
Chapter 3 Silurian

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 (Hoeg, 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 Permian 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 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 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 Permian (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.

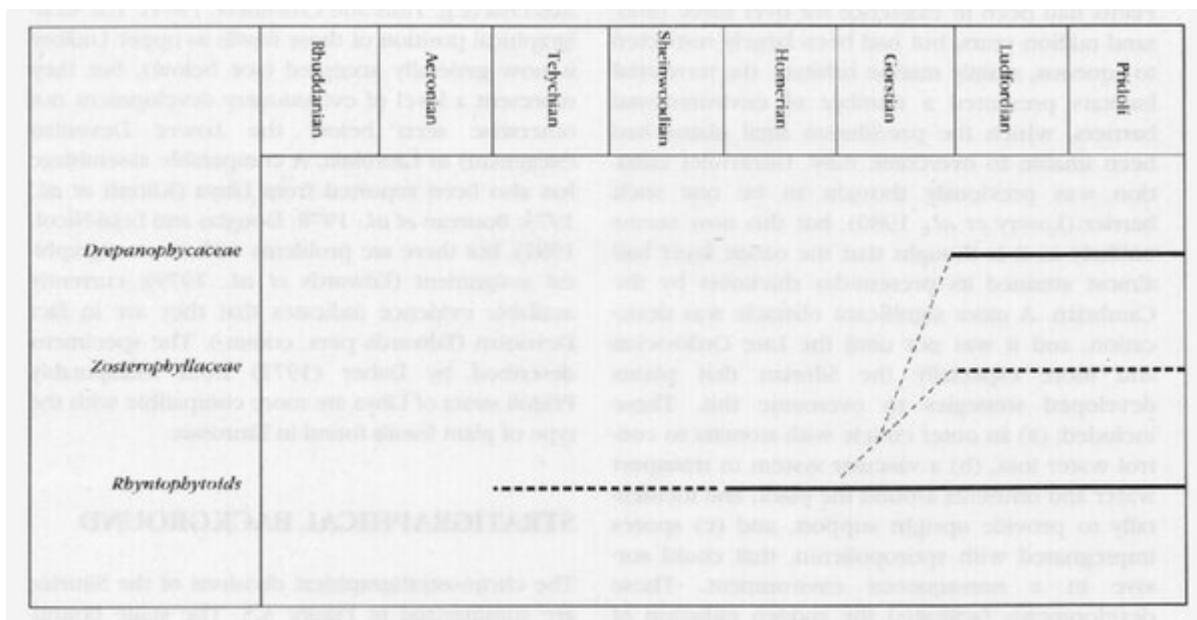
In contrast to the terrestrial vegetation, our knowledge of Silurian marine algae remains poor (Johnson and Konischi, 1959). It is known that thalloid algae occurred as far back as the Cambrian Period, mainly through the fossilized remains of forms that secreted a calcareous skeleton, such as the dasyclads. 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

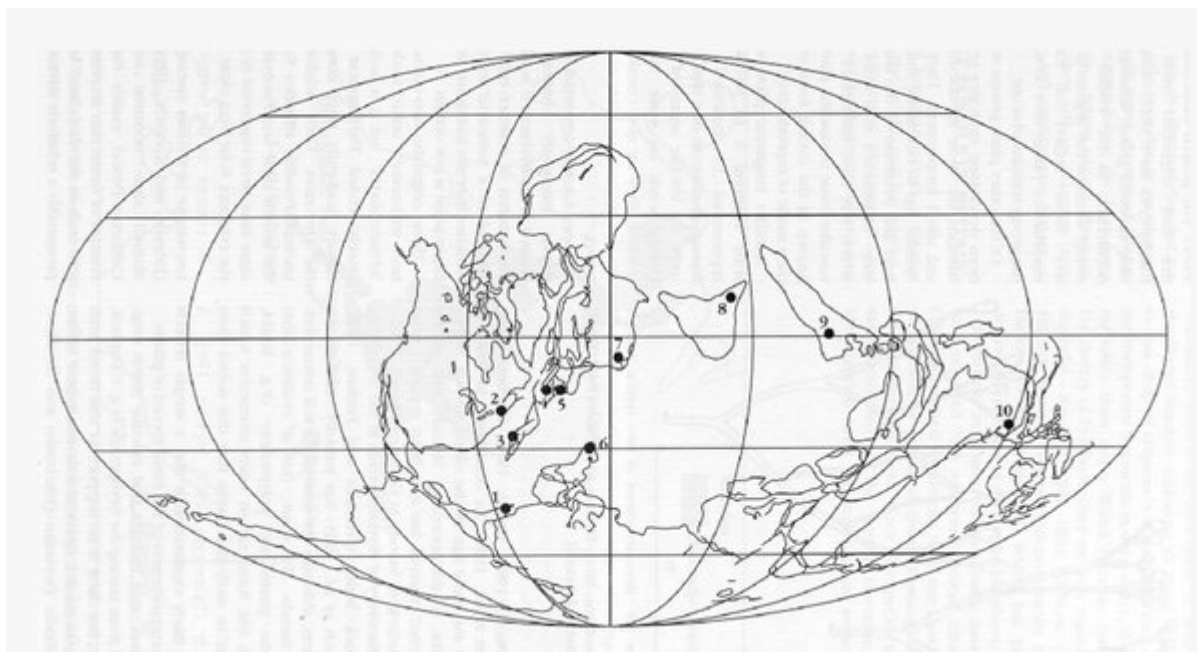
Britain has the most complete record of Silurian land-plant fossils in the world, and has played a central role in developing a phylogenetic and palaeoecological model for the terrestrialization of vegetation. Most of the sites occur in Wales and the Welsh Borders, including all those described in this chapter (Figure 3.4) and (Figure 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 Pridoli 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 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.

