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Evolution and Environment in the Late Silurian-Early Devonian: The Rise of the Pteridophytes [and Discussion]

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Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes

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[Plate 1]

A brief review of the major advances since 1979 in Silurian and Devonian palaeobotany is followed by a preliminary report on a Gedinnian assemblage from the Welsh Borderland. This is dominated by rhyniopsids and includes several species of *Cooksonia* and *Salopella*. Spores have been isolated from a number of taxa. The assemblage is used to illustrate the problems of recognition and classification of early vascular plants. Parallel sedimentological and palaeogeographical studies permit speculation on the ecology and life histories of the plants that colonized the Old Red Continent. It is concluded that the lack of well preserved and independently dated assemblages from elsewhere in the world (an exception being the *Baragwanathia* flora of Australia) prevents the detection of any provincialism in the late Silurian and early Devonian and makes generalizations on the early history of vascular plants premature.

Introduction

Such is recent interest in the colonization of land surfaces and the early evolution of vascular plants that the record of megafossils in the late Silurian and early Devonian is already well documented (for example, Gensel & Andrews 1984). We will therefore briefly review the major palaeobotanical advances of the last five years and describe some new research on a Gedinnian locality in the Welsh Borderland to illustrate both the nature of the problems encountered in the investigation of early pteridophytes and the possibilities for an integrated approach.

The description of the Rhynie Chert plants, arguably the most important single contribution to studies of the history of vascular plants, revolutionized concepts of early pteridophytes, and was followed by 50 years of accumulation of data from fragmentary and far less informative compression fossils in Silurian and Devonian allochthonous sediments. The accrued data were summarized and ordered by Banks (1968, 1975*a*) when he reclassified the psilophytes. Such a *fait accompli* might well have stunted progress but Banks opened another Pandora's box and provided the impetus for further even more critical investigation and extensive debate in two papers (1975*b*, 1975*c*) concerning the acceptable evidence for the existence of vascular plants. The ensuing controversy has been considerably invigorated by Gray and Boucot, whose publications although mainly involving microfossils, have done much to focus attention on the diverse nature of early land vegetation and to challenge conclusions on land plant evolution centred on evidence from the northern hemisphere (Gray & Boucot 1977, 1978; Boucot & Gray 1982; Gray *et al.* 1982; Edwards *et al.* 1979; Taylor 1982; Thomas 1984).

The biostratigraphic potential of Siluro-Devonian plants was reviewed by Chaloner & Sheerin (1979) and Banks (1980), who proposed seven biozones or generic assemblages. The three zones relevant to this account are:

zone I, *Cooksonia* Zone: late Ludlow to Přídolí;
zone II, *Zosterophyllum* Zone: Gedinnian to middle Siegenian;
zone III, *Psilophyton* Zone: middle Siegenian to Emsian.

The scheme was adopted by Chaloner and Sheerin, who cited the ranges of further genera, added their geographical occurrences and outlined the major features of Devonian vascular plant phylogeny. They also developed Chaloner's alternative biostratigraphy (Chaloner 1970) in which the first appearances of anatomical and morphological characteristics (for example, spiral tracheids, stomata, elongate sporangia, microphylls) were plotted stratigraphically. Such plant megafossil zonation was complemented by McGregor's on miospores (McGregor 1979) in which he recorded the stratigraphical ranges of species and made a preliminary attempt at correlation. For the vast majority of the spores cited, the parent plants remain unknown (see, however, Allen 1980; Gensel 1980), but some progress has been made to the understanding of their life cycles (Remy 1982). Remy & Remy (1980) described a gametophyte *Lyonophyton rhyniensis* with plausible antheridia, but less convincing archegonia from the Rhynie Chert. On the grounds of anatomical and morphological similarities and from association, they tentatively related it to *Horneophyton*. They also revived earlier suggestions that *Sciadophyton*, a rosette-like plant widespread on the Old Red Continent, was also a gametophyte (Remy *et al.* 1980). Schweitzer (1983) associated *Sciadophyton* with *Taeniocrada langi* and *Zosterophyllum rhenanum* and produced an illustrated account of the life cycle of the latter. What little is known about Siluro-Devonian palaeoecology and vegetation was summarized by Edwards, D. (1980): more recently Schweitzer (1983) has reconstructed Lower Devonian coastal vegetation based on a locality in the Rhineland.

Since 1980, there have been several descriptions of taxa and new assemblages (Gerrienne 1983 (Emsian, Belgium); Edwards *et al.* 1983 (Wenlock, Ireland); Doran 1980 (Emsian, Canada); Tims & Chambers 1984 (Ludlow, Australia); Geng Bao-yin 1983 (Siegenian, China); Li Cheng-sen 1982 (Emsian, China)), additions to existing ones (Gensel 1982*a*, *b* (Emsian, Canada); Hueber 1983 (Emsian, Canada)) and critical, anatomical and morphological reinvestigations of more familiar species (Cai & Schweitzer 1983 (*Zosterophyllum yunnanicum*); Hueber 1982 (*Taeniocrada dubia*); Edwards, D. S. 1980 (*Rhynia gwynne-vaughanii*); Rayner 1983 (*Sawdonia ornata*); Schweitzer 1980 (*Drepanophycus spinaeformis*); Zacharova 1980 (*Margophyton* (Psilophyton) *goldschmidtii*)). Richardson, McGregor, Streel, Riegel and co-workers have continued their detailed palynological analyses and correlation of marine and continental sediments of the Old Red Continent with the intention of producing a spore-based zonation for the Siluro-Devonian (for example, Richardson *et al.* 1981, 1982). Such studies allow more precise stratigraphic documentation of important plant megafossil assemblages and have modified (usually extended) the ranges of many of the genera cited by Banks (1980) and Chaloner & Sheerin (1979). For example, the Breconian Senni Bed assemblage from the Old Red Sandstone of S Wales (Croft & Lang 1942; Edwards 1970*a*) including *Dawsonites arcuatus*, *Gosslingia breconensis* and *Krithodeophyton croftii*, is now considered early Siegenian (Richardson *et al.* 1982) and the ranges of *Gosslingia* and *Krithodeophyton* have been extended by their discovery in Gerrienne's basal Emsian assemblage from Belgium. Of greater phylogenetic significance are records of *Calamophyton* in the late Emsian of Belgium (Lessuise & Fairon-Demaret 1980), *Drepanophycus spinaeformis* in the late Gedinnian of Germany (Schweitzer 1980) and *Baragwanathia abitibiense* (Hueber 1983) from the Emsian of Canada.

