75, fig. 1). Where intact spine apices are present, they show slightly swollen darkened tips, with a fluted surface (Pl. 74, fig. 3). These tips appear dark in an SEM, possibly on account of a difference in composition, or perhaps simply

EXPLANATION OF PLATE 74

SEM stereo-pairs of *Dawsonites* sporangia and *Sawdonia* axes; magnification given in each case is in the horizontal plane; stub angle ranges from 20° to 70°. I.G.S. stubs: 1, EGP 8742a; 2, 8744a; 3, 8742b; 4, 8745a.

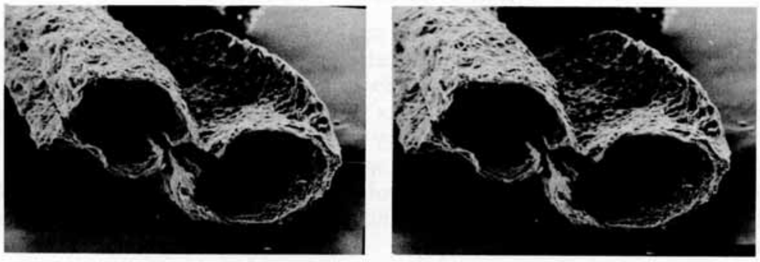
Fig. 1. Pair of sporangia of *Dawsonites* sp., truncated by fracture of the matrix, showing the opposed dehiscence slits (centre), the thick distal wall at either side, and the tapetal membrane lining the sporangial cavity; ×50.

Fig. 2. Tip of a sporangium of *D. arcuatus* (shown at lower magnification on Pl. 75, fig. 7) showing the twisting of the bifid apex; ×50.

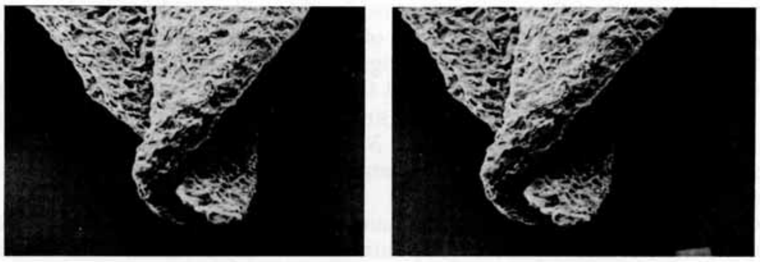
Fig. 3. Spines, flattened in a vertical plane, seen on the upper surface of a compressed *Sawdonia ornata* axis. Note dark spine tips; ×25.

Fig. 4. Stoma of *S. ornata* showing the guard cells lying slightly below the epidermal surface, and the compressed and overhanging sides of the stomatal depression (cf. Pl. 76, fig. 3); ×1000.

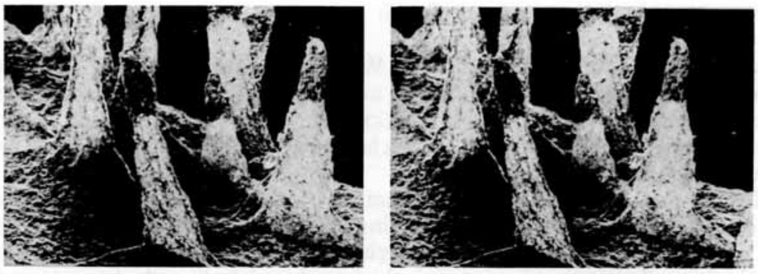
PLATE 74



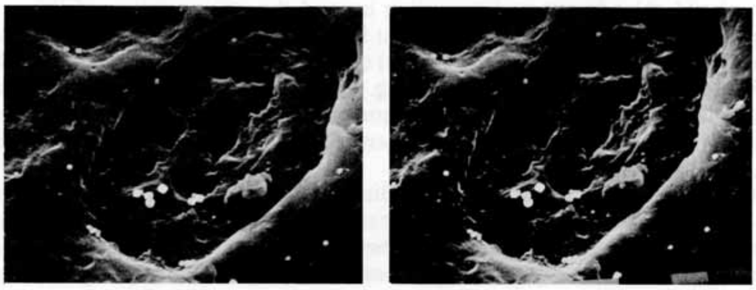
1



2



3



4

CHALONER, HILL and ROGERSON, early Devonian plants

as the effect of a greater thickness at the apex causing a lower intensity of secondary emission. This corresponds to the (optical) darkness of the spine tips seen by transmitted light microscopy (Lang 1931; Zdebska 1972), which appears to be a distinctive feature of the spines which characterizes this species. Lang has discussed fully the possibility that the spine tip was secretory in nature, and emphasizes that the lack of stomata would favour a function of the spine as being something other than simply a photosynthetic emergence. Our own observations under SEM confirm both the swollen aspect of the spine tip and (with all the limitations of such negative evidence) the lack of stomata.

