Palaeozoic Palaeobotany of Great Britain

C.J. Cleal and B.A. Thomas

Department of Botany,
National Museum of Wales,
Cardiff, UK.

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Chapter 3

Silurian

Evidence of pre-Silurian vegetation

The Silurian was a period of great significance for the evolution of the Plant Kingdom (Figure 3.1). Plants had been in existence for over three thousand million years, but had been largely restricted to aqueous, mainly marine habitats: the terrestrial habitats presented a number of environmental barriers, which the pre-Silurian algal plants had been unable to overcome fully. Ultraviolet radiation was previously thought to be one such barrier (Lowry *et al.*, 1980), but this now seems unlikely as it is thought that the ozone layer had almost attained its present-day thickness by the Cambrian. A more significant obstacle was desiccation, and it was not until the Late Ordovician and more especially the Silurian that plants developed strategies to overcome this. These included: (a) an outer cuticle with stomata to control water loss, (b) a vascular system to transport water and nutrients around the plant, and incidentally to provide upright support, and (c) spores impregnated with sporopollenin, that could survive in a non-aqueous environment. These developments facilitated the sudden radiation of plant taxa in the Lower Devonian fossil record (see Chapter 4). Much of this very early history of land vegetation has been demonstrated using fossils found in Britain.

PALAEOGEOGRAPHICAL SETTING

The best available review of Silurian plant fossil distribution is by Edwards (1990). She has shown that most fossils represent equatorial to subequatorial vegetation, particularly of Laurussia (Figure 3.2). In addition to the British localities, there are records from the USA (Schopf *et al.*, 1966; Banks, 1972, 1973; Pratt *et al.*, 1978), Ireland (Edwards *et al.*, 1983), the former Czechoslovakia (Obrhel, 1962, 1968), Ukraine (Ishchenko, 1969, 1975), Kazakhstan (Senkevich, 1975) and China (Edwards, 1990).

Laurussia would have provided an ideal setting for the first migration of plants onto land. The climate was warm and moist, and the extensive delta-systems generated by Caledonian earth movements provided extensive intermediate areas between marine and the drier terrestrial habitats.

An assemblage from Raudfjorden in Spitsbergen was originally considered to be of Late Silurian age (Høeg, 1942), but is now thought to be Early Devonian (Banks, 1972).

Some Silurian plant fossils from Gondwana indicate a quite different and apparently advanced vegetation. The best documented belong to the lower of the *Baragwanathia* assemblages of Australia (e.g. Tims and Chambers, 1984). The stratigraphical position of these fossils as upper Ludlow is now generally accepted (see below), but they represent a level of evolutionary development not otherwise seen below the Lower Devonian (Siegenian) in Laurussia. A comparable assemblage has also been reported from Libya (Klitzsh *et al.*, 1973; Boureau *et al.*, 1978; Douglas and Lejal-Nicol, 1981), but there are problems with its stratigraphical assignment (Edwards *et al.*, 1979); currently available evidence indicates that they are in fact Devonian (Edwards pers. comm.). The specimens described by Daber (1971) from indisputably Přídolí strata of Libya are more compatible with the type of plant fossils found in Laurussia.

STRATIGRAPHICAL BACKGROUND

The chronostratigraphical divisions of the Silurian are summarized in Figure 3.5. The stage boundaries are defined at stratotypes in mainly basinal marine facies, and located on the basis of graptolite zones. However, palynology has allowed detailed correlations to be made between the basinal sequences and the near-shore facies, in which most of the Silurian plant fossils occur (Richardson and Edwards *in* Holland and Bassett, 1989).

The lithostratigraphy of the Silurian strata in Britain is summarized by Cocks *et al.* (1971) and Holland and Bassett (1989).

All of the Silurian plant fossils belong to the *Cooksonia* Zone in the Banks (1980) classification.

EVIDENCE OF PRE-SILURIAN VEGETATION

Microscopic algae inhabited Early Palaeozoic soils (Retallack, 1986). The oldest evidence of macroscopic terrestrial plants is cuticles and spores from the Ordovician (Gray, 1985), while the oldest macrofossils are from the Silurian. The only records of macrofossils from below the Silurian in Britain are from the Ordovician of Pembrokeshire (Hicks, 1869) and Cumbria (Sedgwick, 1848; Nicholson, 1869), but these are poorly documented. From outside this country, the most widely quoted pre-Silurian land plant is *Aldanophyton*, from a Cambrian marine limestone in Siberia (Kryshtofovich, 1953). It was

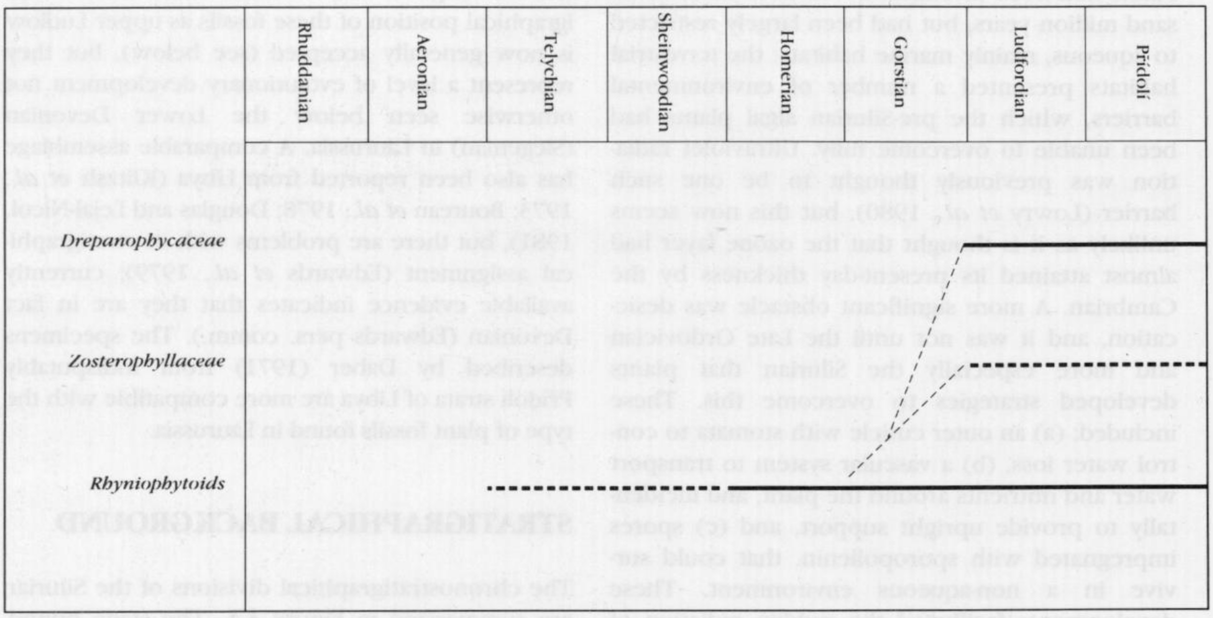

Figure 3.1 The distribution of families of vascular plants in the Silurian. Based on data from Cleal (1993).

initially described as a lycopsid, but this is now generally discounted (e.g. Stewart, 1960, 1983), although its affinities remain a mystery. Records from the Ordovician of Poland (Greguss, 1959; Koslowski and Greguss, 1959) and the former Czechoslovakia (Obrhel, 1959) have been queried by Chaloner (1960). The poorly preserved 'fossils' from an Ordovician sandstone in Kazakhstan (Senkevich, 1963) may not be plant remains.

SILURIAN VEGETATION

Characters that were adaptive to life in the terrestrial habitats appeared in several groups of plants. Most significant were small plants with naked, dichotomous axes, known as rhyniophytoids, and including *Cooksonia* and *Steganotheca* (Figure 3.3). Britain has yielded the most abundant and well-preserved fossils of these small plants, and most of what we know about them is based on British work. Our knowledge of them is still incomplete, though; even their size is a matter of conjecture, although they were probably little more than a few millimetres high. It is generally assumed that they were the earliest known vascular plants. They show undoubted evidence of a cuticle with stomata, and of cutinized spores (Edwards *et al.*, 1986), but no evidence of vascular tissue has been found in the Silurian. They are thus provisionally designated as 'rhyniophytoid', implying that they have the appearance of a primitive vascular plant, but without yielding direct evidence of vascular tissue (Edwards and Edwards, 1986). The oldest examples of well-preserved rhyniophytoid remains are from the Wenlock Series.

Unequivocal evidence of vascular plants in the Silurian of Britain is relatively limited. Slender axes with xylem tissue have been reported from the Ludlow Series (Edwards and Davies, 1976). No fructifications were attached, but it is generally assumed that they are fragments of rhyniophytes, the archetypal simple vascular plants, with naked, branching axes bearing single, terminal sporangia. Outside of Britain, the evidence is more convincing. The most widely discussed example is the lycopsid *Baragwanathia*, which is best known from Australia. Its stratigraphical position has been the subject of much controversy, but a Ludlow age is now widely accepted (Garratt, 1979, 1981; Edwards *et al.*, 1979; Douglas and

