

## LOWER DEVONIAN (DITTONIAN) PLANTS FROM THE WELSH BORDERLAND

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ABSTRACT. Fertile specimens of *Zosterophyllum* Penhallow, *Salopella* gen. nov. (assigned to the Rhyniaceae), and *Prototaxites* Dawson are described from the upper group of the Ditton Series (Lower Devonian, approximately late Gedinnian or lower Siegenian of Europe) of Shropshire. Spores have been isolated from *Salopella* gen. nov., oval and fusiform carbonaceous masses, and from the matrix.

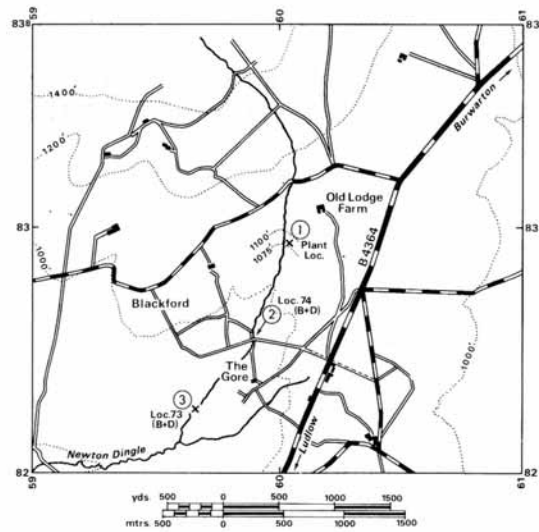
It has recently been suggested by Allen *et al.* (1968) that an investigation of the ranges of plant macro- and microfossils coupled with one on vertebrates might help to solve two major stratigraphic problems of the Lower Old Red Sandstone in the Anglo-Welsh region: first, that of correlation between South Wales and the Welsh Borderland and secondly, the precise delimitation of boundaries within the stages. Croft (1953) defined the Breconian of South Wales on the basis of its flora and fauna (the latter being represented by one fragment of *Rhinopteraspis cornubica*) and the Dittonian and Downtonian lithologically. In the Welsh Borderland, however, the stages have been delimited by vertebrates (White 1950, 1956; Ball and Dineley 1961).

Except for Lang's work on Downtonian floras of the region (Lang 1937), no detailed accounts of plant assemblages have been published, although 'plant debris' is often mentioned in stratigraphical and palaeontological papers (Allen and Tarlo 1963; Ball and Dineley 1961). Richardson and Lister (1969) have described spore assemblages from South Wales and the Welsh Borderland. This report is part of an investigation concerned with the collection and description of both macro- and microfloras throughout the Downtonian and Lower Devonian of the Anglo-Welsh region.

The beds containing the plants described below are exposed in both banks of the stream in the upper part of Newton Dingle, in the area known as The Gore. Ball and Dineley (1961), consider the section found in Newton Dingle to be the most complete for the upper group of the Ditton Series in the Brown Clew Hill regions. The plant locality is just above their locality 74 (see text-fig. 1) and is therefore at about 290 m above the main *Psammosteus* limestone. In the upper of the two cornstones (locality 74) Ball and Dineley found *Althaspis leachi?* and *Europrotaspis crenulata*, typical of the *A. leachi* Zone. Their locality 73 has a more sparse fauna but is still probably in the *A. leachi* Zone. White (1956) tentatively correlated the *A. leachi* horizons with the lower Siegenian of Europe.

### DESCRIPTION OF THE PLANTS

The plants were found in a coarse grey-green, sometimes micaceous sandstone. This is overlain by a cornstone containing very fragmentary remains. The fossils in the less micaceous areas are occasionally associated with malachite. Plant and



TEXT-FIG. 1. Location of plant-bearing horizon in Newton Dingle. Plants occur at locality 1. Positions of fish-bearing cornstone localities 73 and 74 after Ball and Dineley (1961), which occur in the *Althaspis leachi* zone, are indicated.

indeterminate animal fragments either completely cover the bedding planes or are of sporadic occurrence. Plant axes sometimes exhibit parallel alignment. The plants are preserved as iron-stained impressions or black compressions, which revealed little or no structure on maceration with Schulze's solution. Oxidation of the spore masses was more successful.

The axes range between 0.2 mm and 2.5 mm with some fragments as long as 9.0 cm. The narrowest ones (Pl. 40, fig. 10), though parallel sided, are flexuous, but the majority are straight and show dichotomous or, more rarely, pseudomonopodial branching, the latter usually occurring in wider axes. Also in these wider types are central strands. No evidence of tracheids is present. Scattered in the matrix are coiled narrow axes (Pl. 40, fig. 7) and less frequently, hook-like structures. One specimen has a small projection (?axillary tubercle) below a branching point. Perhaps the most exciting find at this locality is a single specimen and its counterpart (70.14G. 3a and b) which look very similar to the Rhynie chert genus *Rhynia*. For reasons outlined below, it was decided to erect a new genus for this type of compression fossil.

Also present are oval- and cigar-shaped spore masses.

All specimens are housed in the Department of Geology, National Museum of Wales, Cardiff.

Division TRACHEOPHYTA  
 Subdivision ZOSTEROPHYLLOPHYTINA Banks 1968  
 Family ZOSTEROPHYLLACEAE Kräusel 1938  
 Genus ZOSTEROPHYLLUM Penhallow 1892  
*Zosterophyllum* sp.

Plate 40, figs. 1, 4, 8, 9

*Material.* Two incomplete fructifications and their counterparts were found.