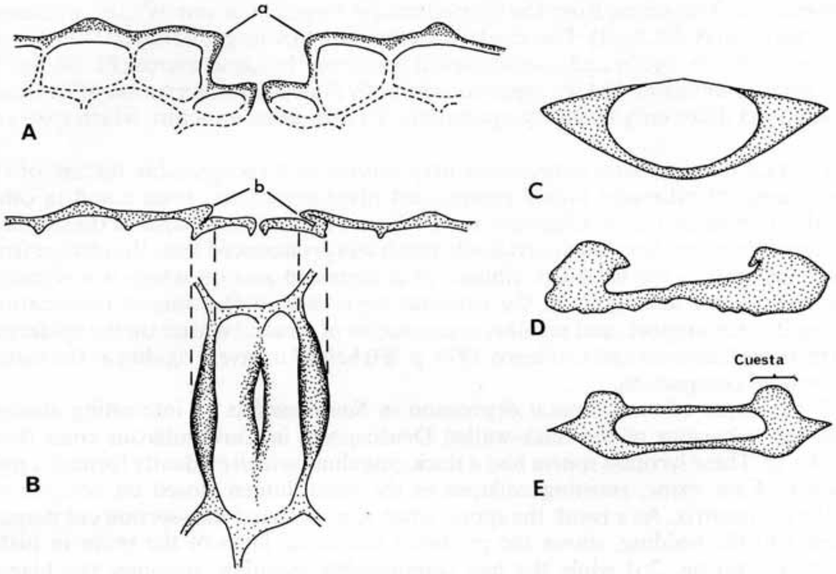
Epidermal papillae. The presence of a single elongated papilla or cuticular ridge on each epidermal cell of *S. ornata* was noted by Edwards (1924) and subsequently by Lang (1931) and Zdebska (1972). SEM observation indicates that these were quite prominent features of the external topography of the stem surface (Pl. 75, fig. 5), and not simply a darkening or internal thickening of the periclinal epidermal cell wall. It is noteworthy that these papillae and the swollen spines tips are lacking in the only other known species of *Sawdonia*, *S. acanthotheca*; so that while they appear to be a helpful specific feature, they cannot be used for separating *Sawdonia* from *Psilophyton* s.s.

We have found no evidence of the hair bases described by Edwards (1924) and Zdebska (1972). However, as our observations were only based on a few minute areas of cuticle, this negative evidence is not very significant. It may be noted that Lang (1931) was also unable to find evidence of the hair bases in Gaspé material, although he was aware of Edwards' record of their occurrence.

Stomata. Stomata were observed in the Witney material, both in SEM observation of the outer stem surface (Pl. 74, fig. 4), and in small fragments of stem cuticle prepared by oxidation with Schulze's solution (Pl. 76, fig. 1). The cuticle so prepared was very fragile and we were unable to get large fragments of the size of those prepared by Edwards (1924) from Gaspé.

Edwards first noted the interesting feature of what appear to be two crescentric cuticular thickenings more or less encircling the stomatal pore. He figures these (1924, fig. 2; our Pl. 76, figs. 2, 3 are of his material) and remarks that 'the outer walls of the cells flanking the stomatal pores are thickened and frequently have a crescentric form'. Zdebska (1972) has made a very searching study of the stomata in the Polish material and extends our understanding beyond the interpretation of Edwards and Lang. She notes the important point that Edwards's crescentric thickenings, as seen in careful focusing, are above the general cuticular surface. Our own observation on the Witney macerated cuticle (Pl. 76, fig. 1) confirms this point. On this basis she suggests that the stomatal aperture was surrounded in life by a cuticular ridge on the epidermal surface forming a low rim encircling the stomatal aperture (Zdebska 1972, text-fig. 5).

Our SEM observations of the unoxidized outer stem surface suggest a different possible explanation for these crescentric ridges. The stereo-pair (Pl. 74, fig. 4) makes it clear that the guard cells were sunken below the general stem surface (text-fig. 2A); the lateral walls of this stomatal depression were steep, even overhung (text-fig. 2A*a*),



TEXT-FIG. 2. A, diagrammatic section of the epidermis of *Sawdonia* as it was in life; the cuticle is stippled; the stoma lies in a depression (*a*). B, diagrammatic sectional view and (below) a surface view of the fossil cuticle showing the effect of collapse during compression; the originally steep sides of the stomatal depression have buckled to form folds (*b*) protruding slightly above the cuticle surface; these are seen as dark crescentic features on either side of the guard cells (below). C–D, diagrammatic views of a Carboniferous Densospore, showing analagous behaviour on compression; the uncompressed spore, C, collapses in a coal matrix so that the equatorial thickening (cingulum) is left as a prominent feature of the compressed spore, D (drawn from a vertical section of a British Upper Carboniferous coal, × 700). This has been interpreted by some authors as an original feature of the spore (a 'cuesta') protruding from the proximal surface (E). It is here suggested that as in the *Sawdonia* cuticle, this less compressible feature is a product of collapse on compression, and was not a prominence on the original object.