Considering the two floral–faunal paradoxes discussed by Chaloner & Sheerin, where faunal evidence suggests an older age than that indicated by the plants, Garratt & Rickards (1984) have reiterated the evidence (graptolites, field relationships, the presence of unquestioned Ludlow assemblages elsewhere in the area) for a Ludlow age for the Lower Plant Assemblage containing *Baragwanathia longifolia*, various Rhyniopsida and Zosterophyllopsida from Victoria, Australia. The authors considered the possibility that certain types of monograptids persisted into the Devonian, but could not match their specimens with post Ludlow forms. Professor H. Jaeger who originally recognised the graptolites in the Upper Plant Assemblage as Devonian species (Jaeger 1966) has also examined the new specimens and identified *Bohemograptus bohemicus* and *Monograptus* ex gr. *uncinatus* respectively for Rickards' identifications of *B. bohemicus* and *M.* aff. *uncinatus* (B. Rickards, personal communication.) No further progress has been made in dating the Libyan assemblage of lycopods and some extremely fragmentary fossils assigned to *Psilophyton* (Klitzsch *et al.* 1973). Boucot & Gray (1982) remain of the opinion that they are Llandovery or possibly Wenlock, although A. Lejal-Nicol (personal communication) considers them to be probably younger.

Evolution and environment in the early Devonian: a palaeobotanical case history from the Old Red Continent

We accept the criticism that many of the conclusions relating to the phylogeny of early vascular plants are based on fragmentary fossils from widely distributed and rarely coeval localities concentrated on the Old Red Continent (North Atlantic Realm; Boucot & Gray 1982) and appreciate that the chances of the earliest land plants becoming preserved as megafossils are extremely low. We therefore agree that the timing of the invasion of the land may well be best documented by microfossils that reflect anatomical adaptations to the land environments, but point out that the affinities of the plants that produced these microfossils remain conjectural and their gross organization unknown. While aware that the land colonization and possibly the origin of vascular plants occurred before any Old Red Sandstone sediments were deposited in Europe, we consider that the Siluro-Devonian strata of the Old Red Continent provide an excellent opportunity to trace the early stages in the colonization of a major land-mass (Edwards 1979*a*). Whether such events reflect contemporary plant history in other parts of the world or whether they represent successive migrations, evolution having occurred elsewhere, will only be resolved by the collection and description of new assemblages with well-documented stratigraphy: investigations of the type currently being undertaken in Australia (Garratt & Rickards 1984; Tims & Chambers 1984).

The first detailed account of megafossils from the Anglo-Welsh region was Lang's classic paper on Downton (Přídolí) assemblages (1937). We have collected from Lang's localities and extended the project into Ludlow strata from S Wales. All the megafossil assemblages are dominated by rhyniopsids or rhyniophytoids (plants of the aspect of rhyniopsids, but lacking proven tracheids) (Pratt *et al.* 1978) with an increase in numbers of taxa accompanied by a very slight increase in diversity towards the end of the Silurian (Edwards 1979*b*; Edwards & Davies 1976; Edwards & Rogerson 1979; Edwards *et al.* 1979). We present here an analysis of plants and sediments from an early Gedinnian locality, Targrove Quarry on the drive leading to Downton Hall near Ludlow. It is of some historical interest in that it was from here that Lang (1937) described *Cooksonia hemisphaerica* and illustrated *in situ* tracheids in an associated axis (Edwards *et al.* 1979). He considered the strata to be part of the uppermost Downton, but Ball & Dinely (locality 105, 1961) map it 175 feet (*ca.* 60 m) above the main 'Psammosteus' limestone in the lower group of the Ditton Series, which on the basis of fish and spores (J. B. Richardson, personal communication) correlates with the Gedinnian of Europe. Records of *Traquairaspis symondsi* and *Pteraspis rostrata* var. *trimpleyensis* place the exposure towards the base of the *crouchi* Zone in the Dittonian. The sediments are typical of the distal alluvial facies of the Old Red Sandstone (Allen 1979). At certain horizons (see below) bedding planes are almost completely covered by fragments of axes, occasionally terminating in sporangia, and patches of organic material some of which may be of animal origin. In this account we concentrate on the plants with axial organization, which are considered pteridophytes in that some contain tracheids and are homosporous (but see below, Discussion). Also present are spheres of *Pachytheca*, rounded billets of *Prototaxites* and black films of irregular outline covered by *Nematothallus* cuticles. The abundance of the latter suggests that the parent plant was an important part of terrestrial vegetation in the early Devonian, but we know little of its gross morphology and affinities (Edwards 1982; Edwards & Rose 1984).

Preservation, techniques and descriptions of plants

The fossils are coalified compressions: cells are sometimes visible on the surface and are most conspicuous when infilled with limonite. In one or two instances only, *in situ* tracheids have been observed in this form of preservation. Cellulose nitrate film pulls were prepared from axes and sporangia. The former occasionally show fragments of cuticle, with outlines of epidermal or cortical cells, but never stomata. Spores isolated on film pulls were examined by light and scanning electron microscopes.

Sterile axes

These are fragmentary, rarely more than 30 mm long and 2.0 mm wide. Most are parallel-sided, smooth and unbranched. One isolated circinate tip has been found (figure 16, plate 1). A few axes branch dichotomously (*Hostinella*); asymmetric branching is rare. One displays a K-branch (figure 15) characteristic of *Zosterophyllum*. Figure 14 shows a striated axis with one row of small blunt teeth. Some of the axes bear a central darker line, but as yet we have failed to isolate any tracheids.

Fertile specimens

Most are fragmentary, comprising a short, unbranched, smooth axis with a single terminal sporangium. A few specimens show dichotomous branching either in the base of the sporangium itself or in the axial system. Sporangia fall into three major categories; short and wide, elongate, and bifurcate.

Short, wide sporangia

The majority of sporangia terminate short lengths of unbranched axis, a few, dichotomously branching axes and, in two more complete specimens, sporangia, are borne terminally on lateral branches. These will be described first.

V. 58024. The complete specimen, 30 mm long, comprises a ‘main’ axis, 0.6 mm wide, which at the base has divided equally to produce by overtopping a ‘lateral’ branch system (figure 6). The latter displays two further dichotomies, with one branch terminating in an almost complete oval sporangium, 2.4 mm wide and 1.8 mm high, with narrow distal border and probably convex junction with subtending axis.

V. 58013. This specimen (7.5 mm long) also shows overtopping; two closely spaced dichotomies near the base result in a trifurcation in which two short lateral branches terminate in oval sporangia. A further division occurs near the edge of the rock: one branch possibly terminates in a sporangium, the other plunges into the rock (figure 7).

Sporangial characteristics (size, shape and border) suggest affinities with *C. caledonica* and should these sporangia have been found detached in sediments of this age they would probably have been assigned to that genus, our only reservation being that the sporangium–stalk junction is not clearly visible in the Targrove specimens. However the overall branching system more closely resembles that in *Renalia* and so we conclude that the Targrove specimens have closer affinities with that genus.

Cooksonia-like sporangia

See figures 1–5. By far the most numerous sporangia conform in shape to that in Lang's diagnosis for *Cooksonia*, although the subtending axis, if present, rarely shows dichotomous branching. The problems of distinguishing species in fossils so simple that they present few, well-defined characters have been outlined elsewhere (Edwards 1979*b*; Edwards *et al.* 1983). Here we scored for overall shape, presence or absence of border (?dehiscence line), nature of the sporangium wall, nature and extent of contact between sporangium and subtending axis, features of the subtending axis including proximity of branching and *in situ* spores. However, there are relatively few sporangia that are so completely preserved that they show all characters clearly, and many are so small that the dislodging of a few fragments of residue or matrix radically alters their shape. In the large number of short and wide sporangia discovered at Targrove we have recognized several species of *Cooksonia* and attempted an analysis of intraspecific variation including ontogenetic variation. Our problems have been compounded because, having found the *Renalia*-type specimens, we suspect that at least some of the isolated sporangia, for example, those resembling *Cooksonia caledonica*, may originally have been part of much larger plants that fragmented during transport before burial. Thus although we have decided to use the genus *Cooksonia* for such sporangia we have also considered the possibility of erecting a new genus for forms where short and wide sporangia terminate short lengths of unbranched axes.