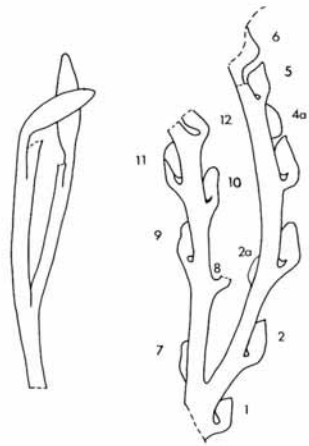
*Description.* Specimen 70.14G.1a originally consisted of an apparently single axis bearing sporangia, but removal of the matrix revealed a bifurcation in the base of the fertile region giving rise to an additional branch to the left of the original (Pl. 40, fig. 1). Part of the counterpart (70.14G.1b) showing two basal sporangia was found (Pl. 40, fig. 4). The fossil is preserved partly as a carbonaceous compression and partly as an impression stained with limonite. No structure is present. A drawing of the uncovered specimen, in which the numbers assigned to the sporangia correspond to those in Table 1, is given in text-fig. 2. The specimen is 35.0 mm long with the width of the fertile axis ranging between 1.0 mm and 2.7 mm immediately below the dichotomy.

The left-hand branch bears six widely spaced sporangia, alternately inserted, but in the right-hand one, five sporangia are attached to one side of the axis. The two remaining sporangia (2a and 4a) are almost completely covered by the axis. It seems probable that there is a two-rowed arrangement here also, but with the rows borne on the same side of the axis. This assumption is supported by the arrangement in specimen 70.14G.2a and b. Further uncovering is undesirable since the specimen is likely to break up. One sporangium occurs below the dichotomy.

The sporangia are borne on distinct stalks which are attached to the fructification axis at an acute angle though sometimes almost at a right angle. They are curved distally so that the sporangia are held upright with their long axes parallel to that of the fructification axis. In almost all cases the sporangia are seen in side view, with approximately one-half of one valve visible. This is because the valves are folded towards the axis. The majority of the sporangia are partially overlain by the fructification axis. This phenomenon was seen in *Zosterophyllum fertile* of Leclercq (1942) and in the new Scottish occurrence of that species (Edwards 1972).

A narrow border (0.1 mm wide) can be seen in some sporangia (e.g. 4 and 4a).

The second specimen 70.14G.2 is more compact (Pl. 40, figs. 8, 9). It is 14 mm long and bears six closely packed sporangia, which overlap each other and the



TEXT-FIG. 2. *Left:* *Salopella allenii* gen. et sp. nov. A composite drawing from part and counterpart (70.14G.3a and b),  $\times 3.3$ . *Right:* *Zosterophyllum* sp. A line-drawing of specimen 70.14G.1a with sporangial numbers corresponding to those in Table 1,  $\times 4.5$ .

TABLE 1. Dimensions of sporangia and stalks in *Zosterophyllum* sp. from the Welsh Borderland.

	No. (in text-fig. 2b)	Stalk (in mm)		Sporangium (in mm)	
		Max. length (outer margin)	Width	Height above stalk attachment	Width
Specimen 70.14G.1	1	2.0	0.6	1.3	0.9
	2	1.5	0.6	2.8	1.2*
	3	2.0	0.7	2.8	1.7*
	4	2.0	0.7	2.1	1.7*
	4a	..	..	2.5	..
	5	>1.0	0.9	2.3	1.7*
	6	..	..	..	1.7*
	7	2.0	0.8	..	..
	8	2.0	0.9	..	..
	9	1.5	0.9	2.0	0.8*
	10	1.3	0.5	2.0	1.2
	11	1.5	0.6	2.1	0.9*
12	1.2	0.4	..	1.2	
Specimen 70.14G.2 numbering from basal sporangium upwards	1	..	0.8	2.2	2.0†
	2	..	..	2.2	..
	3	..	..	2.1	2.0†
	4	..	..	2.0	1.1
	5	not uncovered	..	..	..
	6	1.2	0.8	2.2	1.5

\* Margin of value covered by axis.

† Face view.

fructification axis. Before development three sporangia could be seen. These were in side view as in 70.14G.1. Removal of the axis in the basal region has revealed two further sporangia, this time in face view. These alternate with the others.

A third sporangium in the upper region has not been uncovered. The uncovered sporangia are almost circular in outline and have a border *c.* 0.1 mm wide. They are illustrated in Plate 40, fig. 9. Thus this specimen also has two rows of sporangia, alternately arranged, but not borne on opposite sides of the axis. This is possibly similar to the arrangement of sporangia in the right-hand branch in 70.14G.1.

*Discussion.* Recent papers by one of us (Edwards 1969*a, b*, 1972) have illustrated the difficulties of identification of isolated compressed *Zosterophyllum* fructifications. The present specimens are no exceptions. Although the variation in sporangial arrangement has a parallel with *Zosterophyllum llanoveranum* (Croft and Lang 1942; Edwards 1969*a*) sporangial size, shape, and insertion are quite different. There is a superficial similarity with the plants described from the Breconian, called *Z. cf. fertile* (Edwards 1969*b*). They have in common the bifurcation at the base of the fertile region and type of sporangial insertion and arrangement. The difference in sporangial shape could be due to preservation. The sporangia are borne closer to the axis in the new specimens. In this respect they are intermediate between *Z. cf. fertile* and *Z. fertile*, where the stalks are at right angles to the axis and curve through 90° distally (Leclercq 1942). Indeed, the sporangia in face view are very similar to those illustrated by Leclercq. The Welsh Borderland specimens are again slightly larger than *Z. cf. fertile* and sporangium shape in side view is not identical. There is

no dichotomy in the fertile region in the Belgian plant. Leclercq found one specimen only, so there is no evidence for variation in sporangial arrangement. The new specimens are therefore thought possibly related to *Z. fertile*, but as differences exist should be left as *Zosterophyllum* sp. Schweitzer (personal communication, 1971) has been reinvestigating the Lower Devonian Rhenish flora. In addition to *Zosterophyllum rhenanum*, he has found a new type of fructification, which he will publish as a new *Zosterophyllum* species. This has many characteristics in common with both the Welsh Borderland and Brecon Beacons fructifications. It differs in that the sporangia do not appear to be folded in side view, so that the dehiscence line is visible.

Subdivision RHYNIOPHYTINA Banks 1968  
Family RHYNIACEAE Kidston and Lang 1920  
Genus SALOPELLA gen. nov.