while those at the poles of the stoma were at a more gentle gradient. While we therefore endorse Zdebska's (1972) observation that the ridges (text-fig. 2B*b*) are a genuine diagnostic feature of the fossil cuticle we believe that their 'raised' character may be a product of collapse of the cuticle on the vertical sides of the stomatal depression rather than a structure elevated above the stem surface in life, as she suggests. If, as we believe, our material is conspecific with that from Opole (Poland), we interpret the stomatal structure described by Zdebska as due to collapse (the effect of compaction of plant-plus-matrix) of sunken stomata, producing a ridge where the more competent vertically orientated cuticle of the depression margin resisted this collapse.

As Zdebska (1972) points out, the thickenings adjoining the stomata (collapsed sides of the stomatal depression, in our interpretation) may not be equally developed on either side of the stoma (e.g. her pl. 8, figs. 1, 2). We believe that this is a result of the epidermis lying somewhat obliquely in the matrix, as the sediment underwent compaction. The stoma from the cleared cuticle fragment of our Witney specimens is of this type (Pl. 76, fig. 1). This can be matched with a comparable stoma from Gaspé *S. ornata* (Pl. 76, fig. 2) and a symmetrical one from the same source (Pl. 76, fig. 3). We would emphasize that we agree entirely with Zdebska's observation of her fossil cuticle, and differ only in the interpretation of the original structure which gave rise to it.

The fact that stomatal depressions may survive as a recognizable feature of the topography of otherwise highly compressed plant organs has been noted in other plant compression fossils (Chaloner and Collinson 1975). The collapse of the stomatal depressions in our *Sawdonia* is evidently much less pronounced than the change from the cylindrical to the flattened 'ribbon' of compressed axis on which it is situated. No doubt some matrix lay in the stomatal depression at the time of fossilization, giving it some support; and possibly encrustation of mineral matter on the epidermal surface (see Chaloner and Collinson 1975, p. 89) helped to give it rigidity as the matrix underwent compaction.

The collapse of the stomatal depression in *Sawdonia* has an interesting analogy with the behaviour of the thick-walled Densospores in Carboniferous coals (text-fig. 2C–E). These lycopod spores had a thick cingulum, which evidently formed a rigid feature of the exine, resisting collapse as the spore lumen closed on compaction of the coal matrix. As a result the spore, when seen in a coal thin-section cut perpendicular to the bedding, shows the proximal and distal faces of the spore in juxtaposition (text-fig. 2D) while the less compressible cingulum becomes the highest feature of the flattened spore. This produces the distinctive outline of Densospores seen in a coal section which has been referred to as 'biconcave' or 'dumb-bell shaped' (Schopf *et al.* 1944). The ridge around the spore lumen resulting from this differential collapse phenomenon can be seen in spores extracted by maceration, being the first part of the spore to give a sharp image on focusing down on to it from above. Staplin and Jansonius (1964) have referred to this feature in Densospores as a 'cuesta' (cf. text-fig. 2E). We believe that the cuesta (like the cuticular ridge observed by Zdebska) of some fossil Densospores appeared as a topographic feature only after compression, rather than having been an original feature of the topography of the uncompressed spore (cf. text-fig. 2B*b* and D). We interpret both Zdebska's ridge and

EXPLANATION OF PLATE 75

SEMs of *Sawdonia ornata* and *Dawsonites arcuatus*; magnification given in each case is in the horizontal plane; stub angle ranges from 17° to 68°. I.G.S. stubs: 1, EGP 8744b; 2, EGP 8743a; 3 and 4, EGP 8743b; 5, EGP 8745b; 6, EGP 8745c; 7, EGP 8744a.

Fig. 1. Circinately coiled tip of *S. ornata* (apex at top right, truncated axis at top left); note varied spine length; ×12.

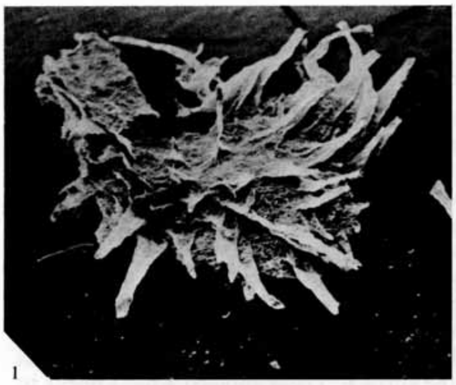
Figs. 2–4. Spines from lower surface of compressed axis of *S. ornata* shortened by compaction of matrix. 2, ×40. 3, detail from lower surface of another specimen showing fluting of spine base; ×300. 4, circular cross-section where spine was broken off; ×140.