Cooksonia hemisphaerica. The commonest and most easily identified sporangia belong to this species (figure 1). From Lang's diagnosis and illustrations, which were also based on Targrove material, the sporangia terminal on dichotomously branching smooth axes, are hemispherical (almost as high as wide) with flat contact area between sporangium and axis, and have thick walls. Edwards (1979*b*) also included slightly wider, that is, elliptical, sporangia. The new specimens show some variation in shape (some being a fraction longer than wide) and in size (including both larger and smaller examples). The thick, heavily coalified central region comprising spore-mass plus wall is often surrounded by a narrow, lighter halo, thought to represent only wall, but there is no evidence for a predetermined dehiscence line. In most specimens there is a marked distinction between sporangium and axis, but where this is missing, measurements must be approximate and identification of *C. hemisphaerica* less certain. Smooth-walled spores isolated from some of the sporangia have provisionally been assigned to the dispersed spore genus, *Ambitisporites*.

Dichotomous branching is recorded in only a few specimens; the longest one described by Lang shows two branch points. We have no evidence that the fragmentary plants were parts of the lateral branch system of a much more complex organism as reconstructed by Stepanov (1975) although it is possible that fragmentation occurred during transport (Gensel 1976).

Cooksonia pertoni. In this species, the sporangia terminating smooth, dichotomously branching axes are considerably wider than high (figure 2). Most of Lang's Downton specimens show an extensive and flat junction between sporangium and axis and a subtending axis which decreases rapidly in width below the sporangium. The considerable variation in sporangial outline and size noted for the Downton specimens is also seen in Targrove. Film pulls reveal details of both spores (*Ambitisporites*) and sporangial wall. Most of the surface cells are isodiametric, but at the convex border, anticlinally elongate, thick-walled cells form a thick band, which may have been involved in dehiscence (*cf. Renalia*, Gensel 1976). Fortuitously compressed sporangia provide some evidence for two valves and indicate that the sporangia were probably ellipsoidal not discoidal. Such preservation forms when lacking a dehiscence line perhaps account for the specimens that appear intermediate between *C. pertoni* and *C. hemisphaerica*. Considering Stepanov's reconstruction of *C. pertoni* (1975), evidence from the Welsh Borderland, and in particular from new specimens found at the type locality, makes it very unlikely that this was the organization in *C. pertoni* and we conclude that the Russian specimens are better assigned to another genus.

Cooksonia cambrensis. A small number of sporangia with circular or elliptical outlines terminate axes that are parallel-sided and show little or no increase in width below the sporangium (figure 5). These resemble the Downton sporangia (Edwards 1979*b*) placed in two forms (α and β) of a new species, *C. cambrensis*. Additional similarities include the narrow area of contact between sporangium and axis and the lack of branching close to the sporangium. A number of specimens lack these two last characteristics: whether or not they should be assigned to the Welsh species is conjectural. Indeed as both *Ambitisporites* and *Retusotriletes* have been isolated from Targrove sporangia assigned to α and β forms of *C. cambrensis* (but not from a single sporangium) there is a likelihood that more than one species is present, unless the sporangia were preserved when the spores were at different stages of development.

Cooksonia caledonica. The sporangium illustrated in figure 3 has the characteristics of the

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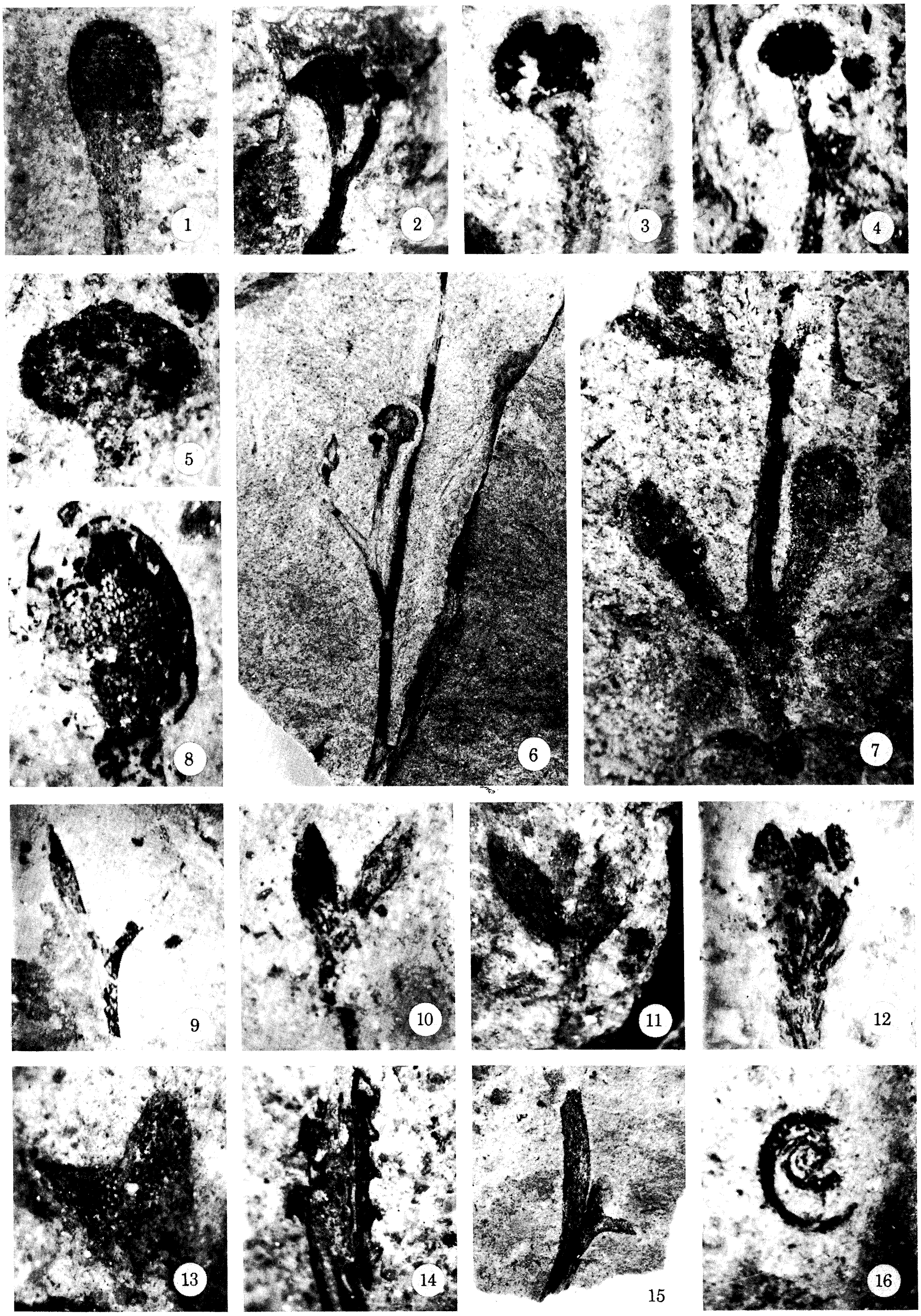
DESCRIPTION OF PLATE 1

