Llanover Quarry

Highlights

Llanover Quarry has yielded one of the most diverse examples of a *Psilophyton* Zone (Siegenian) flora from Britain. It is the type locality for *Zosterophyllum llanoveranum* Croft and Lang, the only *Zosterophyllum* for which three-dimensional internal anatomy is known. This site has also yielded important information on the form and structure of *Uskiella, Drepanophycus, Gosslingia* and *Deheubarthia.*

Introduction

This small Old Red Sandstone exposure lies about 5 km south of Abergavenny, Gwent, Wales [SO 298 079]. Plant fossils were first discovered by Wickham King, who then showed the site to the palaeobotanist William Croft. Croft's collection was the basis of the classic study on the so-called Senni Beds flora (Croft and Lang, 1942). Further collecting has proved difficult, due to the small outcrop and awkwardly positioned tree roots, but some subsequent work on the assemblage has been done (Edwards, 1969a, b, 1970a, 1981; Edwards *et al.,* 1989; Shute and Edwards, 1989).

Description

Stratigraphy

The exposed sequence consists of about two metres of red sandstones and mudstones of the Brownstone Group (*sensu* Heard and Davies, 1924), which are correlatives of the Senni Beds of the Brecon Beacons. They were deposited on an alluvial plain crossed by fast, low sinuosity streams (Kelling *in* Owen *et al.,* 1965; Allen, 1979). No animal fossils have been reported, but the plant and microfossils suggest a Siegenian age (Croft and Lang, 1942; Mortimer, 1967; Richardson and Lister, 1969). The plant fossils occur in or near sediments of the fluvial channel (Allen, 1979), and probably originated from a variety of habitats (Edwards, 1979b).

Palaeobotany

The plant fossils are mostly preserved as compressions and iron oxide stained impressions, with no cuticles preserved, but some limonite petrifactions also occur. The following assemblage has been described to date:

Phaeophycophyta(?):

Prototaxites cf. *caledonianus* (Lang) Kräusel and Weyland

Nematothallus sp.

Chlorophycophyta(?):

Pachytheca sp.

Rhyniophytoids:

Sporogonites exuberans Halle

Taeniocrada sp.

Rhyniopsida:

Uskiella spargens Shute and Edwards

Zosterophyllopsida:

Zosterophyllum llanoveranum Croft and Lang

Z. cf. *australianum* Lang and Cookson

Z. cf. *fertile* Leclercq

Gosslingia breconensis Heard

Deheubarthia splendens Edwards, Kenrick and Carluccio

Devonian

Lycopsida:

Drepanophycus spinaeformis Göppert

Trimerophytopsida:

Dawsonites arcuatus Halle

Uncertain affinities:

Sciadophyton cf. *steinmannii* Kräusel and Weyland

Sennicaulis hippocrepiformis Edwards

'spherical or circular bodies *incertae sedis*'

Interpretation

Coalified spheres of *Pachytheca* are common at Llanover. They are generally poorly preserved, but the cortical and medullary regions can sometimes be distinguished (Croft and Lang, 1942, pl. 11, fig. 78). Croft and Lang also reported some *Pachytheca*-like specimens with tuberculate surfaces, referring to them as 'spherical bodies *incertae sedis*'.

A feature of the Llanover assemblage noted by Croft and Lang is the presence of elongate, slender specimens of *Prototaxites.* The dimensions of the tubes and the presence of 'medullary spots' invite a comparison with *P. caledonianus* and with *Prototaxites* described from the Silurian of the Welsh Borderland (Lang, 1937) and the Devonian of Germany (Kräusel and Weyland, 1934).

The Rhyniaceae is represented here by *Uskiella spargens* Shute and Edwards (1989). It was first identified as *Cooksonia* sp. (Croft and Lang, 1942), but has quite a different shape and structure of the sporangia. Shute and Edwards interpreted it as a small plant of determinate growth-pattern, with naked, dichotomous axes forking at a wide angle (60–90°) and bearing ellipsoidal, terminal sporangia. Petrifaction from Llanover were particularly instructive in showing details of the sporangia, including the presence of a zone of differentiated cells around the major circumference, which may have been linked with dehiscence. This type of bivalved sporangial structure evidently had an adaptive advantage, perhaps because it maximized the area of spores exposed to the atmosphere after dehiscence, since it seems to have evolved independently in several other groups of plants, as well as the Rhyniaceae (reviewed by Shute and Edwards, 1989).

Several specimens of *Sporogonites* sporangia were described by Croft and Lang, from which they were able to prepare spores. One example was also found to have stomata preserved on the stem just below the sporangia. Their affinities are still unknown, and are currently being re-investigated by Shute and Edwards.

Croft and Lang's record of the rhyniophytoid genus *Taeniocrada* sp. is based on slender, flattened stems from a lenticular band of mudstone at Llanover. In the absence of fertile structures, it has been impossible to place them in a particular species, and even their generic assignment cannot be regarded as proven (Edwards, 1981).