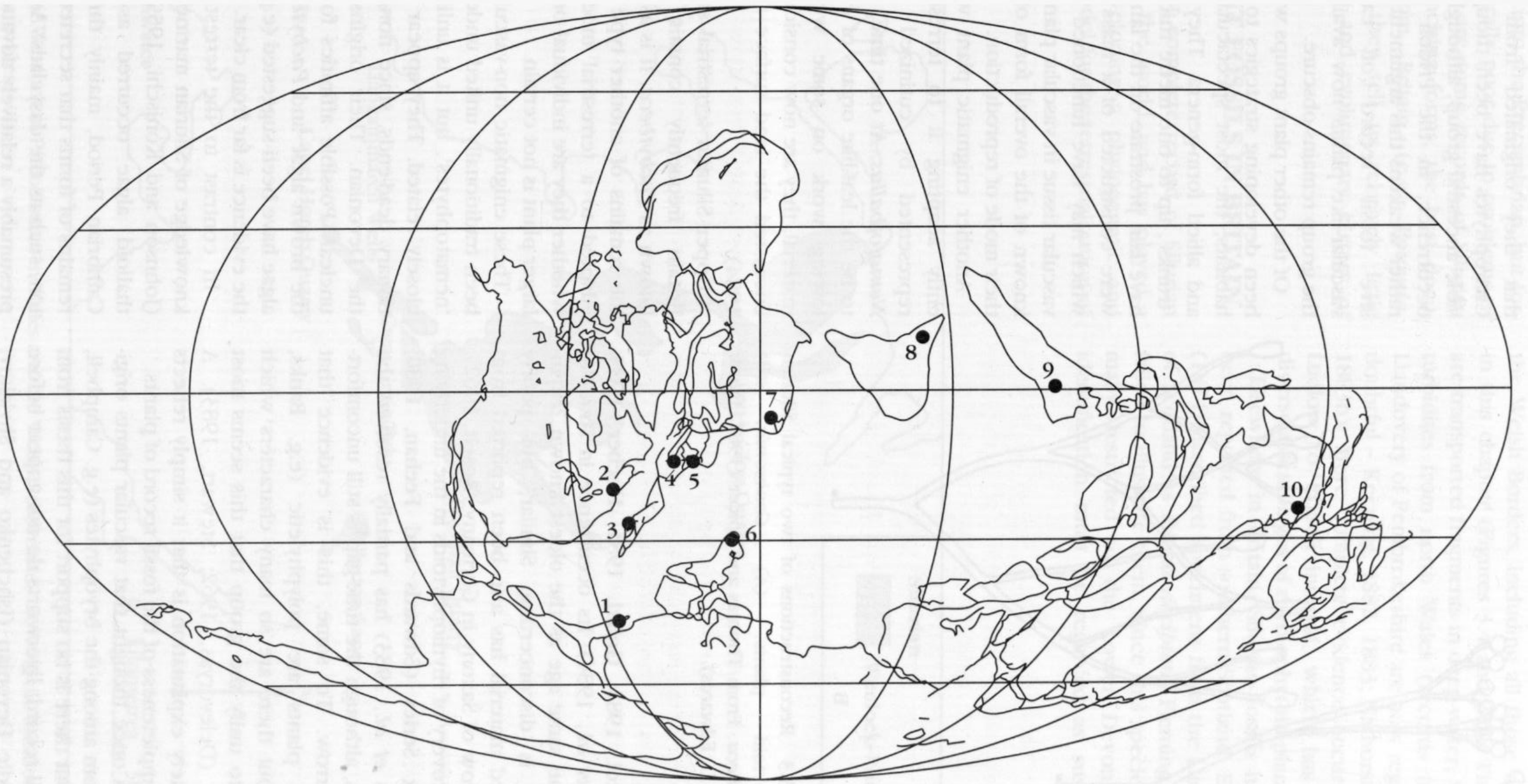

Figure 3.2 The palaeogeography of the Silurian, showing the location of the major fossil floras of this age. 1 – Virginia; 2 – Maine; 3 – New York State; 4 – Tipperary; 5 – Wales; 6 – Bohemia; 7 – Podolia; 8 – Kazakhstan; 9 – Xinjiang; 10 – Victoria. Based on Scotese and McKerrow (1990).

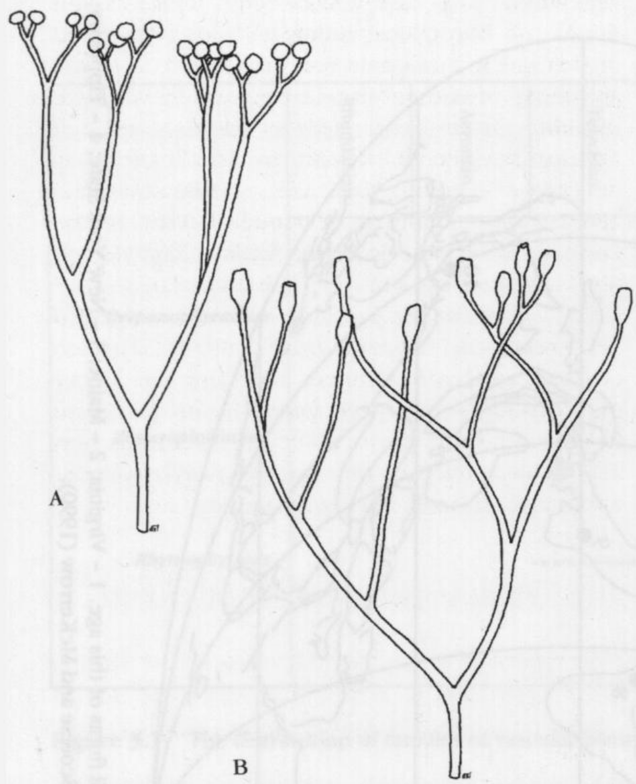

Figure 3.3 Reconstructions of two typical Silurian rhyniophytoid plants. (A) *Cooksonia*. (B) *Steganotheca*. From Thomas and Spicer (1987, figure 3.1; after D. Edwards).

Lejal-Nicol, 1981; Gould, 1981; Hueber, 1983; Garratt *et al.*, 1984). Its occurrence in strata of about the same age as the oldest known ?rhyniophytes is disconcerting. Similar, but poorly preserved material has also been reported from the Ludlow of Saxony in Germany (Roselt, 1962). The discovery of rhyniophytoids in the underlying Wenlock Series (Edwards and Feehan, 1980; Edwards *et al.*, 1983) has partially resolved the problem, although the time-gap is still uncomfortably narrow. To some, this is evidence that vascular plants are polyphyletic (e.g. Banks, 1968), but there are so many characters which appear to unify the group that this seems most unlikely (Delevoryas, 1962; Stewart, 1983). A more likely explanation is that it simply reflects the incompleteness of the fossil record of plants.

It was once thought that vascular plants originated from among the bryophytes (e.g. Campbell, 1895), but there is no support for this thesis from the fossil record; liverworts do not appear before the Middle Devonian (Ishchenko and Shylakov, 1979). The general consensus now seems to be that they originated from the green algae. Charophytes have been thought to be one possible ancestral group, although their lowest fossil occurrence, in the Přídolí (Ishchenko, 1975), rather weakens this argument. Despite the extensive fossil record of early vascular and vascular-like plants now available, the origin of the group remains obscure.

Of the other plant groups which appear to have been developing strategies to adapt to terrestrial habitats, the most spectacular was *Prototaxites* and allied form-genera. They had thick axes or 'trunks', up to one metre thick, which appear to have lain prostrate on the land surface. The axes were constructed of a mass of tubes, some of which may have functioned in a similar way to vascular tissue in vascular plants. However, little is known of the overall form of these plants or of their mode of reproduction.

Another enigmatic plant with features apparently adapting it to terrestrial conditions, is represented by cutinized sheets known as *Nematothallus*. At one time, these were thought to be the leaf-like organs of *Prototaxites* but, following work on some well-preserved British material, they are now considered to be thalli that encrusted the land surface (Edwards and Rose, 1984).

Upper Silurian terrestrial sedimentary rocks in Britain frequently contain spherical objects known as *Pachytheca*. It is assumed that they are the remains of another type of plant becoming adapted to a terrestrial mode of life, although whether they are individual organisms or part of a larger plant is not certain.

These enigmatic non-vascular land plants have been traditionally united under the umbrella-term 'nematophytes', but it is unlikely that they were closely related. They appear to represent evolutionary dead-ends, since none are known above the Devonian. Their origins and affinities are unclear. Possible affinities for *Prototaxites* with the brown algae and *Pachytheca* with the green algae have been suggested (e.g. Taylor, 1981), but the evidence is far from clear.

In contrast to the terrestrial vegetation, our knowledge of Silurian marine algae remains poor (Johnson and Konischi, 1959). It is known that thalloid algae occurred as far back as the Cambrian Period, mainly through the fossilized remains of forms that secreted a calcareous skeleton, such as the dasyclads. As lime secretion was presumably a relatively advanced specialization, it is likely that macroscopic branching algae occurred well back into the Precambrian, but fossil evidence is generally poor due to problems of preservation. There are some records of Silurian non-calcareous branching forms, the best documented being from Britain (e.g. *Powysia*, *Inopinatella*), but they tell us relatively little about the diversity and evolutionary history of such algal plants.

SILURIAN PLANT FOSSILS IN BRITAIN

Britain has the most complete record of Silurian land-plant fossils in the world, and has played a central role in developing a phylogenetic and palaeoecological model for the terrestrialization of vegetation. Most of the sites occur in Wales and the Welsh Borders, including all those described in this chapter (Figures 3.4 and 3.5). The oldest are transported fragments in deep-water, Wenlock turbidites from north Wales (records from the Llandovery of Pembrokeshire are now regarded as doubtful – Keeping, 1882, 1883; Nathorst, 1883a, 1883b). More complete evidence occurs in the Ludlow to Přídolí interval, which has yielded diverse assemblages of rhyniophytoid plants.

Elsewhere in Britain, Silurian fossils have also been reported from southern Scotland. Etheridge (1874) described specimens from the Llandovery of Scotland as *Parka decipiens* Fleming, but he failed to illustrate them. Since this species is normally restricted to the Lower Devonian, the identification must be regarded as suspect. A