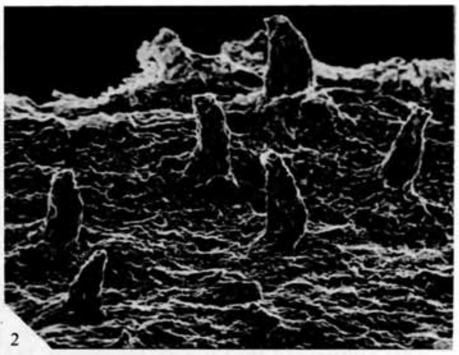
Fig. 5. Papillae on axial surface; ×280.

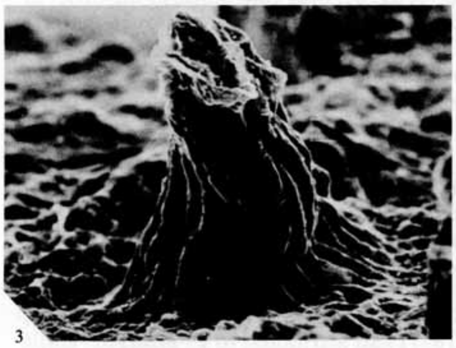
Fig. 6. Xylem elements removed on latex replica from fractured surface of stele of *S. ornata* showing spiral (or ?annular) thickenings replaced by pyrite; ×130.

Fig. 7. Sporangium of *D. arcuatus*, with fractured base of paired sporangium at top left; ×12. A different view of the apex (bottom right) is shown in Plate 74, fig. 2.

PLATE 75

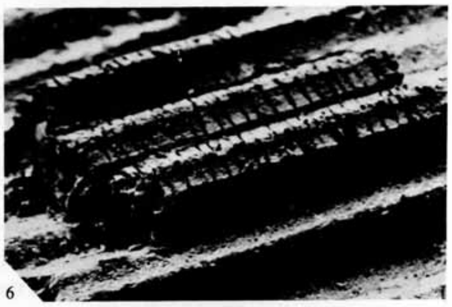

1


2


3


4


5


6


7

CHALONER, HILL and ROGERSON, early Devonian plants

the Densospore 'cuesta' as products of the same mechanism of differential resistance to collapse on fossilization.

Stelar anatomy. Several of the axes evidently underwent partial permineralization with pyrite before biological degradation of the internal structure was complete. Where this occurred, compression of the stem tissue did not progress as far as in non-pyritized specimens (cf. Pl. 76, fig. 7 with fig. 8, where localized pyritization has occurred in the stele and in some of the spines, which have resisted collapse). Several axes were encountered on cut polished faces (see Matten 1973) showing imperfectly preserved steles suggesting a more or less ellipsoidal cross-section, but the exarch/endarch character could not be clearly discerned. One axis showed pyritized vascular elements seen in a longitudinal fracture plane. A single spine seen at the edge of the axis confirmed that it was *Sawdonia.* Pyritized xylem elements were pulled from this axis while trying to take a latex replica of the surface. These showed what appear to be spiral or possibly annular thickening (Pl. 75, fig. 6); they thus confirm the observations of fragmentary xylem elements of *S. ornata* seen by light microscopy in material from New York (Hueber and Grierson 1961) and Poland (Zdebska 1972). It is interesting to note the difference between these elements and those of *Psilophyton dawsonii* Banks *et al.*, 1975, which show very distinctive pit-like areas between their scalariform thickenings.

Division TRACHEOPHYTA
Genus incertae sedis DAWSONITES Halle
Dawsonites arcuatus Halle, 1916

Plate 74, fig. 2; Plate 75, fig. 7; Plate 76, fig. 6

Discussion. The name *Dawsonites* was instituted by Hallé (1916) for clusters of fusiform sporangia of the type that Dawson (1871) had attributed to *P. princeps*. Hallé, doubting this connection with *Psilophyton*, proposed a distinct name so that such sporangia could be referred to without presupposing their affinity with that genus. Høeg (1967) has given a very full review of the species attributed to *Dawsonites*, taking a rather broader generic concept than that of earlier authors. Hueber and Banks

---

EXPLANATION OF PLATE 76

Sawdonia ornata and *Dawsonites arcuatus* from the Witney Borehole and Gaspé, Canada.