*Type species.* *S. allenii* sp. nov.

*Derivation of name.* From Salop, an alternative name for the county of Shropshire.

*Diagnosis.* Plant consisting of naked dichotomously branching axes, preserved as compression fossils with terminal, probably erect fusiform sporangia containing miospores (probably isospores). Anatomy unknown.

*Salopella allenii* sp. nov.

Plate 40, figs. 2, 3; Plate 41, figs. 1-3

*Diagnosis.* Plant at least 24 mm high with naked dichotomously branching axes up to 2.0 mm wide in the basal regions and 1.1 mm wide below the sporangia. Branching angles small (c. 15°). Dichotomous branching immediately below sporangia, which are long and narrow; 2.0 mm at widest point in mid-region and up to 9.0 mm long. Spores azonate with thin exine variously covered with probable tapetal residue.

*Locality.* Newton Dingle, Brown Clew Hill, Shropshire. Exposures in banks of stream just below North Lodge Farm, in area known as The Gore (SO 58 60048295). Plant horizon, grey-green micaceous sandstone basal 5 cm with malachite flecks associated with grey-green siltstone. Overlain by brown sandstone with grey-green siltstone intercalation.

*Holotype.* Specimens 70.14G.3a and b, Department of Geology, National Museum of Wales, Cardiff.

*Derivation of name.* After J. R. L. Allen who took us to the locality.

*Description of material.* The generic and specific diagnoses are based on a single specimen and its counterpart. The axes are preserved as casts, but the sporangia are completely compressed. When the rock was split no sporangia were visible. Uncovering revealed two out of a probable four sporangia. (The two missing ones were probably lost in a rock sliver on splitting the rock.) Considering 70.14G.3a, the sporangium is erect, 9.0 mm long and tapering at base and apex. It attains a maximum width at its mid-point, where it is 2.0 mm wide. A dichotomy is seen 1.0 mm below the sporangium, but a line extends a further 3.5 mm beyond this along the centre of the axis. Because of the very narrow branching angle it is not known where the actual separation of the axes occurs. The axes above the dichotomy are considerably narrower than those below.

The second sporangium was uncovered on the counterpart (70.14G.3b). Here the sporangium is bent over because the axis immediately below it is curved. The sporangium again has a maximum width of 2.0 mm and is 7.0 mm long, but is incomplete at the apex because of irregular rock fracture. A reconstruction of the specimen is given in text-fig. 1a. There is no anatomy preserved in the axes, but spores have

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been isolated from the sporangia (Pl. 41, figs. 1-3). (The spores isolated from the sporangia 70.14G.3 are mounted on slides 70.14G.7 and 8.) These are simple and azonate; have a circular to subcircular amb; trilete mark indistinct but faint sutures are present and the exine is sometimes split along these rays. Exine thin, not exceeding  $1\ \mu\text{m}$  and usually less, secondary compression folds common; exine laevigate but usually partially, or entirely, covered by irregular elements, possibly tapetal residue. Size range 23 (29-7)  $37\ \mu\text{m}$ . Possibly curvatural thickenings are present but this is uncertain as preservation is poor. The thin nature of the wall, presence of possible tapetal material, and lack of features comparable to dispersed spores may be a reflection of immaturity.

*Discussion.* It is immediately obvious that this plant with its naked dichotomously branching axes and terminal sporangia has affinities with members of the Rhyniaceae. Of the genera listed by Banks (1968) it most closely resembles *Rhynia* itself and possibly *Hedeia*.

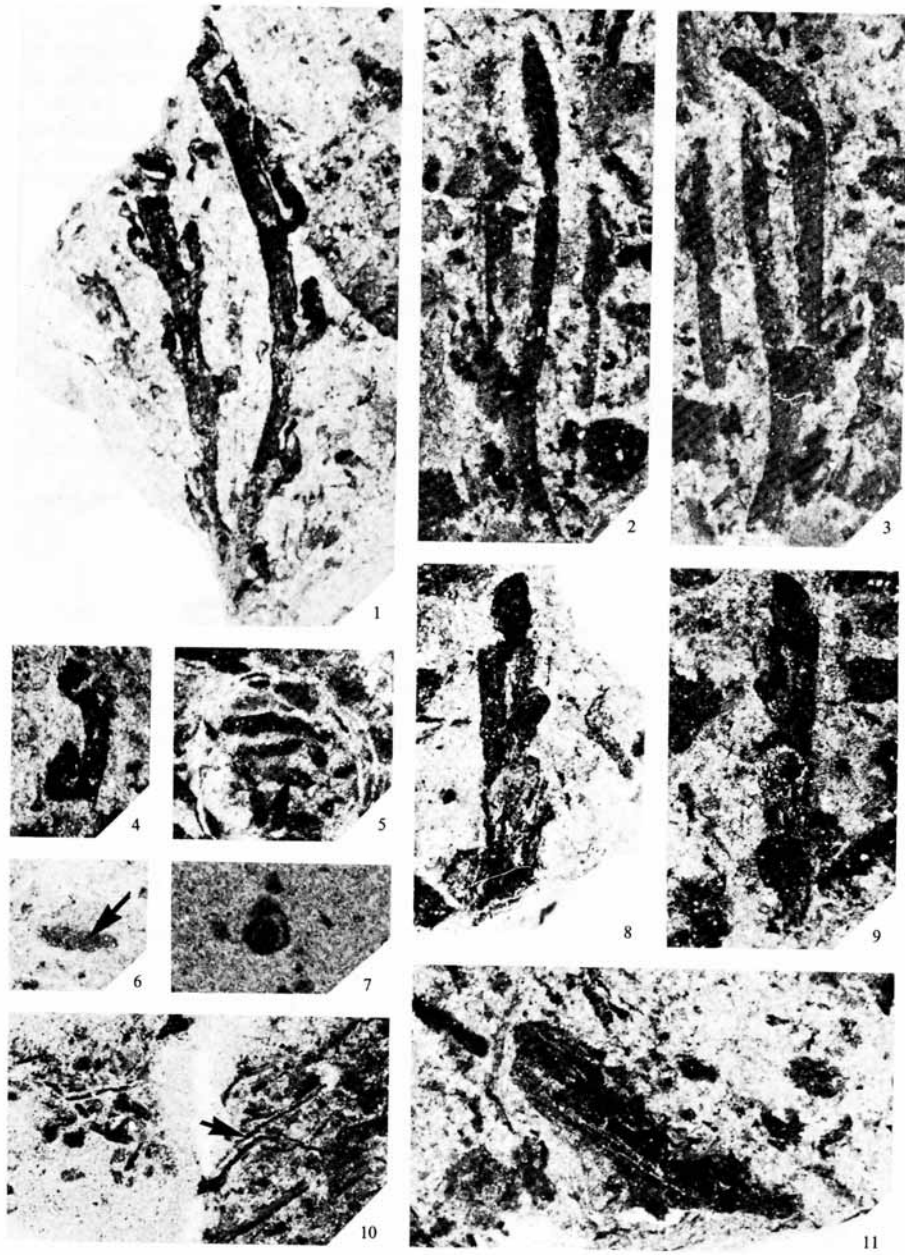
The remarkable preservation of the Rhynie chert petrification flora allows almost complete anatomical descriptions of the plant present. Comparison with compression fossils is therefore difficult, particularly when, as in this case, external shape is almost the only available diagnostic character. While sporangial shape and branching are similar to those in *Rhynia*, the absence of any anatomical data makes it impossible to assign the plant to that genus with any certainty. The axes dimensions are intermediate between the two *Rhynia* species (Kidston and Lang 1917, 1920), while the sporangia are perhaps slightly closer to *R. gwynne-vaughanii*. However, no hemispherical protuberances nor adventitious branching have been seen.