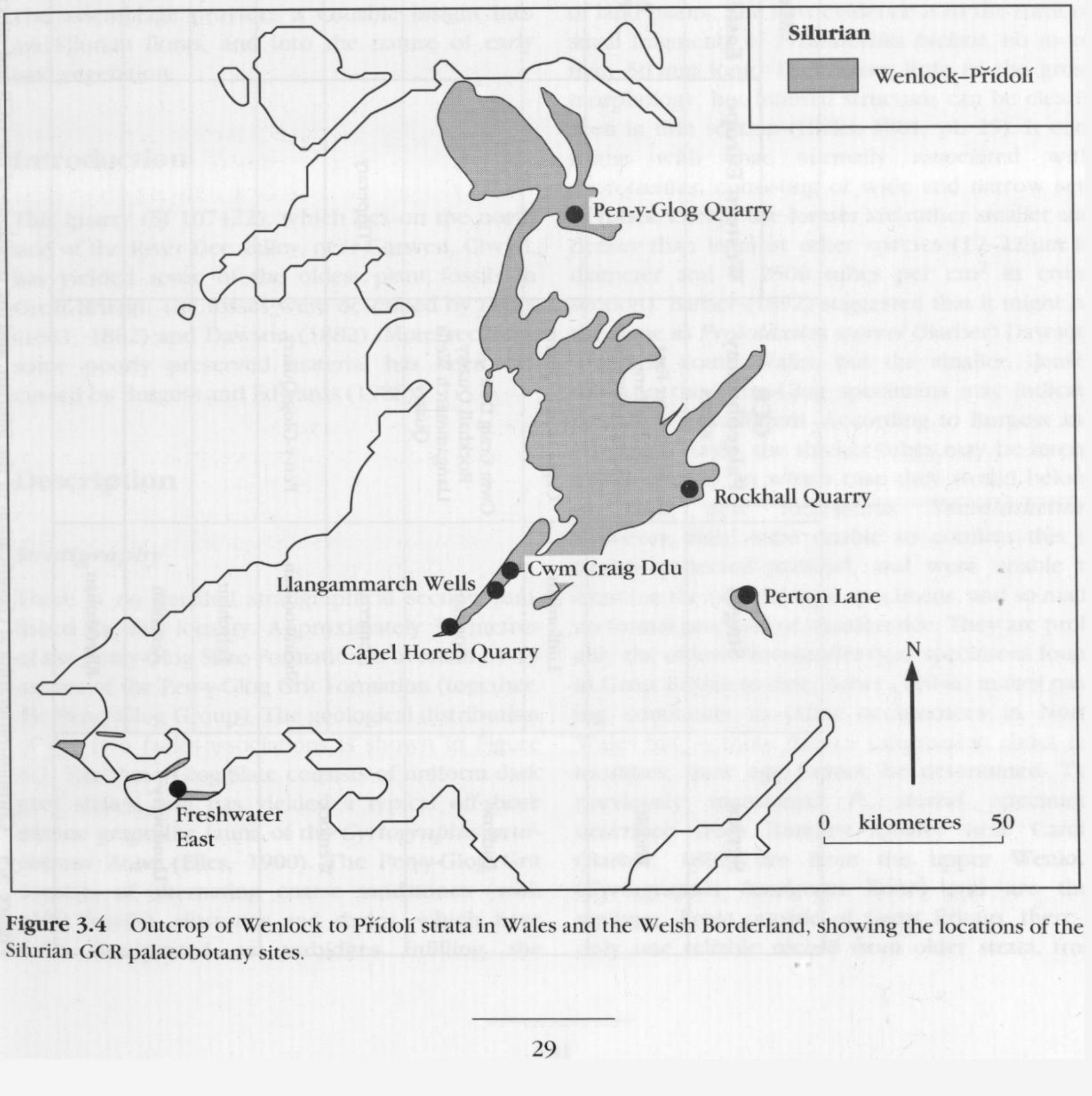

Figure 3.4 Outcrop of Wenlock to Přídolí strata in Wales and the Welsh Borderland, showing the locations of the Silurian GCR palaeobotany sites.

Series	Stages	GCR Palaeobotany sites	Main areas outside Britain			
			Western Europe	Eastern Europe	Asia/Australasia	North America
Přídolí		Freshwater East Perton Lane Capel Horeb Quarry		Bohemia Podolia	Kazakhstan Xinjiang	New York State
Ludlow	Ludfordian	Capel Horeb Quarry				
	Gorstian	Cwm Craig Ddu Quarry Rockhall Quarry Llangammarch Wells Quarry			Victoria	
Wenlock	Homerian		Tipperary			
	Sheinwoodian	Pen-y-Glog Quarry				
Llandovery	Telychian					Maine
	Aeronian					
	Rhuddanian					Virginia

Figure 3.5 Chronostratigraphical classification of the Silurian, and the positions of the GCR and other major palaeobotanical sites in this system.

variety of other problematic plant fossils have been recorded from the Hagshaw Hills and Lesmahagow area of Scotland (Crookall, 1930; Ritchie, 1963), which are probably late Llandovery or early Wenlock in age (Cocks *et al.*, 1971). Crookall's record of *Taitia* from here was the only one to be adequately described and illustrated, and even this is difficult to interpret, and may not even be a plant.

PEN-Y-GLOG QUARRY

Highlights

Pen-y-Glog Quarry has yielded the oldest, well-preserved *Prototaxites-Pachytheca* assemblage in Great Britain, and the oldest preserved as petrifactions from anywhere in the world (Figure 3.6). It has also yielded a number of other enigmatic plant fossils, including *Berwynia carruthersii* Hicks. The assemblage provides a valuable insight into mid-Silurian floras, and into the nature of early land vegetation.

Introduction

This quarry (SJ 107422), which lies on the north side of the River Dee valley, near Corwen, Clwyd, has yielded some of the oldest plant fossils in Great Britain. The fossils were described by Hicks (1881, 1882) and Dawson (1882). More recently, some poorly preserved material has been discussed by Burgess and Edwards (1988).

Description

Stratigraphy

There is no detailed stratigraphical section published for this locality. Approximately 30 metres of the Pen-y-Glog Slate Formation is overlain by 15 metres of the Pen-y-Glog Grit Formation (together, the Pen-y-Glog Group). The geological distribution of the two facies-associations is shown in Figure 3.7. The Pen-y-Glog Slate consists of uniform dark grey shales, and has yielded a typical off-shore marine graptolite fauna of the *Cyrtograptus murchisoni* Zone (Elles, 1900). The Pen-y-Glog Grit consists of alternating coarse sandstones (with plant fossils), siltstones and shales, which have been interpreted as turbidites infilling the Denbigh trough (Cummins, 1957), and which contain a *Monograptus riccartonensis* Zone fauna (Elles, 1900). The biostratigraphical evidence suggested is clearly indicative of a lower Sheinwoodian (early Wenlock) age.

Palaeobotany

The best preserved specimens are petrifactions from the sandstones, and include *Prototaxites hicksii* (Etheridge) Dawson and *Pachytheca* sp., together with some enigmatic spherical bodies. The underlying shales have yielded *Berwynia carruthersii* Hicks.

Interpretation

Other than some spores and cuticle fragments (Burgess, 1991; Burgess and Richardson, 1991), Pen-y-Glog has yielded the oldest known evidence of land plants. The best evidence is in the form of small fragments of *Prototaxites hicksii*, no more than 50 mm long. They show little of the gross morphology, but internal structure can be clearly seen in thin section (Hicks, 1881, pl. 25). It conforms with that normally associated with *Prototaxites*, consisting of wide and narrow sets of tubes, except the former are rather smaller and denser than in most other species (12–22 μm in diameter and *c.* 2500 tubes per cm^2 in cross-section). Barber (1892) suggested that it might be the same as *Prototaxites storrei* (Barber) Dawson, found in South Wales, but the smaller, denser tubes in the Pen-y-Glog specimens may indicate that they are different. According to Burgess and Edwards (1988), the thicker tubes may be internally thickened, in which case they would belong to their new form-genus *Nematasketum*. However, they were unable to confirm this in freshly collected material, and were unable to examine the original type specimens, and so made no formal proposal of transference. They are probably the oldest *Prototaxites*-type specimens found in Great Britain to date. Arber (1904a) makes passing comments to other occurrences in North Wales but, without further information about the localities, their age cannot be determined. The previously mentioned *P. storrei* specimens described from Rumney Quarry near Cardiff (Barber, 1892) are from the upper Wenlock (*Cyrtograptus lundgreni* Zone) and are thus younger. From outside of Great Britain, there is only one reliable record from older strata, from

Figure 3.6 Pen-y-Glog Slate Quarry. Cleaved Pen-y-Glog Slates in the lower part of the quarry face, that have yielded *Berwynia*. These are overlain by turbidites of the Pen-y-Glog Grits, that contain *Prototaxites*. (Photo: C.J. Cleal.)

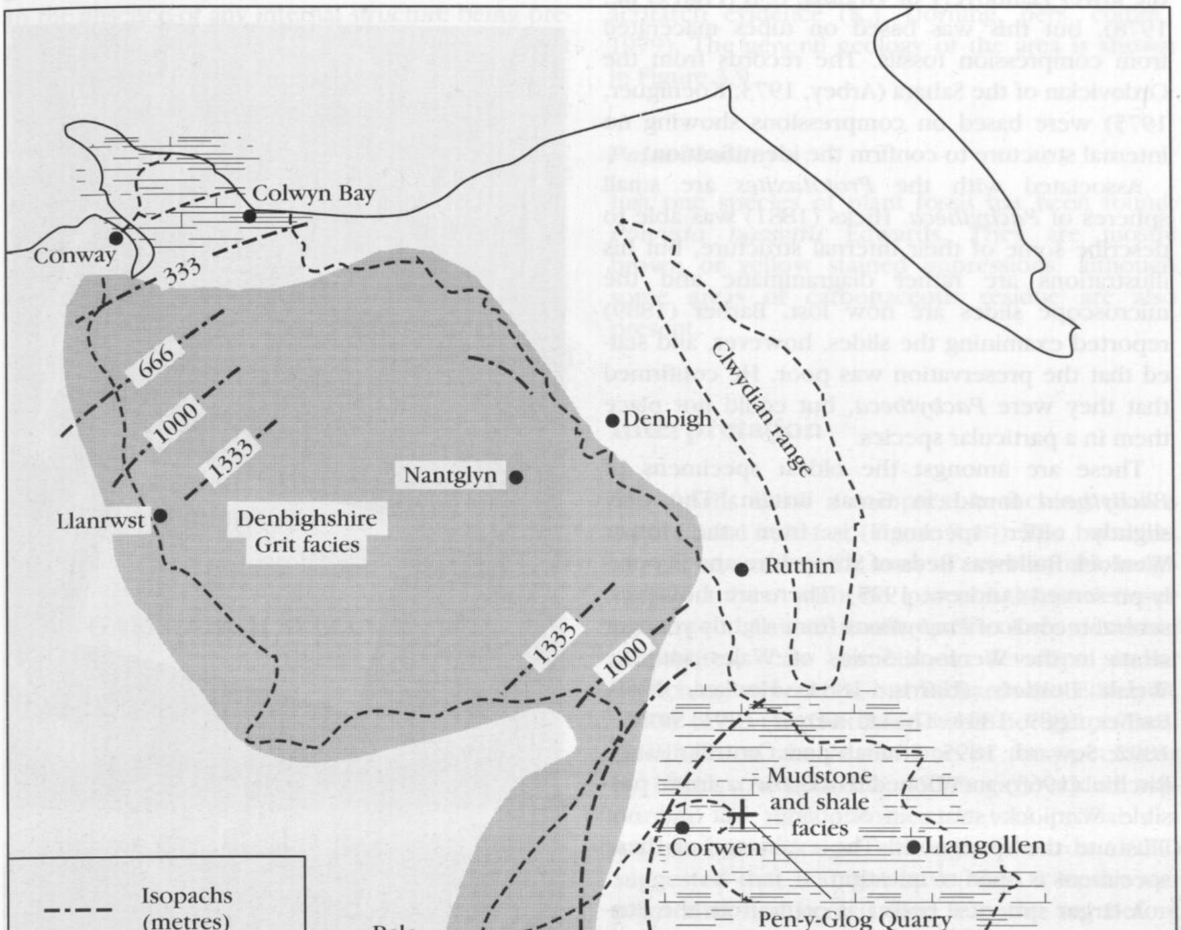

Figure 3.7 Distribution of grit and shale facies in the Wenlock of North Wales, showing the position of Pen-y-Glog Slate Quarry. Based on Smith and George (1961, figure 20).

the lower Llandovery of Virginia, USA (Pratt *et al.*, 1978), but this was based on tubes macerated from compression fossils. The records from the Ordovician of the Sahara (Arbey, 1973; Koeniguer, 1975) were based on compressions showing no internal structure to confirm the identification.