[References](#)



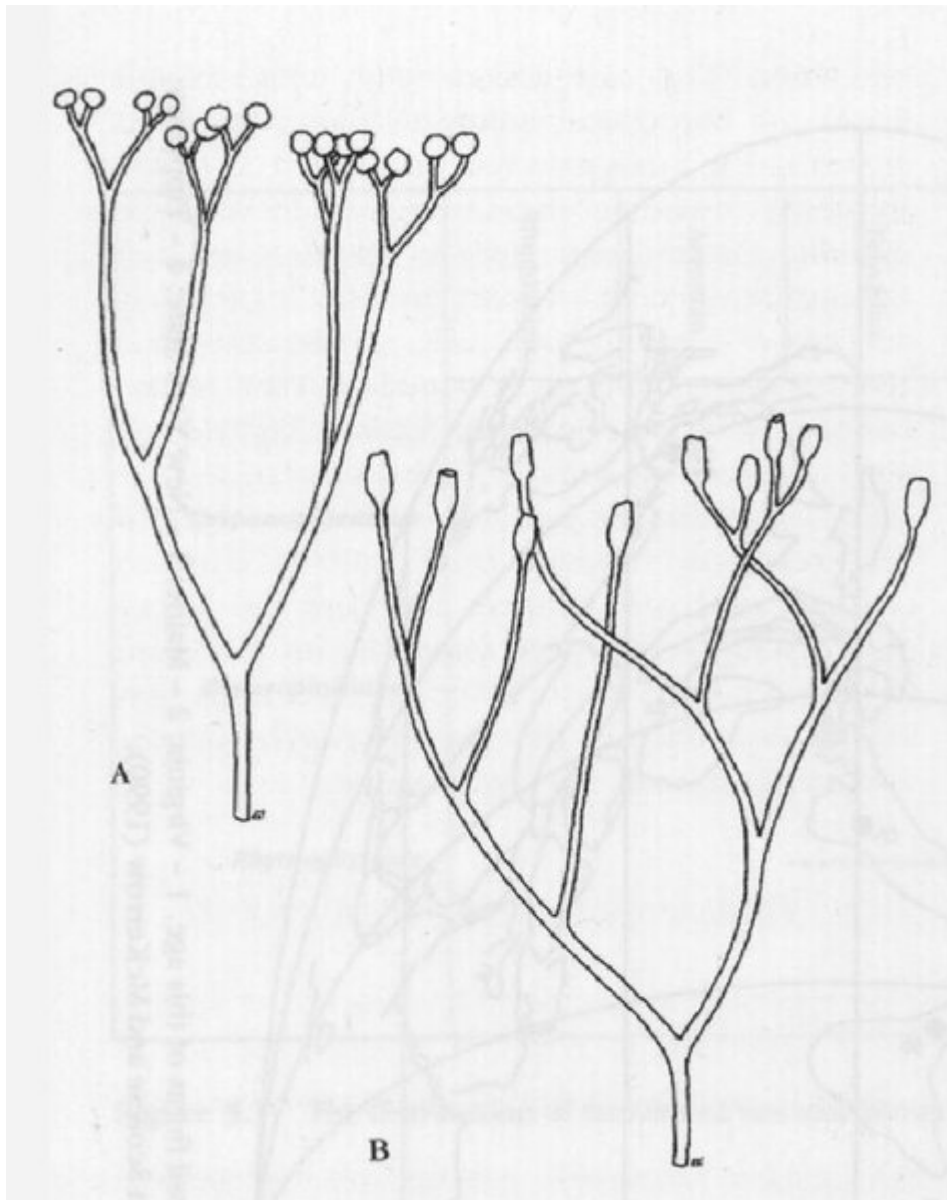
(Figure 3.1) The distribution of families of vascular plants in the Silurian. Based on data from Cleal (1993).