Spores have been previously described from two species of *Rhynia*, *R. gwynne-vaughanii* and *R. major* (A. A. Bhutta 1969, unpublished Ph.D. thesis, University of Wales) but no precise comparisons can be made because of the nature of the *Salopella* spore material. However, Bhutta's description of the spores of the *Rhynia* species reveals that both show retusoid characters but whereas the spores of *R. gwynne-vaughanii* show '... Curvaturae present in most of the specimens' in *R. major* spores '... Curvaturae have been noticed in only one specimen'. Also they appear to have a similar ornamentation to spores released by bulk maceration from the Newton Dingle sample which are here referred to the dispersed spore species *Perotrilites microbaculatus* Richardson and Lister 1969.

The dimensions of the sporangia and axes of *Hedeia corymbosa* (Cookson 1935) are similar to the Dittonian ones, but branching is much more frequent. In an Australian specimen of similar height, four or five dichotomies occur, producing a much-branched structure with some of the axes terminating in sporangia while the remainder are sterile. The comparable Dittonian specimen has only two dichotomies.

#### EXPLANATION OF PLATE 40

- Figs. 1, 4, 8, 9. *Zosterophyllum* sp. 1, fructification,  $\times 3.3$  (70.14G.1a). 4, fragment of counterpart illustrated fig. 1,  $\times 3.4$  (70.14G.1b). 8, 9, part and counterpart of a fragment of fructification. 8,  $\times 4.4$  (70.14G.2a). 9,  $\times 4.2$  (70.14G.2b).  
 Figs. 2, 3. Part and counterpart of fertile *Salopella*. 2,  $\times 2.5$ . 3,  $\times 2.8$  (70.14G.3a and b).  
 Figs. 5, 6. Compressed spore masses in plant debris (indicated by arrow on fig. 5). 5,  $\times 3.0$  (70.14G.4a). 6,  $\times 1.6$  (70.14G.4b).  
 Fig. 7. Isolated circinate tip,  $\times 3.5$  (70.14G.5).  
 Fig. 10. Narrow sterile axes (indicated by arrow),  $\times 1.8$  (70.14G.6).  
 Fig. 11. Debris with *Prototaxites* sp., showing longitudinal striations,  $\times 2.9$  (70.14G.2a).



EDWARDS and RICHARDSON, Lower Devonian plants



tomies with a possible maximum of four sporangia, although, of course, the specimen could be part of a much larger branching system. The shapes of the sporangia in Cookson's illustrations are not clearly seen and the sporangia are often incomplete. Thus it is considered unwise to place the new Dittonian fossils in either *Rhynia* or *Hedeia*. Furthermore, it is thought there is a need to erect a new genus to accommodate this type of organization in a compression fossil. The specimens named *Rhynia major* by Ishchenko (1969) might also be placed in this genus as there was no anatomical justification for her identification (Banks 1972).

INCERTAE SEDIS (?Algae)  
Genus PROTOTAXITES (Dawson 1859)

Longitudinally, but irregularly, furrowed axes, up to 35.0 mm wide are commonly found (Pl. 40, fig. 11). On maceration, longitudinally running tubes are recovered. The fossils are therefore assigned to the genus *Prototaxites*, but specific identification is impossible. Sections through small fragments reveal large, but not small, tubes. The plant frequently occurs as irregularly shaped, heavily carbonized flakes, scattered among plant axes and animal fragments.

*Pachytheca*, although usually common in the Welsh Borderland Lower Devonian, has not been recorded from this locality.