Associated with the *Prototaxites* are small spheres of *Pachytheca*. Hicks (1881) was able to describe some of their internal structure, but his illustrations are rather diagrammatic and the microscope slides are now lost. Barber (1889) reported examining the slides, however, and stated that the preservation was poor. He confirmed that they were *Pachytheca*, but could not place them in a particular species.

These are amongst the oldest specimens of *Pachytheca* found in Great Britain. The only slightly older specimen is from the lower Wenlock Buildwas Beds of Shropshire and is poorly preserved (Andrew, 1925). There are, however, several records of *Pachytheca* from slightly younger strata in the Wenlock Series of Wales and the Welsh Borders (Harris, 1884; Hooker, 1889; Barber, 1889, 1891; Thiselton-Dyer, 1891; Storrie, 1892; Seward, 1895; Strahan and Cantrill, 1912). Ritchie (1963) mentioned *Pachytheca* from possible Wenlock strata in Scotland, but did not illustrate the specimens. The exact age of these specimens is open to question.

A larger spherical body has come from the Pen-y-Glog sandstones (British Geological Survey collections, specimen no. zl 363); it is not well-preserved, but is larger (*c.* 8 mm in diameter) than the *Pachytheca* spheres found here, and does not show the characteristic two-layered structure of that genus. In a letter (dated 19th February 1946) kept with the specimen, W.H. Lang wrote that there was little doubt that it was a plant, but that it could not be identified beyond 'sphaerical body *incerta sedis*'.

The species from the sandstones are all of uncertain affinity, but both *Prototaxites* and *Pachytheca* are widely believed to be land plants. Their presence in mid-basinal marine sediments may be due to the sandstones being turbidites, the plant fragments having been transported into the deeper parts of the Welsh Basin by turbidity currents from a landmass, probably somewhere to the south.

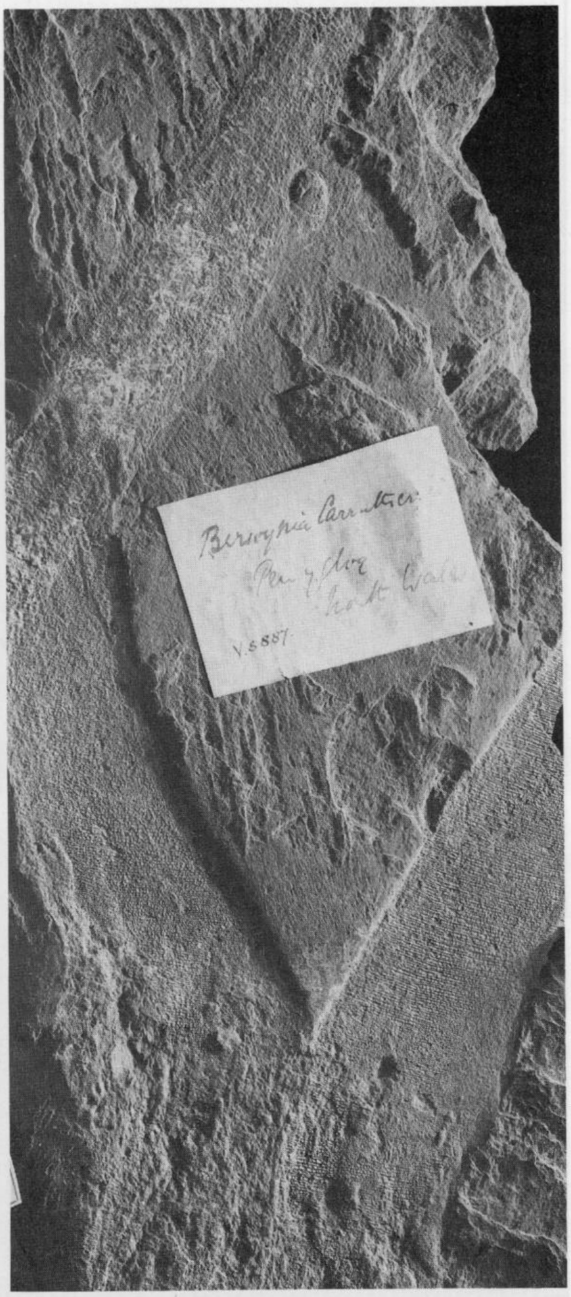

Figure 3.8 *Berwynia carruthersii* Hicks. Enigmatic, possibly algal plant; Natural History Museum, London, specimen V.5887. Pen-y-Glog Slate Formation (Wenlock), Pen-y-Glog Slate Quarry. × 0.5. (Photo: Photographic Studio, Natural History Museum, London.)

Berwynia carruthersii Hicks (Figure 3.8) represents parallel-sided, sometimes branching axes, preserved as anthracitic coal (Hicks, 1882). Many have a rugose surface, which Hicks interpreted as spirally arranged leaf bases, but it is too irregular for this to be likely. Also visible are zones along the margins of the axes, which show a rather finer patterning. However, this and the irregular rugose patterning are probably just a taphonomic effect. In the absence of any internal structure being preserved, it is impossible to be certain as to what group of plants *Berwynia* belongs.

Hicks (1882) described some other enigmatic fragments from the Pen-y-Glog shales as *Parka*, but they are too poorly preserved for this to be confirmed.

Conclusion

Other than some spores, Pen-y-Glog has yielded the oldest evidence of land vegetation in Britain, about 427 million years old. The fossils are also the oldest-known land plant fossils in the world that show details of cell structure, but are not closely related to anything living today.

LLANGAMMARCH WELLS QUARRY

Highlights

Llangammarch Wells Quarry is the only known locality to yield undoubted specimens of *Powysia bassettii* Edwards, one of only two non-calcareous algae known from the Silurian.

Introduction

This site, a small quarry in lower Ludlow marine siltstones near Llangammarch Wells, Powys (SN 937472), has yielded unusually well-preserved compressions of algae. They were first figured by Bassett and Edwards (1973, p. 4) and were subsequently named and described in full by Edwards (1977).

Description

Stratigraphy

The geology of the quarry has been discussed by Bassett (*in* Baker and Hughes, 1979). The sequence consists of dark grey, graptolitic siltstones and shales, representing a marginal marine setting. The part of the quarry containing the plant fossils has yielded graptolites of the lower *Neodiversograptus nilssoni* Zone, indicating a Gorstian (early Ludlow) age. This is supported by acritarch evidence (K.J. Dorning, pers. comm., 1979). The general geology of the area is shown in Figure 3.9.

Palaeobotany

Just one species of plant fossil has been found: *Powysia bassettii* Edwards. They are mostly brown or yellow stained impressions, although some areas of carbonaceous residue are also present.

Interpretation

The fossils show a complex, branching thallus with a basal hold-fast (Figure 3.10). The branches appear to consist of a mass of intertwined, longitudinal tubes, with no parenchymatous tissue preserved. Animal fossils, particularly dendroid graptolites, can sometimes develop similar branching structures, but Rickards (*in* Edwards, 1977) believed that these were not graptolites. Geochemical analysis of one of the specimens by Niklas (*in* Edwards, 1977) gave added support to its algal affinities. It was probably a marine benthic alga, although Edwards (1977) suggested that it might have been a freshwater plant that had been swept into the sea before burial.

This is the only locality known to yield well-preserved *Powysia*. Specimens in the Department of Palaeontology, The Natural History Museum, London, collected from Wenlock Series beds at Dudley and in the Pentland Hills, show similar branching structures. None, however, show any structural details to confirm that they belong to *Powysia*. It is one of only two fully described non-calcareous algae known from the Silurian, the other being *Inopinatella* (see Rockhall Quarry, below).

Conclusion

Llangammarch Wells Quarry has yielded one of the very few examples of a non-calcareous marine alga (*Powysia*) known from the Silurian (423 Ma). Although a few other sites have yielded fossils of this type, the Llangammarch Wells material is the best preserved, yielding some details of internal structure.