FIGURE 1. *Cooksonia hemisphaerica* (T. 1) with dark line in axis below sporangium, × 12.5.
FIGURE 2. *C. pertoni* (T. 2), × 12.5.
FIGURE 3. *C. cf. caledonica* (T. 3), × 12.5.
FIGURE 4. *C. cf. caledonica* (T. 4), showing possible branching point, × 5.
FIGURE 5. *C. cambrensis* (T. 5), × 12.5.
FIGURE 6. *Renalia*-type specimen (V. 58024) with *Cooksonia*-type sporangia on a lateral branch system, × 3.
FIGURE 7. Fertile specimen with trifurcation (V. 58013), × 8.
FIGURE 8. Incomplete oval sporangium (T. 6) showing cells in sporangium wall, × 13.
FIGURE 9. *Salopella* sp. (T. 7) with pointed sporangia, × 5.
FIGURES 10 AND 11. *Salopella* sp. (T. 8, T. 9) with branching close to sporangia, × 12.5.
FIGURE 12. Cluster of at least three fused sporangia (T. 10), × 32.
FIGURE 13. Bifurcating sporangium (T. 11) with tetrads of spores, × 16.
FIGURE 14. Axis (T. 12) with at least one row of blunt, hooked teeth, × 12.5.
FIGURE 15. Axis with K-branch (T. 13), × 2.5.
FIGURE 16. Circinate tip (T. 14), × 12.5.

Specimen numbers with prefix T are housed at University College, Cardiff, and those with prefix V at the British Museum (Natural History).



FIGURES 1–16. For description see opposite.

Scottish Dittonian species (Edwards 1970*b*), namely, sporangia slightly wider than high with distal border and convex junction between sporangium and stalk. However in common with the majority of sporangia of this type found isolated in the matrix at Targrove, it lacks branching in the subtending axis and we have already considered the possibility that such sporangia were parts of a more complex plant. For the moment we prefer to leave the isolated forms as, cf. *C. caledonica* (figures 3, 4).

Sporangia considerably longer than wide

Salopella sp. In 1974, Edwards & Richardson erected the genus *Salopella* for compression fossils comprising smooth, dichotomously branching axes with terminal fusiform sporangia. In *S. allenii* based on a single specimen from Newton Dingle, another locality in the Welsh borderland, the sporangia were at least 9 mm high and 2 mm wide. The azonate spores sometimes preserved in tetrads in the sporangia could not be assigned to a dispersed spore genus. The large number of fusiform sporangia found at Targrove show a considerable range in size (largest: 4 mm long by 0.7 mm wide; smallest: 0.7 mm by 0.3 mm) but none are as big as those in *S. allenii*. A further diagnostic character of the type species is the presence of branching immediately below the sporangia. This is also seen in Targrove, although in some specimens the branch point occurs some distance below the sporangium and this distance varies between specimens (figures 9–11). There is therefore a very limited number of characters for species determination in *Salopella*. *In situ* spores may be of some use. We have recovered *Ambitisporites* from some sporangia, *Retusotriletes* from others, although the presence of smooth walled tetrads in certain sporangia suggests the possibility of ontogenetic variation.

cf. Yarravia sp. In a few specimens a cluster of elongate sporangia terminates a smooth axis (figure 12). These appear to be fused proximally with free tips. Unfortunately the fossils are small and not well preserved, but superficially they resemble the Australian genus *Yarravia* Lang and Cookson.

Ellipsoidal sporangia. These are numerous, ranging from 0.7 to 2.6 mm long and 0.4 to 1.9 mm wide (ratio of length to width is 1.3–2.1), and most terminate short lengths of unbranched axes (figure 8) although dichotomous branching is sometimes present. There is also some variation in the shape of the sporangium apex (rounded or slightly pointed), the type of spore present (*Ambitisporites*, *Retusotriletes*, tetrads) and the nature of the sporangium wall. The most distinctive has an outer layer of large, thick-walled cells which present a reticulate appearance when infilled with limonite. A dehiscence line has not been observed. Such variation is probably interspecific and we conclude that at least two species of a new genus are present.

Bifurcating sporangia. These are the most unusual sporangia we have found. They are two-lobed with blunt, rounded tips (figure 13). The subtending axis is smooth and widens gradually within the fertile region. Thick-walled elongate cells characterize the sporangium wall, and spores, when present, are associated in tetrahedral tetrads (43–45 μm diameter). Such sporangia will be placed in a new genus.

Of the several hundred sporangia collected at Targrove Quarry, approximately 50% may be assigned to the above taxa. The remainder are incomplete, small, or so poorly preserved that they lack any diagnostic characters. However, they demonstrate an abundance of fertile specimens greater than that previously reported in any assemblage of early land plants. Apart from one specimen with branching typical of *Zosterophyllum* and a fragment of a poorly preserved spike, the assemblage is dominated by rhyniopsids (or rhyniophytoids, see below), but shows more diversity both in numbers of taxa and organization than has previously been recorded in the early Gedinnian of the northern hemisphere. The dispersed spore assemblage is currently being studied by Dr J. B. Richardson who reports that the spores are well preserved and are typical of the *micrornatus–newportensis* zone. The isolation of spores from so many different taxa has been an important part of this investigation but it has been disappointing that all are simple, smooth-walled forms and we remain ignorant of the producers of the more highly ornamented examples in the dispersed spore assemblage.