DESCRIPTION OF MICROFLORA

*Description of spore masses and spores, occurring as compression fossils*

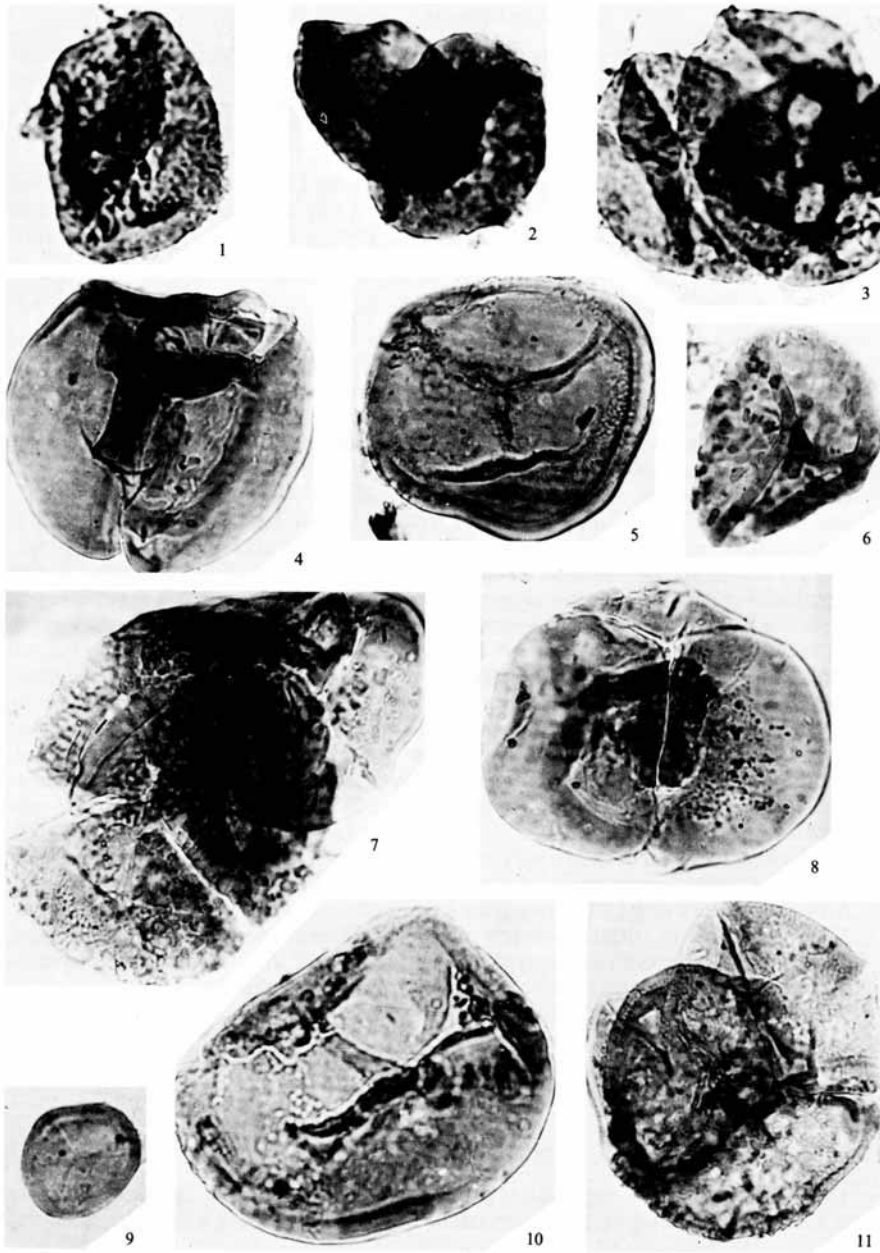
Some of the small fragments of carbonaceous material, abundant in the matrix, have a more definite outline and fusiform shape. Typical examples are illustrated in Plate 40, figs. 5, 6. When the black powdery material is cleared with Schulze's solution, spore masses are recovered but the majority are either fused together or too poorly preserved to be illustrated.

EXPLANATION OF PLATE 41

All magnifications  $\times 1000$  except where stated otherwise. Instrument settings for Zeiss Photomicroscope No. 4709856.

- Figs. 1-3. Spores from sporangia of *Salopella*. 1, slide 70.14G.7/1701099 showing irregular, possibly tapetal, residue loosely adhering to a smooth exine. 2, slide 70.14G.7/1251025, two spores showing nature of possible tapetal residual. 3, slide 70.14G.8/1371100, tetrad; all these spores possibly represent an immature stage since exactly comparable forms have not been seen in dispersed spore assemblages.
- Figs. 4-10. Spores recovered from spore mass after bulk maceration. 4, slide 70.14G.9/1281049, spores similar to the dispersed spore species *Archaeozontriletes chulus* var. *chulus* showing curvatural thickenings. 5, slide 70.14G.10/1621069, cf. *Ambitisporites dilutus*. 6, slide 70.14G.11/1411151, cf. *Ambitisporites avitus* partially covered by 'tapetal' residue. 7, slide 70.14G.9/1601093, cf. *Archaeozontriletes chulus* with tapetal residue. 8, slide 70.14G.9/1921062,  $\times 750$ , tetrad cf. *A. chulus* showing equatorial crassitude (thickening). 9, slide 70.14G.9/1001045, tetrad of *Perotriletes microbaculatus* showing fine granulate sculpture. 10, slide 70.14G.12/1201106, lateral view of specimen of *A. chulus* showing relatively thin proximal surface.
- Fig. 11. Isolated spore found after bulk maceration, slide 70.14G.13/1131086,  $\times 500$ , cf. *Ambitisporites dilutus*.





EDWARDS and RICHARDSON, Lower Devonian spores

Two of these spore masses picked from the rock yielded essentially similar spores (preparations 70.14G.14 and 15) which can be assigned to the dispersed spore genus *Ambitisporites* Hoffmeister 1959 and are of considerable interest because they are similar to *A. dilutus* (Hoffmeister) one of the first, if not the first, trilete land plant spore to appear in the geological record.

Hoffmeister's spores are now regarded as middle Llandovery in age (based on a reassessment of the graptolites by Berry, see Gray and Boucot 1971). The size range of the Newton Dingle spores is 32–44  $\mu\text{m}$  compared with 30–60  $\mu\text{m}$  for Hoffmeister's spores.