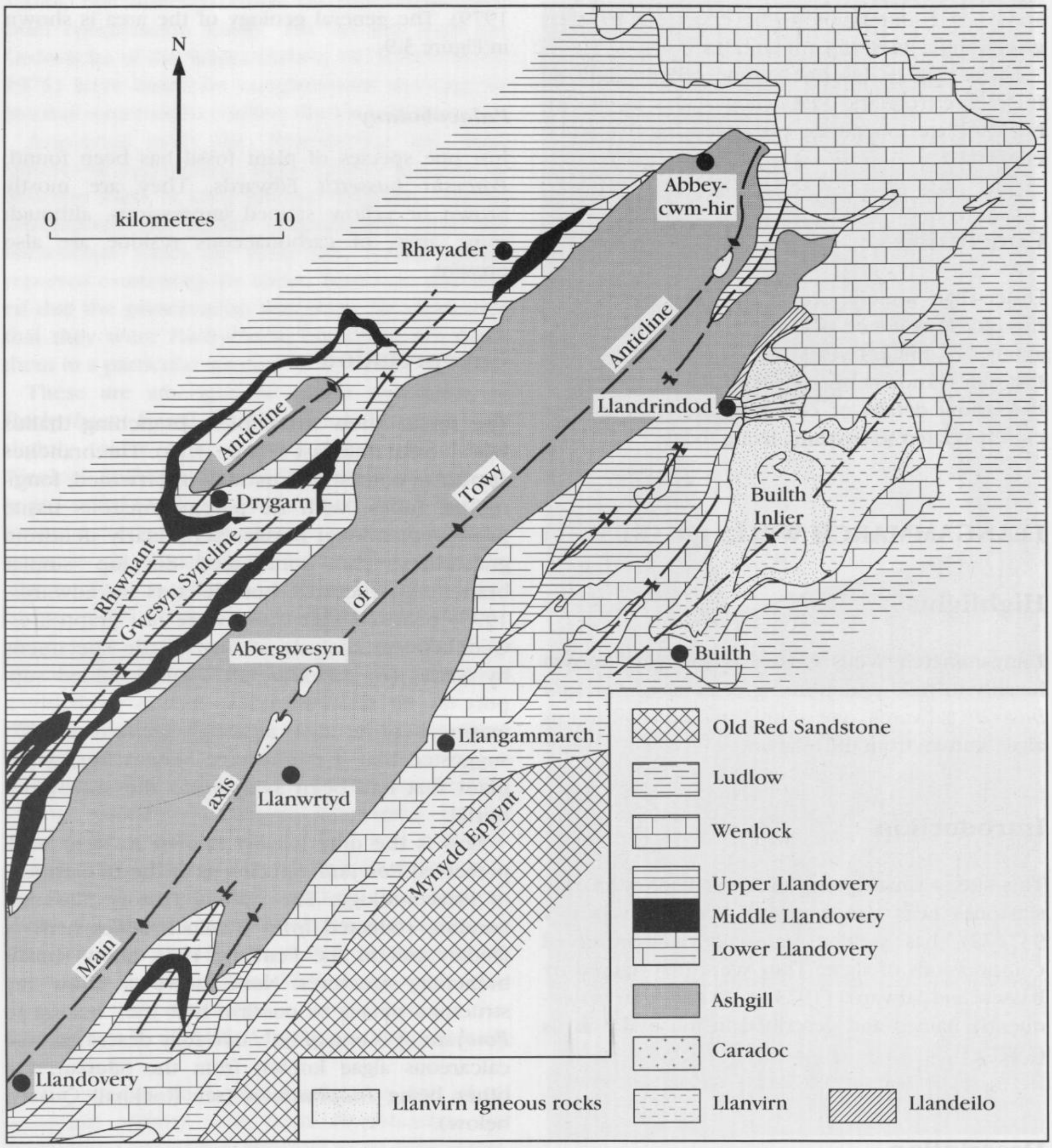

Figure 3.9 Geological map of the area around Llangammarch Wells. The quarry yielding the plant fossils lies just to the east of the village as marked on the map. Based on George (1970, figure 14).

ROCKHALL QUARRY

Highlights

Rockhall Quarry is the only known locality for *Inopinatella lawsonii* Elliott, which is the only Palaeozoic example of what might be a non-calcified dasyclad alga. It is thus potentially significant for helping us to understand the early evolutionary development of this important family of marine plants.

Figure 3.10 *Powysia bassettii* D. Edwards. Enigmatic branched alga; National Museum of Wales, specimen 72.39G1a (holotype). Graptolitic shales (lower *Neodiversograptus nilssoni* Zone - Gorstian), Llangammarch Wells Quarry. × 1.6. (Photo: Photographic Studio, National Museum of Wales.)

Introduction

This Silurian limestone quarry lies just north of the village of Aymestry, in the county of Hereford and Worcester (SO 423655). Plant fossils were described from here by Elliott (1971), who interpreted them as probably algal in origin.

Description

Stratigraphy

This is the type locality for the Aymestry Limestone Formation, which is a lower Gorstian (lower Ludlow) shallow marine deposit (Holland *et al.*, 1963).

Palaeobotany

Elliott (1971) described the plant fossils as *Inopinatella lawsonii* Elliott; they are mostly preserved as coalified compressions.

Interpretation

This is the only locality to yield *I. lawsonii* (Figure 3.11), which probably grew on the edge of a shallow marine shelf. It has a main stem *c.* 0.3 mm wide and more than 30 mm long, and with branches attached in whorls of four. No reproductive structures have been found, but Elliott noted a similarity to the juvenile stages of the extant dasyclad *Neomaris*, and suggested that it may have been a primitive non-calcified example of that family. If correct, then *Inopinatella* is the only known non-calcified dasyclad to have been found in the Palaeozoic. The Dasycladales has a fossil record that extends back to the Cambrian (Meyen, 1987), but the preservation potential of non-calcified forms would be very low, which could explain their absence in the pre-Silurian fossil record.

Conclusion

Rockhall Quarry has yielded the only known examples of a marine alga, *Inopinatella*, which is about 420 million years old. It is thought to belong to the group known as the dasyclads, which have been important components of benthic vegetation for over 500 million years. Most members of the group have a calcified body, and at one time in the geological past (*c.* 200 million years ago) they were major reef-building organisms. *Inopinatella* was not calcified, however, and is thought to have been a primitive, early representative of the group.

Figure 3.11 *Inopinatella lawsonii* Elliott. Non-calcified, possibly dasyclad alga; Natural History Museum, London, specimen V.31287. Aymestry Limestone Formation (upper Gorstian), Rockhall Quarry. × 2. (Photo: Photographic Studio, Natural History Museum, London.)

CWM CRAIG DDU QUARRY

Highlights

Cwm Craig Ddu has yielded the oldest known specimens of *Cooksonia* in Great Britain, and is only marginally pre-dated by the oldest known specimens from anywhere in the world. They represent what is probably the most primitive type of vascular plant, and are thus of key importance for understanding the early phases in the development of vegetation on land.

Introduction

This locality comprises a small roadside quarry in Ludlow-aged siltstones on the north-eastern slopes of Mynydd Eppynt, between Llanwrtyd Wells and Builth Wells, Powys (SN 962475). Plant fragments from here were first reported by Straw (1953), and more were discovered in 1973 during a Geologists' Association field meeting (Baker and Hughes, 1979). The most comprehensive account of the flora is given by Edwards *et al.* (1979), who described a number of sterile and fertile fragments of rhyniophytoid plants (*sensu* Edwards and Edwards, 1986).

Description

Stratigraphy

The geology of this quarry has been discussed by Straw (1930, 1937), Bassett (*in* Baker and Hughes, 1979) and Edwards *et al.* (1979). The exposed sequence belongs to the Pterinea Beds, the basal member of the Wilsonia Shales Formation (Straw, 1937). The beds represent deposits formed on the palaeoslope on the eastern margin of the Welsh basin. It contains a fauna, including rhynchonellid brachiopods, bryozoans, nautiloids, bivalves and rare graptolites, belonging to the *Saetograptus leintwardinesis incipiens* Zone (Straw, 1937; Bassett *in* Baker and Hughes, 1979), indicating a late Gorstian (early Ludlow) age, although acritarchs collected by K.J. Dorning (pers. comm., 1979) have given a mid-Gorstian age.

Palaeobotany

Edwards *et al.* (1979) recorded *Hostinella* sp., *Cooksonia pertoni* Lang, *Cooksonia* sp. and cf. *C. cambrensis* Edwards from here. They are mostly preserved as coalified compressions. Specimens are rare and generally fragmentary, rarely exceeding a few millimetres in size.

Interpretation

The specimens found here have slender, occasionally dichotomous, branching axes. Mostly, they are sterile and thus placed in the form-genus *Hostinella*. A dark central line, suggestive of vascular tissue, occurs along some of them. Even using film pulls, Edwards *et al.* (1979) were unable to obtain microscopic evidence of tracheids to confirm that this is vascular tissue, but they did reveal some evidence of epidermal and/or cortical cells.

Three of the specimens described by Edwards *et al.* showed thin axes terminated by single, small sporangia (one of these specimens is represented by both the part and counterpart). The sporangia varied in shape and were assigned to different 'species', although Edwards *et al.* were clearly uneasy at identifying more than one species from here based on such limited material. There can be little doubt, however, that they belong to the form-genus *Cooksonia* (Figure 3.12).

Cooksonia is widely regarded as the most primitive vascular land plant (Taylor, 1981; Thomas and Spicer, 1987; Edwards *et al.*, 1992). For a time, the Cwm Craig Ddu specimens were the oldest examples of *Cooksonia* known from anywhere in the world. Although older specimens are now known from the Wenlock of Ireland (Edwards and Feehan, 1980; Edwards *et al.*, 1983), they are still the earliest found in Great Britain. They are thus of considerable interest for charting the early history of the British land floras and demonstrating the morphological simplicity of the first vascular plants to appear on land in this part of the world. They contrast with the more advanced plants found in approximately coeval strata in Gondwana (the *Baragwanathia* flora) and suggest that even at this early time there was a clear difference between the land vegetation of the southern low palaeolatitudes and the rest of the world.

Conclusion

Cwm Craig Ddu Quarry has yielded specimens of *Cooksonia* that are some 420 million years old, and which are the oldest examples of this primitive land plant to have been found in Great Britain. This is widely thought to be the ancestral form of most if not all land vascular plants. It is only marginally pre-dated by similar fossils in Ireland, which are at present the oldest examples of such plants from anywhere in the world.

Figure 3.12 *Cooksonia pertoni* Lang. Earliest examples of rhyniophytoid land plants known from Great Britain; National Museum of Wales, specimen 79.17G3. Wilsonia Shales Formation (lower Ludlow), Cwm Craig Ddu Quarry. × 5. (Photo: Photographic Studio, National Museum of Wales.)

CAPEL HOREB QUARRY

Highlights

Capel Horeb Quarry has yielded the earliest examples of plant axes with vascular tissue found anywhere in the world (Figure 3.13). This is thus the oldest unequivocal evidence of a land vascular plant.

Introduction

This site is a disused quarry near Llandovery, Powys (SN 844323), and has yielded plant fossils of Ludlow and also possibly Přídolí age. The fossils are usually very fragmentary, and some early descriptions of the site make little or no mention of them (Straw, 1930; Potter and Price, 1965).