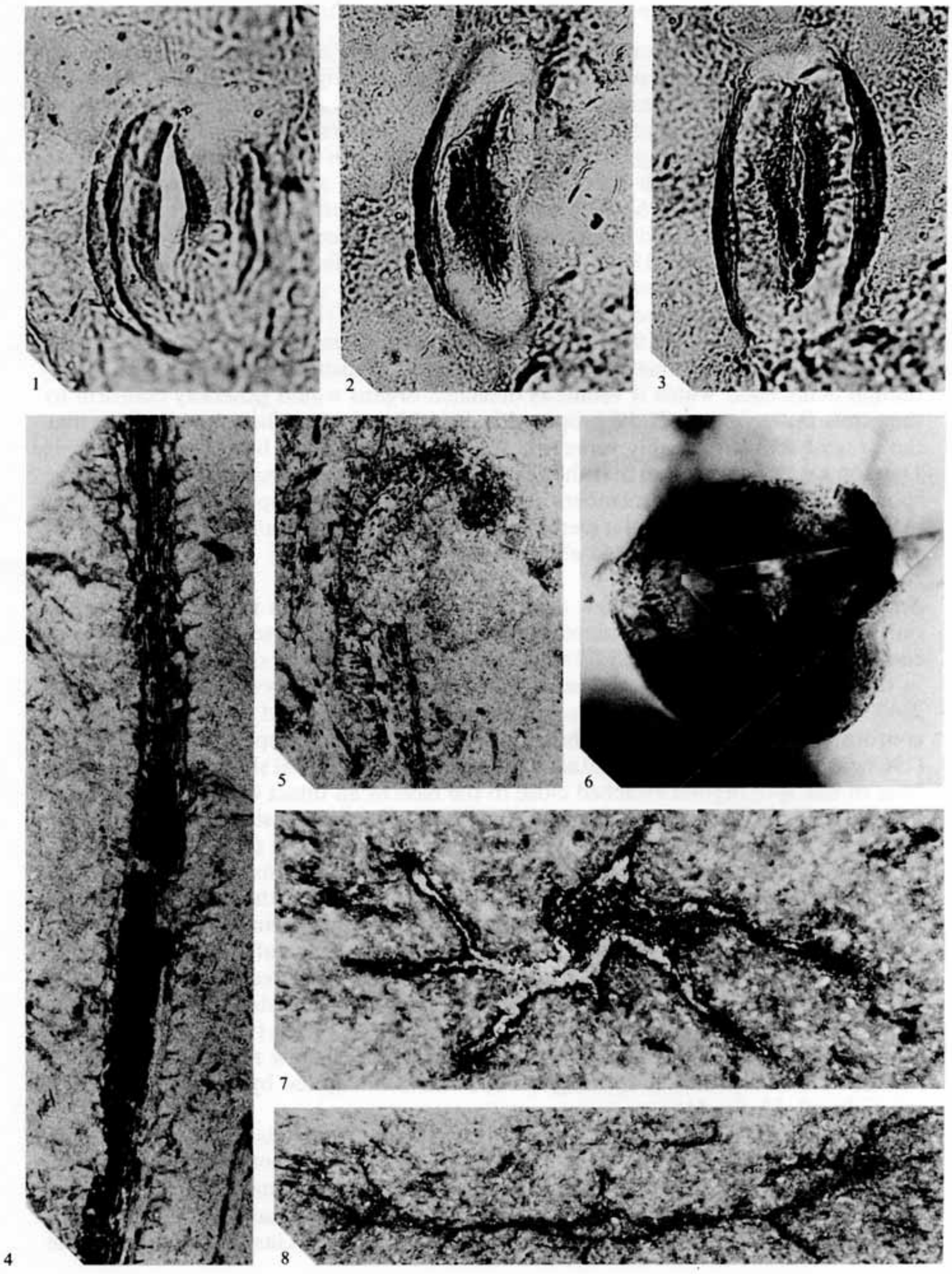
Fig. 1. Macerated cuticle of *S. ornata*, from Witney, showing stomatal aperture and arcuate folds, especially at left, formed by collapse of the stomatal depression; I.G.S. slide PF 4789; ×750.

Figs. 2, 3. Cuticle of *S. ornata* with stomata from Gaspé (figured W. N. Edwards 1924) showing similar folds at one (fig. 2) or both (fig. 3) sides of the stomatal aperture; British Museum (Natural History), Palaeontology Dept., slide V 149180.

Figs. 4, 5. Axes of *S. ornata* exposed on the core surface, photographed under xylene. 4, I.G.S. EGP 8743, ×2. 5, note the circinately coiled apex; I.G.S. EGP 8742, ×2.

Fig. 6. Spore (composite photograph of three focal planes) adhering to the tapetal membrane from a sporangium of *D. arcuatus*; I.G.S. slide PF 4790, ×1000.

Figs. 7, 8. Transverse sections of axes of *S. ornata* (seen in polished vertical sections of cores); both I.G.S. EGP 8744. 7, axis with spines, showing pyritization at centre extending into spine bases; ×30. 8, more completely collapsed axis without pyritization; note slight concavity of stem cross-section (cf. text-fig. 1B); ×20.