#### *Spore masses released by bulk maceration*

Both spore masses and spores were released by bulk maceration. Some of the best-preserved spores were from the spore masses which revealed spores of three types. The spores are assigned to the dispersed spore species *Perotrilites microbaculatus* Richardson and Lister 1969 (preparations 70.14G.11 and 9), spores with a thick exine and a microbaculate-granulate 'perispore'; *Archaeozonotriletes chulus* (Cramer) 70.14G.16, size range 49–78  $\mu\text{m}$ , laevigate spores with a thin diaphanous proximal surface and a broad equatorial crassitude; and *Ambitisporites dilutus* 70.14G.17, size range 40–49  $\mu\text{m}$ , laevigate spores with a narrow equatorial crassitude. It is possible that only one species is present and all the spores may come from one parent plant. Firstly, *Archaeozonotriletes chulus* and *Ambitisporites* cf. *dilutus* both have an equatorial crassitude and may intergrade and, secondly, these spores may represent the inner bodies of the spores assigned to *P. microbaculatus*. The inner bodies of the latter although imperfectly seen through the 'perispore' are laevigate with thick distal walls and an equatorial crassitude similar to spores assigned to the *Ambitisporites-Archaeozonotriletes chulus* complex.

The spore species mentioned above also form a prominent part of the dispersed spore assemblage which is dominated by laevigate spores. Species recorded in addition to those mentioned above are *Retusotriletes warringtonii*, *R.* cf. *minor*, *Apiculiretusispora microconus*, *A.* cf. *spicula*, *Acinosporites salopiensis*, and one specimen of *Emphanisporites*, *E.* cf. *micronatus* (see Richardson and Lister 1969). The total assemblage is thus a very restricted one consisting of a total of nine species compared with twenty-seven species recorded from the middle Ditton Group. A further feature is the strikingly poor representation of the genus *Emphanisporites*. The species present, although clearly unrepresentative of the spore flora of the upper part of the Ditton Group, are typically Dittonian and show no specific differences with previously described Dittonian spores from lower horizons.

It is noteworthy that the number of dispersed spore species identified is small compared with the number of species from a good siltstone or shale assemblage. This paucity of species and lack of variety is probably largely preservational and/or depositional due to the coarseness of the sediment and sorting factors.

#### GENERAL DISCUSSION

This flora is of interest because it is the first detailed record from the Dittonian rocks of the Welsh Borderland. It is intermediate in age between Lang's Downtonian floras

(Lang 1937) and the very extensive Senni Bed floras of South Wales (Croft and Lang 1942; Edwards 1970a). Lang's plants were found at various localities in Pembrokeshire and the Welsh Borderland ranging through King's horizons I1-I8. He described *Prototaxites*, *Pachytheca*, *Nematothallus*, *Parka*, two *Cooksonia* species, and cf. *Zosterophyllum myretonianum*, the last two genera having most significance for this account. The age of the rock in which the *Zosterophyllum* specimen (represented by an H-branch) was found is uncertain. Lang considered it to be from the I8 horizon, i.e. from the upper Downtonian of Caldy Island, Pembrokeshire, but it is possible that it comes from younger rocks. Our own collections from Lower Dittonian localities have so far yielded *Parka*, *Pachytheca*, and *Prototaxites*. Dichotomous branching predominates in the presumed vascular axes and there is a noticeable increase in axis diameter in younger rocks. This new Dittonian flora, possibly lower Siegenian, contains *Zosterophyllum* and *Rhynia* ( $\equiv$  *Cooksonia*) types of organization and therefore shows little advance on the Downtonian assemblages. In contrast, the Breconian floras of neighbouring South Wales are strikingly different, including members of the Rhyniophytina, *Zosterophyllophytina*, *Lycophytina*, *Trimerophytina*, and *Barinophytaceae*. As it is not yet known to what extent the Newton Dingle assemblage is representative of the upper Dittonian flora of the region, a discussion of the evolutionary significance of these differences is perhaps premature.

Unfortunately there are very few floras of identical age in other parts of the world which could be used for comparison. That described by Leclercq (1942) from Belgium, containing *Hostimella*, *Taeniocrada decheniana*, and *Zosterophyllum fertile* is possibly the only one. Strel (1967) gives its age as lowermost Siegenian. It is interesting that the types of plant present are similar to those in the Newton Dingle assemblage. The slightly younger lower Siegenian floras described by Stockmans (1940) are more extensive including *Psilophyton*, *Drepanophycus*, and *Sporogonites* species (Strel 1967). These, together with the Siegenian floras of Germany, have more in common with the Breconian floras of South Wales (Edwards 1970a). The floras from Canada, U.S.A., Australia, and most of the U.S.S.R. (Chaloner 1970; Petrosyan 1968) are also much younger.

Earlier Gedinnian floras have been reported from Scotland, Czechoslovakia, and Spitzbergen. A rather restricted flora dominated by *Zosterophyllum myretonianum* (Lang 1927), *Prototaxites* species (Lang 1926), and *Parka decipiens* (Don and Hickling 1915) occurs in the Dundee formation in the Arbuthnott group of the Lower Old Red Sandstone (Dittonian) (Armstrong and Paterson 1970). More recently, two further species, *Cooksonia caledonica* (Edwards 1970b) and *Zosterophyllum fertile* (Edwards 1972) have been described. Thus, during the Gedinnian times in Scotland, two basic types of vascular plant organization have emerged, naked dichotomously branching axes with terminal sporangia and naked axes with lateral sporangia, aggregated into terminal spikes. A similar pattern is seen in the Gedinnian of Spitzbergen (Høeg 1942; Friend 1961) where the assemblage includes *Pachytheca*, *Prototaxites*, *Taeniocrada*(?) *spitzbergensis*, and sterile *Zosterophyllum* sp. In the Gedinnian of Czechoslovakia, however, only the *Cooksonia* type of organization is present (Obrhel, 1968).

A further plant *Taeniocrada decheniana* Kräusel and Weyland is recorded from

probable Gedinnian rocks in Germany (Schmidt and Teichmüller 1954). Here somewhat recurved sporangia are borne in terminal clusters and Banks (1968) places the plant with *Cooksonia* in the Rhyniophytina. As Chaloner (1970) points out, the sporangia may be regarded as terminal on overtopped lateral branches and may perhaps be considered as intermediate between the two basic types of organization.