Figure 3.13 Capel Horeb Quarry. The bedding plane on the left of the picture is of upper Ludlow beds of the Upper Roman Camp Formation. These are overlain by upper Ludlow or lower Přídolí beds of the Long Quarry Formation. (Photo: C.J. Cleal.)

Better preserved material has been found, as described by Heard (1939), Edwards (1970b, 1982), Edwards and Davies (1976) and Edwards and Rogerson (1979).

Description

Stratigraphy

The geology of this site has been described by Straw (1930), Potter and Price (1965), Edwards and Richardson (*in* Friend and Williams, 1978) and Edwards and Rogerson (1979). The lower part of the sequence consists of shallow marine siltstones and sandstones with a restricted shelly fauna, and belongs to the Upper Roman Camp Formation. Faunal evidence discussed by Potter and Price (1965) suggests a late Ludlow (mid-Ludfordian) age for these strata, a conclusion supported by the microfossils (Dorning *in* Edwards and Davies, 1976). Lying unconformably above these beds is the Long Quarry Formation (Figure 3.14), which has been interpreted as either upper Ludlow (Richardson and Lister, 1969) or lower Přídolí (Potter and Price, 1965). They are probably littoral siltstones and sandstones. The topmost part of the sequence belongs to the Red Marls Formation.

Palaeobotany

The following plant fossils have been reported from the Upper Roman Camp Formation here:

Phaeophycophyta(?):
- *Nematothallus* sp.
- *Nematoplexus* sp.

Rhyniophytoids:
- *Cooksonia hemisphaerica* Lang
- cf. *C. caledonica* Edwards
- *Steganotheca striata* Edwards

The Long Quarry Formation has yielded the following rhyniophytoids:

- *Cooksonia* cf. *pertoni* Lang
- *S. striata* Edwards
- cf. *Renalia* sp.

The thalloid-like structure described by Heard and Jones (1931a) as *Eohepatica dyfriensis*, and by Heard and Jones (1931b) as *Thallomia llandyfriensis*, is now believed to be part of a dictyocarid arthropod (Rolfe, 1969).

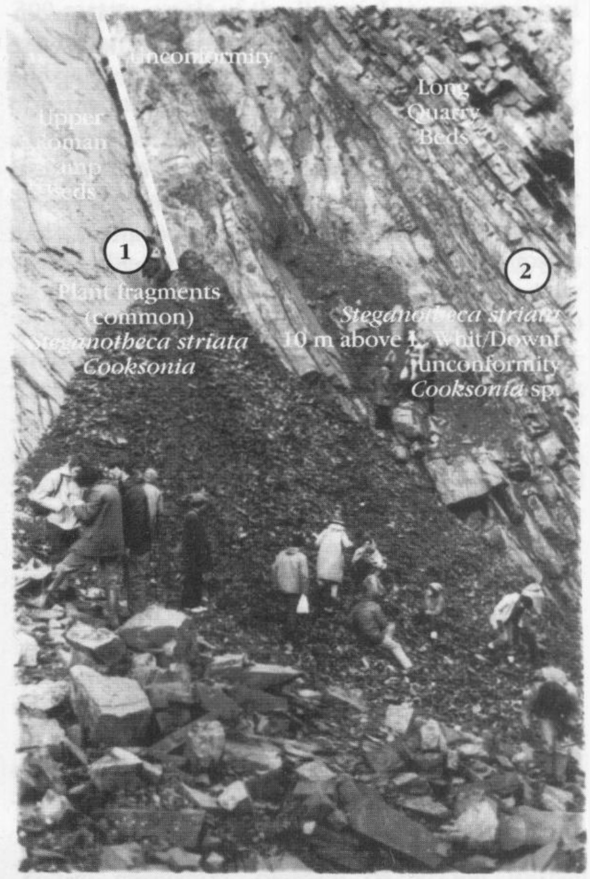

Figure 3.14 Close-up of part of the face of Capel Horeb Quarry, showing the relationship between the two plant-bearing intervals. (Photo: B.A. Thomas.)

Interpretation

The Upper Roman Camp flora appears to be dominated by what are probably non-vascular land plants, such as *Nematothallus*. Bulk maceration has yielded cuticles showing a reticulate pattern on their inner surface, characteristic of the genus (Edwards, 1982). There is considerable variation in this patterning, but it is not yet clear whether more than one species is present. The evidence from Capel Horeb suggests that *Nematothallus* was a thalloid, encrusting plant, rather than a leaf-like structure of a *Prototaxites*, as suggested by Lang (1937) and Jonker (1979).

Edwards (1982) also found a variety of fine tubes in her bulk maceration samples. The majority were isolated tubes of uncertain affinity. There were, however, some clusters of tubes that resemble those found in *Prototaxites* axes. These were named *Nematoplexus* by Edwards, following the nomenclature of Lyon (1962).

Rhyniophytoid plants are represented here by a number of different taxa recognized on the basis of their reproductive structures. The most abundant belong to *Cooksonia*. The specimens from the Upper Roman Camp Formation have mostly globose sporangia, which can be identified as *C. hemisphaerica* (Edwards and Rogerson, 1979), although one was assigned to cf. *C. caledonica* (Edwards and Rogerson, 1979, pl. 1 fig. d). Other specimens from these strata had more elongate sporangia, which lie outside the circumscription of *Cooksonia* as defined by Lang (1937), and were not identified by Edwards and Rogerson. *C. hemisphaerica* is known to have a variety of sporangial shapes (Edwards, 1979a) and the possibility that these slightly more elongate forms belong there cannot be excluded.

Only one fertile specimen of *Cooksonia* has been reported from the Long Quarry Formation here (Edwards and Rogerson, 1979, pl. 1 fig. h). This showed squatter sporangia than those from the Upper Roman Camp Formation and was identified as *C.* cf. *pertoni* Lang.

This is the type locality for another type of rhyniophytoid plant: *Steganotheca striata* Edwards, 1970b (fig. 8b and Figure 3.15). It occurs in both the Upper Roman Camp and Long Quarry formations. Like *Cooksonia*, it has slender, dichotomous axes with terminal sporangia. The sporangia are, however, elongate and less well individualized, and usually show a heavily carbonized, lenticular structure at the apex. It is at present unclear whether this structure is simply due to compression of the sporangial tip, or is evidence of a dehiscence structure. Because of the elongate shape of the sporangia and isotomous branching, Edwards (1970b) initially placed *Steganotheca* in the Rhyniaceae, but it has subsequently been described as rhyniophytoid (Pratt *et al.*, 1978; Edwards and Edwards, 1986).

The holotype of *Cooksonia downtonensis* Heard, which originated from Capel Horeb (Heard, 1939), was transferred to *S. striata* by Edwards (1970b). It is arguable that Heard's name for this species should take priority, but this is not the place to propose a new combination.

A single specimen from the Long Quarry Formation (Edwards and Rogerson, 1979, pl. 1 fig. i) shows a more complex branching pattern than the other rhyniophytoid species found at Capel Horeb. Edwards and Rogerson compared it with *Cooksonia hemisphaerica* Ananiev and Stepanov, 1969, *non* Lang, which Gensel (1976) has in turn compared with *Renalia*. The latter shows characters intermediate between the Rhyniaceae and Zosterophyllaceae and there has been some disagreement as to its taxonomic position. However, Edwards and Edwards (1986) have recently argued that it belongs to the Rhyniaceae, and that its zosterophyll-like characters are due to evolutionary convergence.

Figure 3.15 *Steganotheca striata* D. Edwards. One of the earliest known land plants; National Museum of Wales, specimen 69.64G32a (holotype). Upper Roman Camp Formation (upper Ludlow), Capel Horeb Quarry. × 1.5. (Photo: Photographic Studio, National Museum of Wales.)

Far commoner than the fertile rhyniophytoid specimens discussed above are unbranched and dichotomous axes without sporangia. Being sterile, it is impossible to identify them beyond *Hostinella* sp. However, examples from the Upper Roman Camp Beds have been shown to have *in situ* tracheids (Edwards and Davies, 1976), the earliest known examples of axes with such tissue. Prior to Edwards and Davies' (1976) study, the oldest known axes with *in situ* tracheids were from the basal Devonian at Targrove

Quarry (Lang, 1937). As with the Capel Horeb specimens, none of the Targrove axes with tracheids bore sporangia and so it has been impossible to confirm their identification. However, they were found in association with fertile specimens of *Cooksonia hemisphaerica*, and it has been widely asserted that they belonged to the same plant (e.g. Taylor, 1981). Dispersed tracheids have been reported from strata as old as the Cambrian (Gosh and Bose, 1952; Jacob *et al.*, 1953) but Banks (1975a) has argued that these cannot be relied on as evidence of the presence of the Tracheophyta, because of possible reworking or contamination. The Capel Horeb specimens are thus the oldest indisputable evidence of land vascular plants.

Conclusion

Capel Horeb has yielded the oldest unequivocal evidence of plants with vascular conducting tissue (xylem) from anywhere in the world; the fossils are *c.* 415 million years old. The development of this tissue was one of the key steps that helped plants overcome the hydraulic problems inherent with living on the land, and thus paved the way for the evolution of land vegetation as we see it today.

PERTON LANE

Highlights

Perton Lane is a classic site for Přídolí Series plant fossils, being the first to be subject to a detailed palaeobotanical investigation. It is the type locality for *Cooksonia*, widely regarded as the most primitive known vascular plant, and the only known locality for *Caia* and the enigmatic *Actinophyllum*.

Introduction

This small roadside exposure of Ludlow and Přídolí shales in the village of Stoke Edith, Hereford and Worcester (SO 598403) is one of the classic sites for British Silurian palaeobotany. There has been some confusion over the name of the site, since it has been referred to as Perton Quarry (e.g. by Lang, 1937). As pointed out by Edwards *et al.* (1979), however, Perton Quarry is a large exposure of middle Ludlow limestones, *c.* 300 metres south of the Perton Lane Section, and the latter name is now generally used for the fossil-bearing outcrop.

Plant fossils from here were first recorded by Phillips (1848) and Phillips and Salter (1848), who described what may be algal fertile structures. Slender, branching axes were described by Brodie (1869, 1871) and were compared by Carruthers (*in* Brodie, 1871) with *Psilophyton*. Plant fossils from here have also been briefly discussed by Barber (1889), Richardson (1907), Stamp (1923) and Straw (1926). Until recently, the most complete account of the assemblage was by Lang (1937). Subsequently, however, there have been significant contributions by Fanning (1987), Fanning *et al.* (1990, 1991) and Burgess and Edwards (1988).