Discussion

The presence and nature of conducting tissues in early land plants

The assemblage at Targrove illustrates the inadequacies of compression fossils for anatomical investigations. We have film-pulled several hundred axes, but have failed to recover any xylem of the type isolated from a single, smooth unbranched axis by Lang (1937) although we have observed a reticulate patterning resembling tracheidal thickenings on a fractured dichotomously branching axis. Such evidence indicates that vascular plants were present in early Gedinnian vegetation of the Old Red Continent, but as we have discovered several fertile taxa at the locality, Lang's conclusion that *Cooksonia hemisphaerica* was a vascular plant (Edwards *et al.* 1979) must now be regarded with reservation although similarities in gross morphology with more completely known rhyniopsids, for example, *Rhynia gwynne-vaughanii* suggest pteridophyte affinities. By using the same reasoning the pteridophytic–rhyniopsid nature of the remaining fertile taxa at the locality must also be queried. Similar problems were encountered when identifying the *Cooksonia*-type fossils from the Wenlock of Ireland (Edwards *et al.* 1983) and it was concluded that such minute plants are perhaps better described as rhyniophytoid (Pratt *et al.* 1978). Raven (1977) had postulated that the earliest colonizers of the land, intermediates between the green algae and vascular plants, may have been similar in gross morphology to the latter but with a hypodermal sterome for support and lacking xylem. He cited *Eohostimella* as an example (Schopf *et al.* 1966), but Strother & Lenk (1983) cast doubt on whether that fossil is even of plant origin. We have evidence from scanning electron microscope studies that the outermost tissues of some of the axes at Targrove are indeed thick-walled, a feature characteristic of the majority of the vascular plant colonizers of the Old Red Continent in Siegenian–Emsian times. One of us (Edwards, D. 1980) suggested that this sterome would have complemented the structural role of the often massive conducting strand during drier periods and would also have reduced water-loss. The nature of the tissue remains problematic although its very preservation suggests that it was probably lignified. Niklas (1976) considering the possible combinations of biochemical and morphological (including anatomical) attributes of the earliest land plants proposed one model in which, following the evolution of the biosynthetic pathway of lignin, the polymer would first have been incorporated into the walls of peripheral tissues, with non-lignified elongate cells forming a central water-conducting strand: then as size increased these elongate cells would also have developed lignification. Should such a phylogenetic sequence have occurred, the detection of lignin residues in chemical analyses of intact coalified axes of early land plants can no longer be regarded as unequivocal evidence for their vascular status.

Finally, there is increasing evidence that in the initial phases of the colonization of the land a variety of morphological and physiological strategies were evolved which fall outside our concepts of land plants based on extant tracheophytes and bryophytes. Examples are the organism that was covered by *Nematothallus*-type cuticles (Edwards 1982; Edwards & Rose 1984) and the far better known *Rhynia major*, which presents a new combination of characters, namely, a sporophyte of pteridophyte organization except for the presence of a moss-like central conducting strand (Edwards 1976; Hebant 1977). Even when differentially thickened presumed water conducting cells are present, they may not conform exactly to the organization of primary and secondary walls characteristic of the tracheids and vessels of extant plants. This is the case for *Taeniocrada dubia* (Hueber 1983) and even *Psilophyton dawsonii* (Hartman & Banks 1980). Although occasional specimens of *C. hemisphaerica* at Targrove show a distinct dark central line in the axis immediately below the sporangium (figure 1) we have failed to isolate tracheids from it and thus still have no direct evidence that *C. hemisphaerica* was a vascular plant.

Indeed there are puzzling features in the tracheids which Lang illustrated from Targrove and attributed to *Cooksonia*, and which he described as annular. The vertical walls, presumably representing two fused adjacent primary walls, are of approximately the same thickness and colour as the horizontal annular thickenings and thus closely resemble the scalariform tracheids recovered on film pulls of axes from Siegenian strata (Edwards 1970*a*). The far more fragmentary tracheids recorded from Ludlow strata in South Wales (Edwards & Davies 1976) appear similar. Our failure to discover further tracheids at Targrove is therefore all the more frustrating as it is obviously necessary to isolate them from film pulls for more detailed investigation.

Sedimentology and palaeoecology

The Targrove assemblage occurs in typical fluviatile sediments (distal facies) of the Lower Old Red Sandstone of the Welsh borders (Allen & Tarlo 1963; Allen 1979). In the same sequence are thin carbonate units, concretionary cornstones, thought to be of pedogenic origin (Allen 1973). Although there are records of branching vertical channels interpreted as roots or rhizomes in the cornstones, plant megafossils are found only in the reworked examples. At Targrove the most abundant plant remains occur in channel-fill sandstones, which overlie a metre or so of conglomerate, composed of reworked cornstone clasts, rip-up clasts from adjacent flood plain deposits and, just above the scoured base, rounded billets of *Prototaxites*. So much organic material (cuticles of plants and animal origin, isolated sporangia and short lengths of axis) is present in the sandstone that at some horizons cover is almost complete and the sandstone in section has a laminated appearance. Plants are also preserved in the laterally equivalent flood plain deposits but are less frequent and characterized by larger sheets of cuticles(?) and occasional axes. Larger axes are sometimes recovered from the less fissile sandstones. Isolated blocks on the quarry floor show bands of comminuted material concentrated at the bases of ripples, and probably originated from higher in the channel fill.

Climatic interpretations based on studies of modern calcretes (Goudie 1973; Allen 1974) indicate that the whole of the L.O.R.S. in the Welsh borderland was deposited in a warm to hot climate (mean annual temperature 16–20 °C, with seasonal rainfall of 100–500 mm). From the distribution of evaporites, palaeomagnetic studies and comparisons with modern rivers, it is suggested that there may have been rapid changes of discharge over one or perhaps two orders of magnitude between a short flood(?) and long dry season. The calcrete horizons, however, if pedogenic would not have been flooded by sediment-laden flood waters for considerable periods (in the general order of 10^4 years) but would have been subjected to alternate periods of wetting and drying. In such a system where an active main river system crosses slightly raised broad interfluvial plains with calcrete surfaces (Allen & Williams 1979), the plants probably grew in the flood plain in the immediate vicinity of rivers, on banks and point bar systems etc. The fragmentary nature of the remains suggests they have travelled considerable distances, while their abundance implies that the area must have been heavily vegetated, although frequency of plant fragments would also be a function of concentration by flowing water. The possibility that the simplicity of these plants is not primitive, but the result of reduction associated with adaptation to swamp or arid environments would fit in with colonization of calcrete crusts, today characterized by highly adapted xerophytic angiosperms. However the fossilization potential of such plants would be low and conditions of growth so hostile, that we conclude that the more likely habitats would be close to the larger rivers with year-round flow (Edwards, D. 1980). In the younger Lower Old Red Sandstone sediments of the Brecon Beacons (medial alluvial facies) parallel alignment of well-preserved axes of a single species preserved in near-channel overbank deposits suggests that the plants grew in dense monotypic waterside stands and were flattened by sudden floods (Edwards 1979*b*, 1980). Greater diversity is seen in the tangled masses of transported material, although here plants are more fragmentary and usually sterile.

Sorting during transport

We appreciate that transport from the original habitat to site of fossilization will produce a highly biased sample of the source vegetation. Here the situation is further complicated because we have little information on the complete plants (except that they were quite unlike the vast majority of land plants today) or on their hydraulic characteristics (Spicer 1980). We suspect that the plants were fragmented during transport (the size of the comminuted organisms varies noticeably between successive bedding planes), with pieces of cuticle from thalloid organisms and detached sporangia being carried further. This would explain the lack of larger axes at Targrove, whereas approximately coeval assemblages in the Welsh borderland contain intact *Cooksonia* and *Zosterophyllum* specimens together with larger and wider axes, although the number of specimens is much smaller.