The preceding Downtonian floras are admirably summarized by Banks (1972) who emphasizes that the only vascular plants present at this time were members of the Rhyniophytina.

In conclusion, therefore, on the limited evidence at present available, the uppermost Gedinnian-basal Siegenian floras have more in common with the earlier Gedinnian floras than with later Siegenian ones, and that soon after the beginning of the Siegenian great diversification occurred, resulting in the extensive and varied floras of later Siegenian times.

#### *Miospore assemblages*

So far, the volume of work on miospore assemblages is not great for the early part of their record in the Silurian and Lower Devonian. However, published data from the British Isles, Canada, western Europe, North Africa, and the U.S.S.R. is consistent in showing the same trends of development with closely similar spore assemblages occurring in strata of the equivalent age from these different areas. The assemblages show the gradual increase in diversity of miospores from their first appearance in the Silurian (Llandovery, or possible Middle Ordovician if the records of *Stenozonotriletes* Timofeev (Timofeev 1963a, b) prove to be trilete spores), through Wenlockian, Ludlovian, Downtonian, and Gedinnian. These assemblages are dominated by small simple spores or spores with a narrow equatorial crassitude but show a progressive increase in the variety of sculptural types present, the increase in diversity of the dispersed spore genus *Emphanisporites* and the temporary appearance of proximal inter-radial papillae in several genera. This latter feature appears in the Downtonian and reaches an acme in the Gedinnian, but rapidly declines in the Siegenian and does not reappear until the Carboniferous when it is a feature of some lycopod spores.

Siegenian spore floras show an increase in size with the incoming of more robust-ribbed *Emphanisporites*, they also show the waning of tripapillate spores and an increasing diversity and mean size of spore species, and the genus *Dibolisporites* makes its first appearance. In the Anglo-Welsh area these changes take place in the Senni beds (lower Siegenian), e.g. the spores from the Storey Arms quarry show these characteristics.

While the most striking change in the Lower Devonian sequence of spore assemblages occurs higher in the succession in beds of Emsian age where in several areas, e.g. Germany (Lanninger 1968; Riegel 1968) and Canada (McGregor 1967) there is a sudden change to spore floras of Middle Devonian aspect, there also seems to be a change of lesser but still of considerable importance somewhere near the Gedinnian and Siegenian boundary. However, since very little has been published on the Siegenian, and this stage represents a considerable period of time, it is too early to be precise. Nevertheless, the changes outlined above for the Anglo-Welsh area seem to reflect a general floral change for the period since it apparently occurs in several

areas, e.g. Canada (McGregor *et al.* 1970), Belgium (Streeel 1967), and North Africa (Jardiné and Yapaudjian 1968).

*Acknowledgements.* We are particularly grateful to Professor J. R. L. Allen for leading us to this and to several other localities in the Welsh Borderland. Dianne Edwards was supported by a University of Wales Fellowship, and is indebted to Professor G. F. Asprey for research facilities at University College, Cardiff. J. B. Richardson gratefully acknowledges financial support from the Natural Environment Research Council to provide a Research Assistant and a Zeiss photomicroscope. He is also indebted to Dr. N. Ioannides for the photography.

## REFERENCES

- ALLEN, J. R. L. and TARLO, L. B. 1963. The Downtonian and Dittonian Facies of the Welsh Borderland. *Geol. Mag.* **100**, 129–155.
- HALSTEAD (TARLO), L. B. and TURNER, S. 1968. Dittonian ostracoderm fauna from the Brownstones of Wilderness Quarry, Mitcheldean, Gloucestershire. *Proc. Geol. Soc. London*, **1649**, 49, 141–153.
- ARMSTRONG, M. and PATERSON, I. B. 1970. The Lower Old Red Sandstone of the Strathmore region. *Inst. Geol. Sci. Rept.* **70** (12), 1–23.
- BALL, H. W. and DINELEY, D. L. 1961. The Old Red Sandstone of Brown Clee Hill and the adjacent area. *Bull. Brit. Mus. (Nat. Hist.), Geol.* **5**, 177–242.
- BANKS, H. P. 1968. The early history of land plants. Pp. 73–107. In DRAKE, E. (ed.), *Evolution and Environment*.
- 1972. The stratigraphic occurrence of early land plants. *Palaeontology*, **15**, 365–377, 1 pl.
- CHALONER, W. G. 1970. The rise of the first land plants. *Biol. Rev.* **45**, 353–377, 3 pls.
- COOKSON, I. C. 1935. On plant remains from the Silurian of Victoria, Australia, that extend and connect floras hitherto described. *Phil. Trans. Roy. Soc. London*, **225B**, 127–148, 2 pls.
- CROFT, W. N. 1953. Breconian: a stage name of the Old Red Sandstone. *Geol. Mag.* **90**, 429–432.
- and LANG, W. H. 1942. The Lower Devonian flora of the Senni Beds of Monmouthshire and Breconshire. *Phil. Trans. Roy. Soc. London*, **231B**, 131–163, 3 pls.
- DAWSON, J. W. 1859. On fossil plants from the Devonian rocks of Canada. *Quart. J. Geol. Soc. London*, **15**, 477–488.
- DON, A. W. R. and HICKLING, G. 1915. On *Parka decipiens*. *Ibid.* **71**, 648–666, 3 pls.
- EDWARDS, D. 1969a. Further observations on *Zosterophyllum llanoveranum* from the Lower Devonian of South Wales. *Amer. J. Bot.* **56**, 201–210, 3 pls.
- 1969b. *Zosterophyllum* from the Lower Old Red Sandstone of south Wales. *New Phytol.* **68**, 923–931, 2 pls.
- 1970a. Further observations on the Lower Devonian plant *Goslingia breconensis* Heard. *Phil. Trans. Roy. Soc. London*, **258B**, 225–243, 5 pls.
- 1970b. Fertile Rhyniophytina from the Lower Devonian of Britain. *Palaeontology*, **13**, 451–461, 4 pls.
- 1972. A *Zosterophyllum* fructification from the Lower Old Red Sandstone of Scotland. *Rev. Palaeobotan. Palynol.* **14**, 77–83, 1 pl.
- FRIEND, P. F. 1961. The Devonian stratigraphy of north and central Vestspitzbergen. *Proc. York. Geol. Soc.* **33**, 77–118.
- GRAY, J. and BOUCOT, A. J. 1971. Early Silurian spore tetrads from New York: Earliest New World evidence for vascular plants? *Science*, **173**, 918–921, 2 figs.
- HØEG, O. A. 1942. The Downtonian and Devonian flora of Spitzbergen. *Norges. Svalbard Ishavs-Undersøk.* **83**, 1–228, 62 pls.
- HOFFMEISTER, W. S. 1959. Lower Silurian plant spores from Libya. *Micropaleontology*, **5**, 331–334, 1 pl.
- ISHCHENKO, T. A. 1969. The *Cooksonia* palaeoflora in the Skala horizon of Podolia and its stratigraphical significance. *Geol. J. (Kiev)*, **29**, 101–109, 10 figs. [In Russian.]
- JARDINÉ, S. and YAPAUDJIAN, L. 1968. Lithostratigraphie et palynologie au Dévonien–Gothlandieu gréseux du bassin de Polignac (Sahara). *Rev. Inst. Fr. Petrol.* **23**, 439–468.