Description

Stratigraphy

The geology of this site is covered by Brodie (1871), Straw (1926), Squirrell and Tucker (1960, 1967) and Edwards *et al.* (1979). The sequence consists of Ludfordian (upper Ludlow) Upper Perton Formation, overlain by Přídolí Rushall Formation. The Rushall Formation, which yields the plant fossils, belongs to interval I.1 in King's (1925) lithostratigraphy. It consists mainly of buff to light grey mudstones with thin sandstone bands, and probably represents littoral deposits.

Palaeobotany

The plant fossils from here are preserved as coalified compressions. The following species have been found to date:

Phaeophycophyta(?):
Nematothallus pseudovasculosa Lang
Nematasketum diversiforme Burgess and Edwards

Chlorophycophyta(?):
Pachytheca sp.

Rhyniophytoids:
Cooksonia pertoni Lang
Pertonella dactylethra Fanning, Edwards and Richardson

Caia langii Fanning, Edwards and Richardson
Salopella sp.
Hostinella sp.

Uncertain affinities:
Actinophyllum sp.

Interpretation

This is the type locality for *Cooksonia pertoni*, which is the type species for the form-genus (Figure 3.16). It is widely believed to be the most primitive known vascular plant. It is difficult to envisage an upright land plant with a simpler morphology, with its thin, isotomously forked aerial shoots, no leaves or other macroscopic emergence, and terminally-borne sporangia lacking a dehisence structure. Specimens from elsewhere (locality details not yet published) have shown evidence of stomata and peripheral supporting tissue around the axes (Edwards *et al.*, 1986) and, most recently, a vascular strand (Edwards *et al.*, 1992).

Evidence from *in situ* spores suggests that at least three species of plant bore *C. pertoni*-type sporangia (Edwards *et al.*, 1986). However, the shape of the sporangia is morphologically indistinguishable in all three and so the name *C. pertoni* may be retained as a form-species for such structures.

Two further species of rhyniophytoid have been described recently by Fanning *et al.* (1990, 1991), both of which are characterized by prominent spines. *Pertonella dactylethra* is morphologically very similar to *C. pertoni*, except for the spinose sporangia. *Caia langii*, on the other hand, has significantly more elongate sporongia, rather resembling *Horneophyton* from Rhynie. Fanning *et al.* gave various suggestions as to possible functions for the spines: (a) they increased the photosynthetic area near the sporangia, where there would be considerable energy-demands; (b) they protected the sporangia from predation; and (c) they trapped moisture, helping to protect the developing sporangia from desiccation.

Fossils of uncertain affinity but given the coral-related name *Actinophyllum* are known only from this exposure. Phillips (1848) compared the genus with the fertile structures of the extant dasyclad alga *Acetabularia* but, as it is only known from isolated specimens, the point is difficult to confirm. Straw (1926), who has provided the best photographic record of these fossils, discussed the possibility of it being a coral, but finally came to the conclusion that Phillips' suggestion was more likely to be correct.

Lang (1937) described some poorly preserved specimens from this locality as *Prototaxites*, but better material has since been obtained by Burgess and Edwards (1988). These new specimens differ from *Prototaxites* principally in the presence of internally differentially-thickened tubes. The functional significance of this feature is still unclear. However, it was regarded as sufficiently different from *Prototaxites* to justify the establishment of a new genus and species, *Nematasketum diversiforme* (holotype from Lye Stream near Morville, Shropshire).

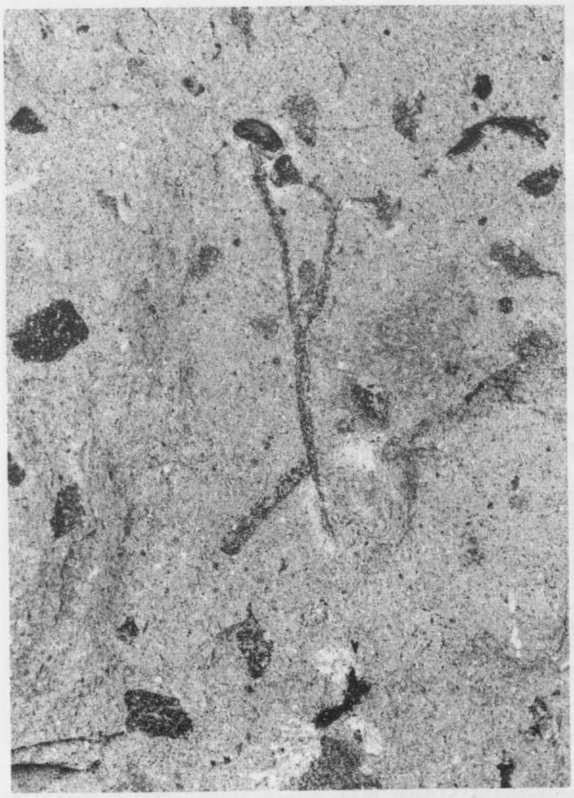

Figure 3.16 *Cooksonia pertoni* Lang. A fertile specimen from the type locality of this important early land plant; Natural History Museum, London, specimen V.58009. Rushall Formation (Přídolí), Perton Lane. × 3. (Photo: Photographic Studio, Natural History Museum, London.)

Conclusion

Perton Lane is the classic locality for the study of the earliest land vegetation, living *c.* 410–420 Ma, and is where W.H. Lang made many of his pioneering discoveries in the 1930s. It is the type locality for *Cooksonia*, which is widely regarded as the archetypal primitive land plant, and is central to any discussion on the earliest evolutionary history of the vascular plants. It is also the only known locality for *Caia*, which has very unusual spiny reproductive organs.

FRESHWATER EAST

Highlights

Freshwater East has yielded the most diverse Silurian flora from anywhere in the world, and is particularly rich in rhyniophytoid species (Figure 3.17). This has proved of great importance for determining the ranges of morphological variation of these primitive land plants, and particularly of their reproductive structures. It is the type locality for *Cooksonia cambrensis* Edwards and *Tortilicaulis transwalliensis* Edwards, and has yielded the oldest known examples of spiny axes.

Introduction

Sandstone exposures on the north side of Freshwater East Bay, Dyfed (SS 024981) have yielded a variety of upper Silurian plant fossils. The fossils were first noted here by Dixon (1921), and a number were included in Lang's (1937) classic study on English and Welsh Přídolí Series floras. A more recent account of part of the flora has been provided by Edwards (1979a).

Description

Stratigraphy

The geology of this site has been described by Dixon (1921). The plant fossils were found in a

Figure 3.17 Freshwater East. View across bay towards the Late Silurian plant-bearing exposures in the Freshwater East Formation. (Photo: C.J. Cleal.)

0.3 m-thick grey sandstone within the Milford Haven Group (Figures 3.18 and 3.19). King (1934) correlated these beds with the Ledbury Marl Formation of the Welsh Borderland, and a Přídolí age has been confirmed by spores described by Richardson and Lister (1969). Allen and Williams (*in* Edwards, 1979a) have interpreted this part of the Freshwater East sequence as having accumulated on coastal mudflats.

Palaeobotany

The following species have been reported from here:

Phaeophycophyta(?):
Nematothallus pseudovasculosa Lang
Prototaxites sp.

Chlorophycophyta(?):
Pachytheca sp.

Rhyniophytoids:
Cooksonia hemisphaerica Lang *emend.* Edwards
C. cambrensis Edwards
cf. *C. caledonica* Edwards
cf. *C. pertoni* Lang
Cooksonia sp.
Tortilicaulis transwalliensis Edwards
cf. *Salopella* sp.
Hostinella sp.
Psilophytites sp.

The specimens are preserved as adpressions. Occasionally, some iron oxide and iron sulphide occurs on them, but no evidence of permineralization has been found (Edwards, 1979a).

Interpretation

This flora is characterized by an abundance of fertile rhyniophytoid specimens. By far the commonest were identified as *Cooksonia* by Edwards (1979a), who used 83 of the most complete examples to analyse the variation in sporangial shape and attachment. This allowed her to identify five form-species from here, one of which (*C. cambrensis*) was new. It also allowed her to emend Lang's (1937) diagnosis for *C. hemisphaerica*. She recognized the problem of identifying species on what are relatively minor differences, but argued that it was the only practical way of analysing such morphologically simple and fragmentary plant fossils. This is by far the most diverse *Cooksonia* assemblage reported from anywhere in the world.

Tortilicaulis transwalliensis was described from a number of unbranched axes bearing terminal, elongate bodies (Figure 3.20). The latter were presumed to be sporangia, although no spores were obtained from them. Neither was any evidence of tracheids found in the axes. A distinctive feature of the species is that the axes have a non-rigid appearance, often seeming to be twisted. It has elongate sporangia, similar to those of *Sporogonites*, but lacks some of the well-defined characters of the latter, such as the longitudinal folds and the sterile basal region. Consequently, Edwards placed it in a separate form-genus. Edwards also found some features shared with certain extant bryophytes, particularly the twisted axes, but again the preservation precluded an assignment.

A small number of specimens were axes, this time showing no evidence of twisting, which bore rather smaller, elongate sporangia. Edwards (1979a) compared these with *Salopella* of Edwards and Richardson (1974), but was unable to place them in any particular species.

As is normal in Přídolí age floras, fragmentary sterile axes are far commoner than the fertile specimens. The most common are smooth, either simple or dichotomous axes, which were identified as *Hostinella* by Edwards (1979a). No evidence of tracheids has been found in these specimens. Edwards also described three specimens showing a cluster of branches, which she compared with the 'K-branching' thought to be from the base of the *Zosterophyllum* plant (Walton, 1964a). However, she emphasized that there was no unequivocal evidence that the Freshwater East specimens were basal structures, and that they could equally be from the aerial part of a plant.

Of considerable interest was Edwards' discovery of four examples of axes, one of which shows a dichotomy, with spines attached (Figure 3.21). In the absence of attached reproductive structures, it was impossible to say what group of plants they belonged to, and so they were placed in the generalized form-genus *Psilophytites*. Their interest is in being the oldest examples of spiny axes recorded from anywhere in the world.