Life cycles and life histories

The plants described from Targrove were probably all sporophytes and in such an allochthonous deposit it seemed unlikely until quite recently that anything, except for *in situ* spores, would be discovered about their gametophytes or life histories. However, *Sciadophyton*, a compression fossil lacking well-preserved cellular detail recorded from numerous geographically widespread Siegenian–Emsian localities around the Old Red Continent (including the Siegenian of South Wales) (Croft & Lang 1942) has recently been interpreted as including the gametophytes of *Zosterophyllum rhenanum* and *Taeniocrada langi* (Schweitzer 1983). Schweitzer recorded sterile axes which he suggested belonged to *Z. rhenanum* in the Gedinnian of Germany. In a detailed reconstruction of a plant succession deduced from a sedimentological survey of a Lower Emsian locality (Köppen Quarry near Waxweiler) gametophytes (*Sciadophyton*) of *Z. rhenanum* are shown growing at the junction of intertidal and supratidal zones at the edge of a salt marsh. Welsh specimens of *Sciadophyton* occur in the continental medial fluviatile facies of the Old Red Sandstone.

Given the palaeoclimatic regime and range of habitats derived from sedimentological studies of the Old Red Continent it is possible to speculate on the nature of the life histories of the plants. Edwards (1979*a*) suggested that those that grew in relatively unstable flood plain environments in warm and seasonally arid climates may have been opportunists, with rapid sexual maturation of gametophytes in the wet season resulting in the early establishment of the more drought-resistant sporophytes. Niklas *et al.* (1980) employed the terminology of modern population ecology in similar but more protracted deliberations. They postulated that the earliest vascular plants such as *Cooksonia* were small and rapidly growing, expending the minimum amount of energy in vegetative activities, lacking secondary tissues and achieving spore production as soon as possible (the r-life history trait, r-LH) and that as they became more efficient and successfully adapted to the land environments the sporophytes in particular would have gradually adopted the K-LH trait with prolonged vegetative growth. Extant pteridophytes have the potential for extensive rhizomatous development. This could account for the situation so frequently encountered in the Lower Devonian where only one species occurs at a particular horizon. A single plant may have covered a large area resulting in a patchy vegetation locally dominated by one species (Andrews *et al.* 1977). Such plants would thus have relied less heavily on sexual reproduction, but would have produced spores over longer periods. We have no information on the duration of the sporophytic phase. It is possible that the plants were swept over and buried in the next period of flooding. There is some morphological evidence that they had the potential to regenerate by the production of root-like structures on distal vegetative axes (Rayner 1983, work in progress in Cardiff).

Gedinnian floras and palaeogeography

Current palynological studies in conjunction with those on fish faunas are producing a more refined biostratigraphy for the late Silurian and early Devonian and are permitting more accurate correlation between localities on the Old Red Continent (for example, Richardson 1974; Richardson *et al.* 1981). Table 1 based on Richardson *et al.* (1982) and unpublished data from Richardson, shows the relative stratigraphic positions of the major plant localities together with the more important taxa (excluding thallophytes). Nonceveux, the type locality in Belgium of *Zosterophyllum fertile*, occurs near the top of their *micrornatus–newportensis* zone, but is considered slightly older than the Newton Dingle locality in the Welsh borderland on the basis of fish. Less precisely dated is the littoral upper Gedinnian assemblage from Germany (Schweitzer 1983), but it shows greater diversity of organization in that in addition to sterile *Taeniocrada* and putative *Z. rhenanum* it contains sterile *Drepanophycus spinaeformis*, a plant with some lycopod characteristics (microphylls and stellate xylem, Rayner 1984) but with cauline, not axillary sporangia (Schweitzer 1980), a combination of features also seen in *Baragwanathia longifolia* (J. D. Tims, personal communication). Obhrel (1962) recorded *C. downtonensis* Heard (probably synonymous with *Steganotheca striata* Edwards) in the *Monograptus uniformis* zone in marine beds of deeper water (Bohemian) facies of Czechoslovakia, although his illustrations suggest closer similarities with *C. hemisphaerica.* The remaining Gedinnian records on the Old Red Continent (for example, Spitsbergen, Hoeg 1942) comprise sterile unidentifiable remains. Thus the very limited information derived from a few approximately coeval assemblages preserved in a range of facies associated with the Old Red Continent suggests a uniform vegetation dominated by rhyniopsids at the base of the Gedinnian, but becoming more diverse throughout the period, due both to increased kinds of rhyniopsids and the appearance of *Zosterophyllum*. *Drepanophycus spinaeformis* recorded from a number of Old Red Sandstone

Table 1. Stratigraphic and geographical occurrences of important late Silurian and early Devonian plant assemblages in Europe

(Absolute ages based on Holland, this symposium.)

Key
●, plant record
○, species uncertain
?, age uncertain

‘stage’ or series	Spore zone (from data in Richardson *et al.* (1982) and personal communication)	*Zosterophyllum myretonianum*	*Z. fertile*	*Salopella allenii*	*S.* n.sp.	*Cooksonia hemisphaerica*	*C. pertoni*	*C. cambrenisis*	*C. caledonica*	*Renalia* n.sp. 1	*Renalia* n.sp. 2	*Drepanophycus spinaeformis*	*Taeniocrada* sp.	selected plant localities in Britain, Belgium and Germany
L. Siegenian	(III)	·	○	·	·	·	·	·	·	·	·	●	●	Brecon Beacons, Wales
406	BZ	·	○	●	·	·	·	·	·	·	·	·	·	?Newton Dingle, England
U. Gedinnian		·	·	·	·	·	·	·	·	·	·	●	○	?Germany
	MN	·	●	·	·	·	·	·	·	·	·	·	○	Nonceveux, Belgium
L. Gedinnian		·	○	○	○	●	●	●	○	●	●	·	·	Targrove, England
		●	·	·	·	·	·	·	●	·	·	·	·	Myreton, Scotland
412	‘*Apiculiretusispora*’ ?	·	·	·	·	●	●	●	○	·	·	·	·	?Freshwater East, Wales
Downton/Přídolí 414	‘*tripapillatus*’	·	·	·	○	○	●	·	·	·	·	·	·	Perton Lane, England

localities in the Siegenian, which is characterized by far more diverse assemblages, first appears late in the Gedinnian of Germany.

There are some indications that contemporaneous vegetation in other parts of the world was more diverse, but unfortunately the plants are incompletely known and their ages less secure. In the U.S.S.R., Senkevich (1978) reported several new taxa from marine sediments in Kazachstan and gave diagnoses for two, *Cooksonella*, differing from *Cooksonia* in the possession of a sporangium border, and a new fertile species of *Taeniocrada*. Far more intriguing is Stepanov's Siberian '*Zosterophyllum* flora', which includes sterile branching axes assigned to *Zosterophyllum*, a much branched *Cooksonia pertoni* and at least five endemic genera (Stepanov 1975). Should there be independent faunal confirmation of the Gedinnian age for this assemblage, it would provide evidence for provincialism in early Devonian floras. Similar problems arise in assessing the Chinese *Zosterophyllum* flora (Li & Cai 1977). We know of no well-dated Gedinnian floras in the southern hemisphere. J. D. Tims (personal communcation) has examined a possibly Lochkovian assemblage comprising *Baragwanathia longifolia* and new species of *Zosterophyllum* and *Baragwanathia* from Victoria, the age determination based on associated corals.