CHALONER, HILL and ROGERSON, early Devonian plants

(1967) re-examined Dawson's (1871) material and have shown that *P. princeps* s.s. (in contradistinction to *S. ornata*) did indeed bear sporangia of the *D. arcuatus* type. Banks *et al.* (1975) and Kasper *et al.* (1974) discuss fully the tortuous history of the use of the names *Dawsonites* and *Psilophyton.* Andrews and his co-workers have adopted the course of using the generic name *Psilophyton* in a broad sense to include early Devonian plants with either smooth or spiny axes, and terminal ovoid or fusiform sporangia (e.g. *P. forbesii*, *P. microspinosum*, *P. dapsile*). They reserve the name *Dawsonites* in a restricted sense, much as Halle conceived it, for 'fragmentary sporangia' (Kasper *et al.* 1974). Banks *et al.* (1975) similarly acknowledge the need for the form genus *Dawsonites*, for detached fusiform sporangia. We favour this restricted use of *Dawsonites* since a number of genera (including *Psilophyton* s.s.; *Trimerophyton* Hopping, 1956; *Oocampsa* Andrews, Gensel, and Kasper, 1975; and *Rellimia* Leclercq and Bonamo, 1973) bore clusters of fusiform sporangia with longitudinal dehiscence, which if found as detached organs would generally conform to the genus *Dawsonites* as Hallé proposed it. For this reason, although we believe that the present fossils probably represent sporangia of the type borne by *P. princeps* Dawson s.s., we do not feel that the genus *Dawsonites* can be regarded as comprising sporangia borne solely by members of the subdivision Trimerophytina (as suggested in Chaloner 1972). At present it seems preferable to treat *Dawsonites* as a tracheophyte genus *incertae sedis* as indicated above.

Structure of the sporangia. A few detached fusiform sporangia were encountered in our residues; these were examined under the binocular microscope and some were coated and examined under SEM while others were cleaned by oxidative maceration in the hope of obtaining evidence of spore contents. Our sporangia were typically 2 × 7 mm, fusiform in shape with longitudinal dehiscence, and appear generally to conform with the specimens attributed to *P. princeps* from Gaspé figured by Hueber (1968). Although we found no intact pairs of sporangia, several showed the truncated base of one sporangium attached close to the base of an intact one (Pl. 75, fig. 7, at left). Several of the sporangia show what appears to be an extension of the dehiscence slit across the apex of the sporangium to give it a cleft with the two apical lobes twisted across one another (see stereo-pair, Pl. 74, fig. 2). We tried at first to interpret this as being two sporangia twisted around one another (cf. the twisting shown in Hueber's 1968 figs. 16, 17); but an examination of several specimens suggests rather that each sporangium had some mechanical tissue in the wall which imparted a tendency to twist (on drying out?) and thus presumably assisted dehiscence (cf. the two halves of the legume pod of Gorse, *Ulex*, where considerable torsional stress is built up in the carpel causing explosive seed discharge, and a twisting of the pod). We note that two of Hueber's sporangia (1968, fig. 17) show minute apical clefts, similar to ours, as does the sporangium of *P. dawsonii* figured by Banks *et al.* (1975, top right, pl. 23, fig. 51).

A further specimen (Pl. 74, fig. 1) shows what we interpret as a pair of sporangia truncated by fracture of the enclosing rock matrix, with opposed dehiscence slits. We believe that this pair of sporangia, already dehisced, became filled with matrix, which on removal with HF left the sporangia unflattened. Lang (1931) described similar sporangia which he attributed to *P. princeps* s.s. from Gaspé, 'preserved in the round, the cavity being filled with a cast of fine mineral material'. However, we query the assignment of this pair of sporangia to *D. arcuatus* as they are considerably smaller (*c.* 800 μm diameter, less than half that of intact sporangia). They are of interest in showing the opposed dehiscence slits, an inner (tapetal?) membrane detached from the sporangial wall, and showing the greatest thickness of the sporangium walls on the outwardly directed faces. In these three details this pair of sporangia resembles those of *P. dawsonii* Banks *et al.*, 1975, as seen in petrified material from Gaspé.

Spores in situ. We macerated some of the flattened sporangia under Schulze's solution, with only partial success. We obtained no spore masses but only occasional spores adhering to fragments of the rather distinctive 'sacs' (?tapetal membrane) which are evidently similar to those figured by Hueber (1968) and Banks *et al.* (1975) from Canadian *Psilophyton.* Our Witney specimens show the same type of irregular cell outlines, presumably representing the shape of cells at the periphery of the tapetum. The fact that the few spores we found were adhering to this somewhat wrinkled membrane made them difficult subjects for photography (Pl. 76, fig. 6).