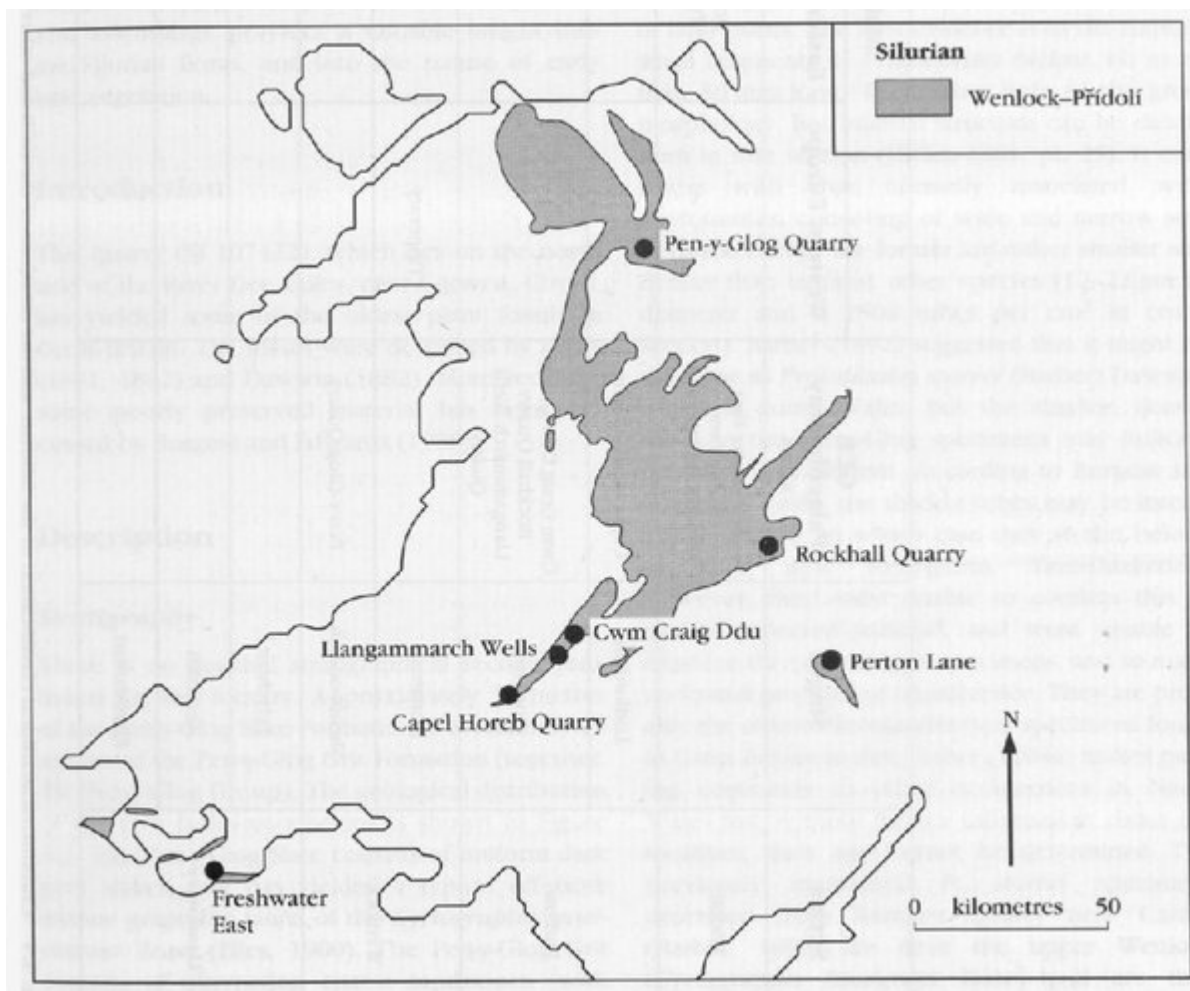
(Figure 3.2) The palaeogeography of the Silurian, showing the location of the major fossil floras of this age. 1 — Virginia; 2 — Maine; 3 — New York State; 4 — Tipperary; 5 — Wales; 6 — Bohemia; 7 — Podolia; 8 — Kazakhstan; 9 — Xinjiang; 10 — Victoria. Based on Scotese and McKerrow (1990).

Series	Stages	GCR Palaeobotany sites	Main areas outside Britain			
			Western Europe	Eastern Europe	Asia/Australasia	North America
Pridoli		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	Homeric		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.



(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).



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