Thus considering world biogeography in Gedinnian times, the pattern seems to follow broadly that of the uppermost Silurian with assemblages of uniform composition in the North Atlantic realm (Old Red Continent) and increased diversity in the Uralian–Cordilleran realm (Boucot & Gray 1982) with the major proviso that for the former only are the assemblages dated with confidence. A similarly deficient record frustrates attempts to detect floral provinces later in the Lower Devonian (Edwards 1973). The most recent, a multivariate statistical analysis of published data on early Devonian plants (Ziegler *et al.* 1981) suggests that there were at least three intergrading floras, of which the cool south temperate Gondwana flora is considered to be the most distinct. However apart from the Australian Victorian assemblages (considered by Ziegler *et al.* (1981) together with Libya as part of the equatorial phytogeographic unit), we know of no assemblage of vascular plants in the Lower Devonian of the southern hemisphere (Anderson & Anderson 1984). Their subdivision of Laurentian (including the Old Red Continent) floras into a temperate or subtropical western-north American flora (including Arizona, Wyoming, Alaska, Bathurst Island and Spitsbergen) and an equatorial one is questionable because of the number of genera common to the two floras. It may simply reflect lack of detailed information on both the plants and their ages in the temperate–subtropical flora.

Quantitative assessments of vascular plant diversity†

With the exception of recent attempts by Niklas *et al.* (1980, 1983) palaeobotanists have mainly been preoccupied with evolution at the organ level and overall relationships of vascular plants (Stewart 1983). Stimulated by quantitative studies on taxonomic diversity in Phanerozoic invertebrates, the American workers applied similar statistical analyses to vascular plant data mainly from Europe and north America, and demonstrated four distinct evolutionary phases (Niklas *et al.* 1983). Additional data accumulated during the course of our studies at Targrove and elsewhere in S Britain offer the possibility for a more detailed analysis of at least part of their first phase, the Silurian to mid-Devonian proliferation of vascular plants, and to discuss some of the problems and sources of error that Niklas *et al.* (1983) recognized in handling

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† Since this paper was written, a paper with a more detailed analysis of early vascular plant evolution has been published by Knoll *et al.* (1984).

their data and that particularly distort quantitative evolutionary assessments within the Silurian and early Devonian.

(i) Absolute time scale: this is obviously essential to such an analysis. McKerrow *et al.* (1984) have recently reassessed published age determinations (table 2) which conveniently cover the relevant period. Values for the whole of the period do not vary greatly (29–34 Ma) however those for some of the subdivisions do and would radically alter the slope of the graph of number of species, for example, within the Přídolí and Gedinnian.

TABLE 2. A COMPARISON OF RECENTLY PUBLISHED AGE DETERMINATIONS FOR THE LUDLOW–EMSIAN PERIOD

		McKerrow *et al.* 1980	Jones *et al.* 1980	Harland *et al.* 1982	McKerrow *et al.* 1985
base of Ludlow to base of Eifelian/Ma		420–390	412–383	421–387	420–391
duration of	Ludlow/Ma	7	7	7	6
	Přidolí	2	4	6	2
	Gedinnian	8	5	7	6
	Siegenian	5	4	7	5
	Emsian	8	9	7	10

(ii) Analysis of data. We have already discussed the problems of species recognition in plants as simple and as fragmentary as *Cooksonia* and *Salopella* and, because in such cases there is a tendency to 'lump' rather than to split, numbers of taxa in the late Silurian and early Devonian are probably underestimated. This in turn may have the effect of apparently slowing down the rate of evolution. Schopf *et al.* (1975) claim that, for the animal record, the more complex the organism the faster the rate of evolution: in that well-defined morphological changes of the phenotype usually reflect or parallel genome changes, it may well be more difficult to detect changes at the genome level in a series of organisms of extreme morphological simplicity as is seen, for example, in *Cooksonia*. In this paper we extend the range of *Cooksonia pertoni* from the basal Downton into the Gedinnian with some confidence. We are less confident about extending it into the Wenlock (Edwards *et al.* 1983) where comparably shaped, but much smaller, sporangia are recorded. We have similar reservations about the Wenlock records of *C. hemisphaerica* and *C. cambrensis* from Edwards *et al.* (1983). It is clearly impossible to decide whether the taxa are conspecific with younger representatives yet such a decision has profound effects on patterns of diversity and estimates of rates of evolution in early pteridophytes. Another source of error is in the scoring of sterile remains (for example, *Hostinella*, *Aphyllopteris*, *Psilophytites*) so that in compiling numbers of taxa caution would again result in a conservative estimate. On the other hand, in the Downton and early Gedinnian where departures from dichotomous branching occur, this does not necessarily indicate an increase in numbers of species as a single plant may have possessed more than one form of branching.

(iii) Age considerations and correlation. Refinement of evolutionary patterns within the late Silurian and Lower Devonian requires precise correlation, which is gradually being attained particularly through complementary palynological and faunal studies. This has resulted in a more accurate analysis of numbers of taxa against time. Determinations of species durations are less satisfactory owing to problems associated with species recognition (see (ii)) and the fact that there is a large number of single records (for example, Rhynie Chert assemblage). Single occurrences may affect calculations of origination rates (Niklas *et al.* 1983) based on numbers of appearances and extinctions, particularly in a time interval as short as the Downton.

Niklas *et al.* (1983) concluded that some of the slowest rates of speciation and the longest durations of species occurred in the early vascular plants. Our own observations and calculations suggest that although there are a few long-ranging species, for example, *Sawdonia ornata*, *Drepanophycus spinaeformis* and *Taeniocrada decheniana* among Devonian plants, it is perhaps premature to formulate any generalizations particularly for the rhyniopsids. However the approaches adopted by Niklas and co-workers will certainly provoke further thought and stimulate others to assess the value of the plant fossil record more critically.

Epilogue

It is now a matter for history that studies on early pteridophytes began on fossils from the Old Red Continent, that the finest preservation has been found there and that the land mass has been the subject of some classic sedimentological studies. In the evolution of the Phanerozoic earth, the Old Red Continent represents the oldest emergent land mass of any great size whose continental sediments have been studied in detail. The timing of the origin of the continent was such that it could not have provided the stimulus for the invasion of the land or the origin of vascular plants but it may provide information on some of the earliest adaptive radiations of vascular plants. In that it was a seasonally arid continent of low latitudes, it is possible that the record is a biased one, reflecting a highly specialized vegetation. What evidence we have on land vegetation before the middle Silurian is based on microfossils and we know nothing of the type of terrestrial environments involved. Boucot & Gray (1982) believe that the initial invasion of the land occurred at relatively high latitudes (Malvinokaffric Realm) although other workers have queried the premises on which they base their conclusions. We consider it very likely that small islands, isolated and unstable environments, would have provided ideal environments for the establishment of pteridophytes. Indeed, the earliest *Cooksonia*-like plants may well have lived on just such an island, as the remnants of an ancient volcanic arc are thought to have existed in the Irish Sea in Wenlock times. Pteridophytic homosporous reproduction would have facilitated rapid dispersal over quite long distances, both sea and land, and in the absence of competition from seed plants, the earliest pteridophytes are directly comparable to the pioneering bryophytes and pteridophytes of newly formed land surfaces today (Chaloner & Sheerin 1979). Homospory provides the potential for the development of a geographically widespread uniform vegetation, islands provide geographical isolation, varied habitats and thus possibilities for speciation.