We assume that most of our sporangia had shed the bulk of their spores before fossilization, and that the spores attached to the tapetal membrane represent a residue of their contents rather than contaminants. However, in these circumstances, the possibility of contamination cannot be ruled out. The spores show a mean diameter of 50 μm (range for four specimens: 45–55 μm). They have an ornament of minute (1 μm or less) sculptural elements (coni or papillae) over much of the surface. There are imperfectly defined curvaturae and the triradiate suture extends for about two-thirds of the radius. There are three dark patches in the exine in the interradial areas, close to the apex, but at the apex itself the exine is translucent as elsewhere. These spores are generally similar to those figured by Hueber (1968) and Banks *et al.* (1975) from *Psilophyton* sporangia. The closest species of dispersed spore seems to be *Apiculiretusispora brandtii* Streel (see, for example, the specimens from the Emsian–Eifelian Battery Point formation, Gaspé, figured by McGregor 1973). As McGregor points out *A. brandtii* is evidently closely comparable to the spores figured by Lang (1932) from *D. arcuatus* from the Strathmore Group (Emsian) of Scotland.

Our *in situ* spores are also very similar to the slightly larger dispersed spores from adjoining cores in the Witney borehole described and figured by Chaloner (1963) as '*Cyclogranisporites sp.*' It may be noted that this broadly defined genus was used at that time as a designation for spores later segregated as *Apiculiretusispora.* McGregor and Owens (1966), for example, attributed spores from Gaspé to '*Cyclogranisporites sp.*' which McGregor (1973) subsequently assigned to *A. brandtii.*

Banks *et al.* (1975) discuss fully the problem of relating *in situ* spores of their *P. dawsonii* to an appropriate dispersed-spore species; this is aggravated by the tendency of the outer layer of exine to come away, leaving the spore with a sculptureless surface beneath. The same problem is considered in relation to dispersed spores by McGregor (1973). We did not see clear evidence of this detachment of an outer exine layer in our material, but we had access to only a few partially obscured specimens. It is a little disconcerting that spores essentially similar to ours were also reported by Edwards (1968) adhering to sporangial walls of a very different plant, *Krithodeophyton croftii*, from the Siegenian of Wales. We suspect that this is the similarity of spores of basically rather simple organization in unrelated plants rather than being of any systematic significance, or the result of contamination in either case.

Association of Sawdonia *and* Dawsonites. The occurrence of our *Dawsonites* sporangia in the same cores as *S. ornata* repeats an association noted in several occurrences elsewhere. These include Gaspé (the cause of the original confusion of *Psilophyton* and *Sawdonia* in Dawson's material) and the Strathmore Group in Scotland (Lang 1932; see also Zdebska 1972). Since the globose lateral sporangia of *Sawdonia* are so totally unlike the fusiform terminal ones of *Psilophyton* we assume that this association is purely fortuitous in these three instances. At most, it may reflect an ecological association of the two plants.

Acknowledgements. We record our warm thanks to the Royal Society for the Grant-in-aid which made possible the purchase of the SEM used in this work. We are also grateful to the Chief Palaeontologist, I.G.S., and to the Keeper of Palaeontology, British Museum (Natural History) for allowing us to borrow specimens in their care, and to Mr. Richard Packer for technical help with the photography.

REFERENCES

ANANIEV, A. R. and STEPANOV, S. A. 1968. Discovery of spore-bearing organs on *Psilophyton princeps* Dawson emend. Halle in the Lower Devonian of southern Minusinsk Trough (Western Siberia). In *New materials on the stratigraphy and palaeontology of the Lower and Middle Palaeozoic of Western Siberia. Trudy Tomsk. Univ.*, Geol. Ser. **202,** 30–46. [In Russian.]

ANDREWS, H. N., GENSEL, P. G. and KASPER, A. E. 1975. A new fossil plant of probable intermediate affinities (Trimerophyte–Progymnosperm). *Can. J. Bot.* **53,** 1719–1728.

BANKS, H. P., LECLERQ, S. and HUEBER, F. M. 1975. Anatomy and morphology of *Psilophyton dawsonii*, sp. n. from the late Lower Devonian of Quebec (Gaspé), and Ontario, Canada. *Palaeontogr. am.* **8** (48), 77–127.

CHALONER, W. G. 1963. Early Devonian spores from a borehole in southern England. *Grana palynol.* **4,** 100–110.

—— 1972. Devonian plants from Fair Isle, Scotland. *Rev. Palaeobot. Palynol.* **14,** 49–61.

—— and COLLINSON, M. E. 1975. Application of SEM to a Sigillarian impression fossil. Ibid. **20,** 85–101.

—— and GAY, M. M. 1973. Scanning electron microscopy of latex casts of fossil plant impressions. *Palaeontology*, **16,** 645–649.

—— and RICHARDSON, J. B. 1977. South-east England. *In* A correlation of the Devonian rocks of the British Isles. *Spec. Rep. geol. Soc. Lond.* **8,** 26–39.

DAWSON, J. W. 1871. The fossil plants of the Devonian and upper Silurian formations of Canada. *Geol. Surv. Canada*, 1–92, pls. 1–20.