- KIDSTON, R. and LANG, W. H. 1917. On Old Red Sandstone plants showing structure, from the Rhynie Chert bed, Aberdeenshire, Part I. *Rhynia Gwynne-Vaughani*, Kidston and Lang. *Trans. Roy. Soc. Edinburgh*, **51**, 761-784, 10 pls.
- 1920. Part II. Additional notes on *Rhynia Gwynne-Vaughani* Kidston and Lang; with descriptions of *Rhynia major*, n.sp. and *Hornea lignieri* n.g., n.sp. *Ibid.* **52**, 603-627, 10 pls.
- LANG, W. H. 1926. Contributions to the study of the Old Red Sandstone Flora of Scotland. V. On the identification of the large 'stems' in the Carmyllie Beds of the Lower Old Red Sandstone as *Nemato-phyton*. *Ibid.* **54**, 792-799, 2 pls.
- 1927. VI. On *Zosterophyllum myretonianum* Penh., and some other plant remains from the Carmyllie Beds of the Lower Old Red Sandstone. *Ibid.* **55**, 443-452, 2 pls.
- 1937. On the plant-remains from the Downtonian of England and Wales. *Phil. Trans. Roy. Soc. London*, **227B**, 245-291, 7 pls.
- LANNINGER, E. P. 1968. Sporen-Gesellschaften aus dem Ems der S.W. Eifel. *Palaontographica* (B), **122**, 95-170, 7 pls.
- LECLERCQ, S. 1942. Quelques plantes fossiles recueillies dans le Dévonien inférieur des environs de Nonceveux (Bordure orientale du bassin de Dinant). *Ann. Soc. Géol. Belg. Bull.* **65**, 193-211, 3 pls.
- MCGREGOR, D. C. 1967. Composition and range of some Devonian spore assemblages of Canada. *Rev. Palaeobot. Palynol.* **1**, 173-183, 1 pl.
- SANDFORD, B. V. and NORRIS, A. W. 1970. Palynology and correlation of Devonian formations in the Moose River basin, northern Ontario. *Proc. Geol. Ass. Canada*, **22**, 45-54, 2 pls., 3 figs.
- OBRHEL, J. 1968. Die Silur- und Devonflora des Barrandiums. *Paläont. Abh. B*, **2**, 635-701, 5 pls.
- PENHALLOW, D. P. 1892. Additional notes on Devonian plants from Scotland. *Can. Record Sci.* **5**, 1-16, 2 pls.
- PETROSYAN, N. M. 1968. Stratigraphic importance of the Devonian flora of the U.S.S.R. Pp. 579-586. In OSWALD, D. H. (ed.), *Internat. Symposium on the Devonian System, Calgary, Canada, 1967*, **1**.
- RICHARDSON, J. B. and LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and south Wales. *Palaontology*, **12**, 201-252, 7 pls.
- RIEGEL, W. 1968. Die Mitteldevon-flora von Lindlar (Rheinland) 2. Spores dispersae. *Palaontographica* (B), **123**, 76-96, 5 pls.
- SCHMIDT, W. and TEICHMÜLLER, M. 1954. Pflanzen-Reste aus dem Gedinne des Hohen Venns. *Geol. Jb.* **69**, 89-102, 2 pls.
- STOCKMANS, F. 1940. Végétaux éodévoniens de la Belgique. *Mém. Mus. roy. Hist. nat. Belg.* **93**, 1-90, 14 pls.
- STREEL, M. 1967. Associations de spores du Dévonien inférieur Belge et leur signification stratigraphique. *Ann. Soc. Géol. Belg. Bull.* **90**, 11-54, 5 pls.
- TIMOFEEV, B. V. 1963a. Ordovician and Silurian phytoplankton of the Siberian Platform. *Doklady Akad. Nauk SSSR*, **149**, 399-402.
- 1963b. Phytoplankton and dispersed spores of the Ordovician, Silurian and Lower Devonian of the Baltic region, the Gory Swietokvzyskie and Podolia. *Ibid.* **150**, 158-161.
- WHITE, E. I. 1950. The vertebrate faunas of the Lower Old Red Sandstone of the Welsh Borders. *Bull. Brit. Mus. (Nat. Hist.) Geol.* **1**, 51-67.
- 1956. Preliminary note on the range of pteraspids in Western Europe. *Bull. Inst. roy. Sci. nat. Belg.* **32**, 1-10.

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Revised typescript received 15 May 1973