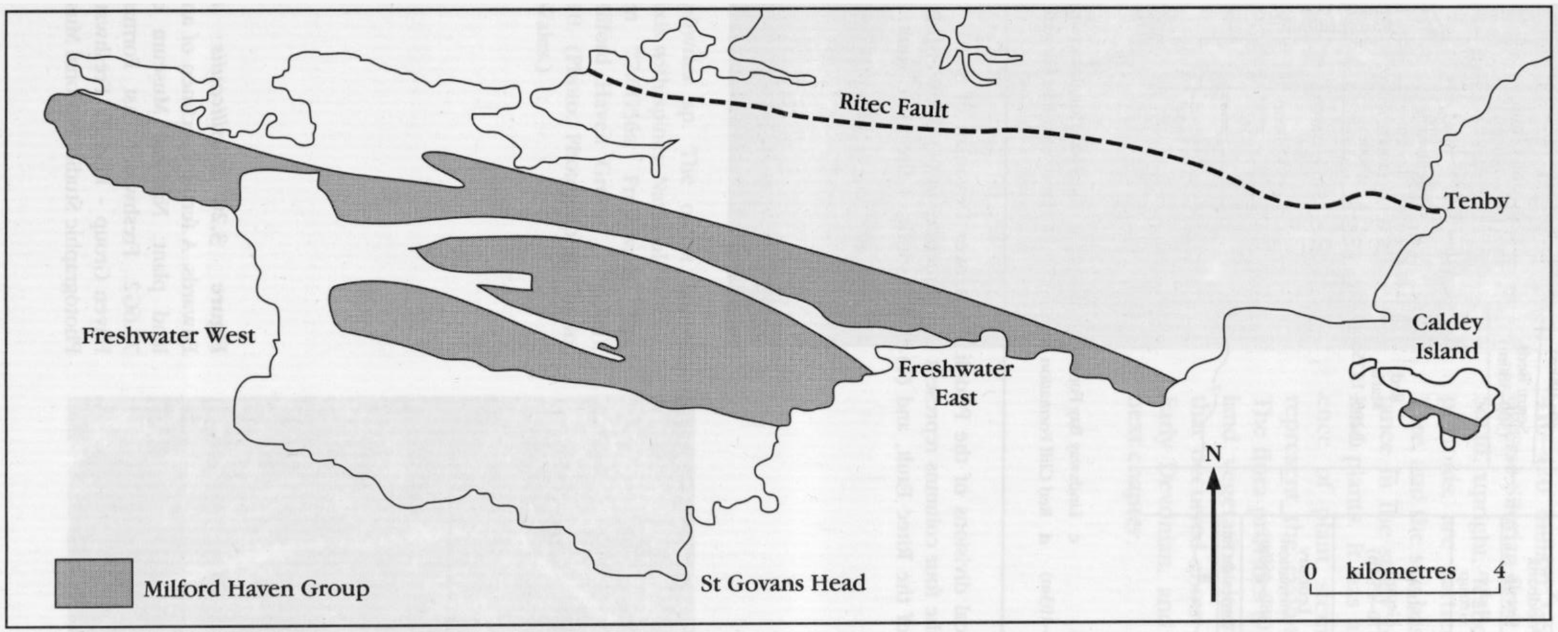

Figure 3.18 The outcrop of the Milford Haven Group (Upper Silurian and Lower Devonian) in Pembrokeshire, showing position of Freshwater East and other localities that yield plant fossils. Based on Williams *et al.* (1982, figure 2).

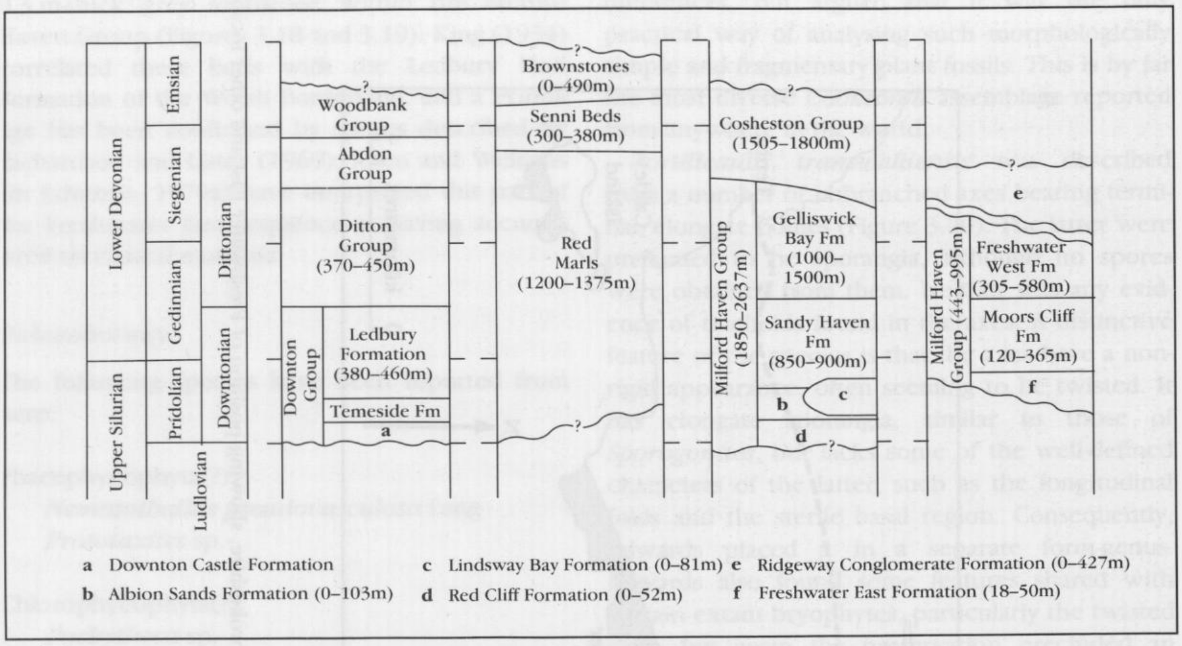

Figure 3.19 Lithostratigraphical divisions of the Přídolí and Lower Devonian of South Wales and the Welsh Borderland. From left to right, the four columns represent the sequences in (1) the Welsh Borderland, (2) central South Wales, (3) Dyfed north of the Ritec Fault, and (4) Dyfed south of the Ritec Fault. Based on Friend and Williams (1978, figure 31).

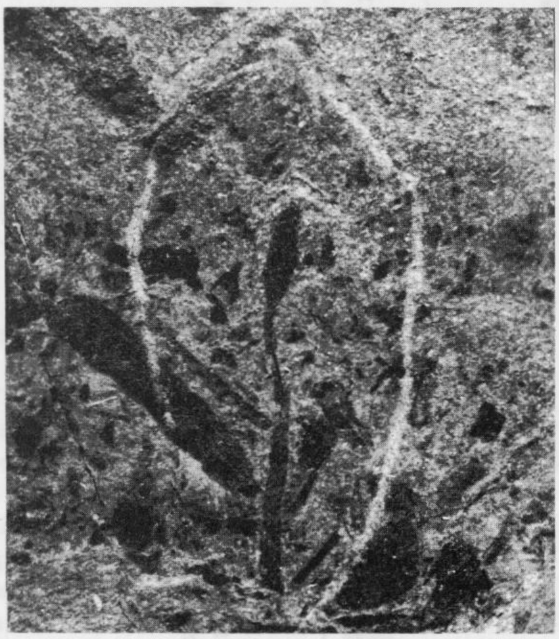

Figure 3.20 *Tortilicaulis transwalliensis* D. Edwards. A fertile specimen of an early rhyniophytoid land plant; National Museum of Wales, specimen 77.6G2. Freshwater East Formation (lower Milford Haven Group – Přídolí), Freshwater East. × 4. (Photo: Photographic Studio, National Museum of Wales.)

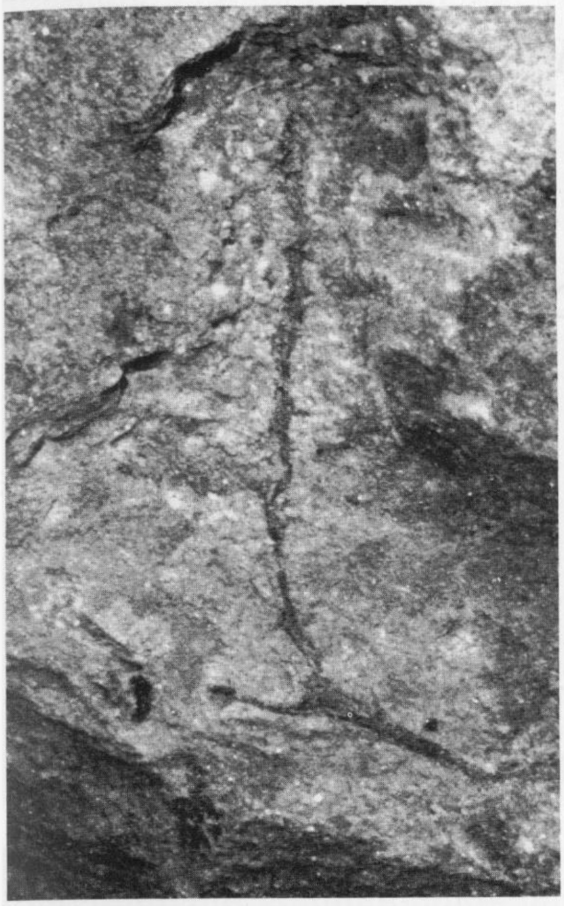

Figure 3.21 *Psilophytites* sp. The oldest known examples of a plant axis with spines; National Museum of Wales, specimen 77.6G56a. Freshwater East Formation (lower Milford Haven Group - Přídolí), Freshwater East. × 10. (Photo: Photographic Studio, National Museum of Wales.)

Conclusion

The Freshwater East plant fossils, which are 410–420 million years old, represent the most diverse Silurian flora from anywhere in the world. Small, upright, leafless plants, known as rhyniophytoids, are particularly abundant and diverse here, and the site has been of considerable importance in the study of these archetypal, primitive land plants. It has also yielded the earliest evidence of plant stems with spines, which may represent the evolutionary precursors of leaves. The flora provides a highly significant insight into land vegetation just before the major radiation that occurred about 10 million years later in the Early Devonian, and which is the subject of the next chapter.