Whether or not the vascular plants are mono- or polyphyletic remains conjectural. In 1954, Professor Suzanne Leclercq wrote ‘the finding of the Silurian flora of Australia has been the thin end of a wedge driven in the foundation of the general monophyletic dogma’ (p. 301). She discussed the possibility that the complex of Lower Devonian plants, then called psilophytes, were not the ancestral group that gave rise to the remaining major pteridophytic lines, but existed alongside them as an evolutionary dead-end. More recently accumulated data suggest that the rhyniopsids produced the trimerophyte complex (Banks 1980*b*) and from these late Lower Devonian plants stemmed ferns, horsetails and eventually, via the progymnosperms, the earliest seed plants. The evolutionary position of the lycopods, if indeed *Baragwanathia* should be considered a member of that group, is now more clouded. Traditionally they have been derived from Rhyniopsida with the zosterophylls as intermediates (Bower 1935; Banks 1968): Schweitzer (1980) presented some alternative lineages following his discovery of cauline sporangia in *Drepanophycus spinaeformis*. The realization that *Leclercqia* with its much-divided leaves, first recorded from Emsian strata, is the earliest true lycopod, in the sense that it has axillary sporangia, has revived the hypothesis that the lycopod leaf has evolved by reduction from a three-dimensional telome truss (Stewart 1983) and fired speculation that the lycopods had a diphyletic origin.

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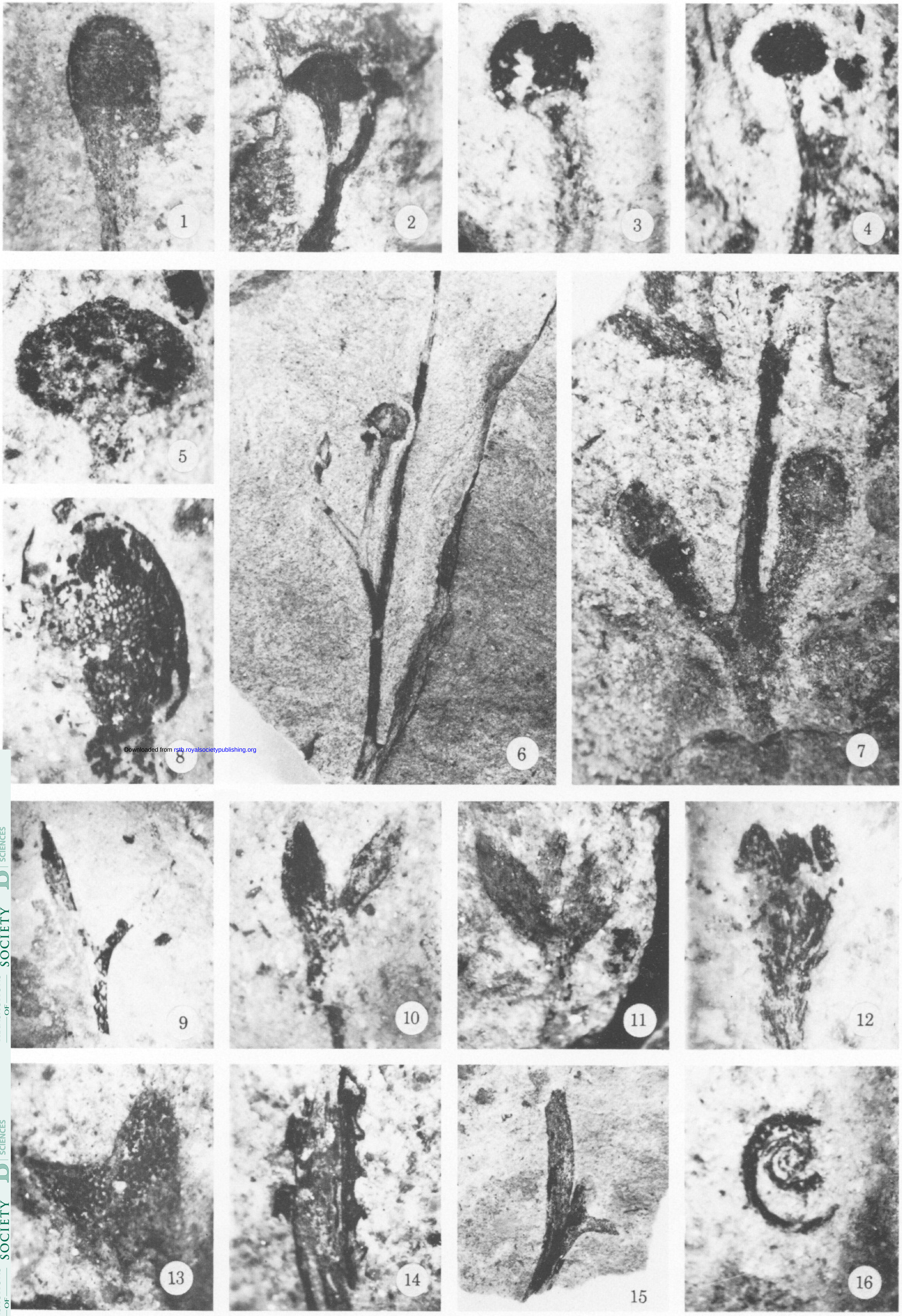
Discussion

W. G. Chaloner, F.R.S. (*Department of Botany, Royal Holloway and Bedford Colleges, Huntersdale, Virginia Water, Surrey, U.K.*). The apparently more or less synchronous appearance of rhyniophytes and (supposedly) Silurian lycopods obviously strengthens the possibility of a polyphyletic origin of vascular plants, as Dr Edwards acknowledges. However, I feel that the strongest evidence for a single common origin for at least the archegoniates comes from living plants rather than fossils. Living archegoniates share such diverse features as the oblique insertion of the flagella, the ubiquitous discoid chloroplast, the stoma and of course, the enclosure of the egg in an archegonium. These shared characters which hold together the bryophytes and tracheophytes and, in part, link them with the Charophytes, point to a single successful land migration by some relative of the latter group, rather than multiple pathways of land migration.

D. Edwards. To a certain extent I agree with Professor Chaloner's opinion that the vascular plants had a common origin and envisage a 'pool of archegoniates' whose gametophytes possessed the characters (apart from stomata) he lists and were thus at a slightly higher level of organization than the charophytes from which they probably derived. Whether or not these plants were true land colonizers or lived in ephemeral shallow ponds is more debatable. The latter possibility would suggest multiple pathways of land migration by tracheophytes, bryophytes and plants with *Rhynia major*-type organization, with the sporophytes exhibiting different responses to the selection pressures of the terrestrial environment. As to the origin of vascular plants themselves I merely resurrect earlier suggestions of a diphyletic or polyphyletic origin, again within the pool of archegoniates, and retire to sit on the fence to wait for more data.



FIGURES 1–16. For description see opposite.