EDWARDS, D. 1968. A new plant from the Lower Old Red Sandstone of South Wales. *Palaeontology*, **11,** 683–690.

EDWARDS, W. N. 1924. On the cuticular structure of the Devonian plant *Psilophyton. J. Linn. Soc.* (Bot.), **48,** 377–385.

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.

HALLE, T. G. 1916. Lower Devonian plants from Rorargen in Norway. *K. svenska Vetens Akad. Handl.* **57,** 1–46.

HARRIS, T. M. 1974. *Williamsoniella lignieri*: its pollen and the compression of spherical pollen grains. *Palaeontology*, **17,** 125–148.

HØEG, O. E. 1967. Psilophyta. *In* BOUREAU, E. (ed.). *Traité de Paleobotanique*, **2,** 193–433.

HOPPING, C. W. 1956. On a specimen of '*Psilophyton robustius*' Dawson from the Lower Devonian of Canada. *Proc. R. Soc. Edinb.*, Ser. B, **66,** 10–28.

HUEBER, F. M. 1968. *Psilophyton*: the genus and the concept. Pp. 815–822. *In* OSWALD, D. H. (ed.). *International symposium on the Devonian System.* Alberta Society of Petroleum Geologists, Calgary, **2.**

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

—— and BANKS, H. P. 1967. *Psilophyton princeps*: the search for organic connection. Ibid. **16,** 81–160.

—— and GRIERSON, J. D. 1961. On the occurrence of *Psilophyton princeps* in the early Upper Devonian of New York. *Am. J. Bot.* **48,** 473–479.

KASPER, A. E., ANDREWS, H. N. and FORBES, W. H. 1974. New fertile species of *Psilophyton* from the Devonian of Maine. Ibid. **61,** 339–359.

LANG, W. H. 1931. On the spines, sporangia, and spores of *Psilophyton princeps* Dawson, shown in specimens from Gaspé. *Phil. Trans. R. Soc.*, Ser. B, **219,** 421–442.

—— 1932. Contributions to the study of the Old Red Sandstone flora of Scotland, VIII. On *Arthrostigma*, *Psilophyton*, and some associated plant remains from the Strathmore beds of the Caledonian Lower Old Red Sandstone. *Trans. R. Soc. Edinb.* **57,** 491–521.

LECLERQ, S. and BONAMO, P. M. 1973. *Rellimia thomsonii*, a new name for *Milleria* (*Protopteridium*) *thomsonii* Lang 1926 emend. Leclerq and Bonamo 1971. *Taxon*, **22,** 435–437.

MCGREGOR, D. C. 1973. Lower and Middle Devonian spores of Eastern Gaspé, Canada. I. Systematics. *Palaeontographica*, Abt. B, **142,** 1–77.

—— and OWENS, B. 1966. Illustrations of Canadian fossils; Devonian spores of eastern and northern Canada. *Geol. Surv. Pap. Can.* **66-30** [i–iii], 1–66, pls. 1–29.

MATTEN, L. C. 1973. Preparation of pyritised plant petrifactions: 'a plea for pyrite'. *Rev. Palaeobot. Palynol.* **16,** 165–173.

POOLE, E. G. 1969. The Stratigraphy of the Geological Survey Apley Barn Borehole, Witney, Oxfordshire. *Bull. geol. Surv. Gt Br.* **29,** 1–104.

RICHARDSON, J. B. 1967. Some British Lower Devonian spore assemblages and their stratigraphic significance. *Rev. Palaeobot. Palynol.* **1,** 111–129.

SCHOPF, J. M., WILSON, L. R. and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Rep. Invest. Ill. St. geol. Surv.* **91,** 1–73.

STAPLIN, F. L. and JANSONIUS, J. 1964. Elucidation of some Paleozoic Densospores. *Palaeontographica*, Abt. B, **114,** 95–117.

WALTON, J. 1936. On the factors which influence the form of fossil plants, with descriptions of the foliage of some species of the Palaeozoic equisetalean genus *Annularia*. *Phil. Trans. R. Soc.*, Ser. B. **226,** 219–237.

ZDEBSKA, D. 1972. *Sawdonia ornata* (= *Psilophyton princeps* var. *ornatum*) from Poland. *Acta palaeobot. Cracov*, **13,** 78–98.

—— 1975. A new Zosterophyll and its bearing on the problem of evolution of the Lycopod sporophyll. *Cour. Forsch. Inst. Senckenberg*, **17,** 92.

W. G. CHALONER and A. J. HILL

Department of Botany
Birkbeck College
Malet Street
London WC1E 7HX

E. C. W. ROGERSON

Department of Botany
University College
P.O. Box 78
Cardiff CF1 1XL
Wales

Manuscript received 11 July 1977
Revised manuscript received 19 November 1977