This is the type locality for *Zosterophyllum llanoveranum* (Figure 4.14). It is the only species of *Zosterophyllum* for which the anatomy is known, following studies by Edwards (1969a) on petrifactions from here and Craig-y-Fro Quarry. Of particular significance was the determination of the form of the vascular strand, which is oval in cross-section and exarch, in contrast to the terete, centrarch strands of the Rhyniopsida and Trimerophytopsida. It was also possible to determine the form of the prominent sporangial dehiscence structure. A few specimens from Llanover have also been identified as *Z* cf. *australianum* and *Z.* cf. *fertile* (Croft and Lang, 1942; Edwards, 1969b), although they may just be morphological variants of *Z. llanoveranum.*

Another member of the Zosterophyllopsida in the Llanover assemblage is *Gosslingia.* Rather better material of this form-genus has been found at Craig-y-Fro Quarry, and from these details of the anatomy have been described (Heard, 1927; Edwards, 1970a; Kenrick and Edwards, 1988a). However, the Llanover specimens have provided some important information on the gross morphology of the plant, in particular the arrangement of the sporangia.

The specimens described by Croft and Lang as cf. *Psilophyton princeps* have laterally attached sporangia similar to those of *Sawdonia ornata* (Dawson) Hueber described from the Gaspe Peninsula (Hueber and Banks, 1967; Hueber, 1968, 1971). unlike .*Sawdonia,* however, they have small bulges or curved branches just below each dichotomy, and lack the characteristic dark tip to the spines. For this reason, they have been assigned to a new genus and species, *Deheubarthia splendens* Edwards, Kenrick and Carluccio (1989).

Croft and Lang described the only fertile axes of *Drepanophycus spinaeformis* known from outside of Germany. Based on the German material, Kräusel and Weyland (1930) originally described the sporangia as being attached adaxially to the leaves. Later, however, Kräusel and Weyland (1935) found sporangia attached to leaf apices, which seems to be confirmed by the Llanover specimens. It is currently believed that the position of attachment of the sporangia is variable (e.g. Meyen, 1987). *Drepanophycus* is regarded by Hueber (1992) as one of the earliest and most primitive lycopsids (order Drepanophycales), being only pre-dated by the Silurian *Baragwanathia* from Gondwana (see Chapter 3).

Isolated trusses of pendant, fusiform sporangia were identified by Croft and Lang as *Dawsonites arcuatus* (Figure 4.15). They are probably the fertile parts of a trimerophyte plant, but in the absence of attached vegetative structures it is impossible to place them in one of the more natural taxa based on whole-plant morphology. They are associated with spiny axes, suggesting possible affinities with *Psilophyton princeps.* However, at least some of these axes were found by Croft and Lang to have laterally attached sporangia, which means that they belong to the zosterophyllalean genus *Deheubarthia* (see above). Until the nature of the vegetative axes which bore these sporangial trusses at Llanover has been determined, they have to be retained within the generalized form-species *D. arcuatus* Halle. The fossils here and at Craig-y-Fro (see below) are the oldest known remains of trimerophytes from anywhere in the world.

A number of specimens were described by Croft and Lang as *Sciadophyton steinmannii.* Such structures are now believed to be gametophytes (Remy, Remy *et al.,* 1980; Remy, Schultka *et al.,* 1980), and have been compared with petrified specimens from Rhynie identified as *Lyonophyton* (Remy and Remy, 1980a, b). Schweitzer (1983a, b) has reported *Zosterophyllum*-like axes attached to German specimens of *Sciadophyton,* suggesting that the latter was a zosterophyll gametophyte. Croft and Lang noted that the Llanover specimens differ slightly from the type specimens of *S. steinmannii* Kräusel and Weyland, 1930 in the sizes of the discs and of the circular scars that they show. Contrary to Croft and Lang, therefore, they are referred to in the above species list as *S.* cf. *steinmannii.*

Sennicaulis hippocrepiformis Edwards, 1981 was described from specimens from both here and from Craig-y-Fro Quarry. Most of the anatomical details of this species were determined from the pyrite petrifaction from Craig-y-Fro, but the Llanover specimens showed certain details of the xylem structure particularly well. The affinities of these isolated axes remain uncertain, but probably lie either with the Rhyniopsida or Trimerophytopsida.

Llanover Quarry has yielded the most diverse *Psilophyton* Zone flora (*sensu* Banks, 1980) in Britain. Croft and Lang (1942) record comparable assemblages from the Den Quarries near Abergavenny, along Kemeys Graig near Newport, from below the dam of Talybont Reservoir near Brecon and from a cliff near Llanthony Abbey in the Black Mountains; but none of these sites has yielded such diverse assemblages as Llanover Quarry and Craig-y-Fro.

These Welsh assemblages belong to the European phytogeographic subunit of the equatorial and low-latitude floras (as defined by Raymond *et al.,* 1985), which characterizes the southern and eastern parts of Laurussia. The closest comparison is with assemblages from Podolia in the Ukraine and the Dniester River in Moldavia (Ishchenko, 1965, 1974), particularly in the presence of *Gosslingia, Sciadophyton* and *Zosterophyllum.* Some comparison is also possible with floras from Belgium (Stockmans, 1940; Gerrienne, 1988, 1990a, b, 1991), although the latter have yielded fewer species.

Other *Psilophyton* Zone assemblages have been found in Britain in a borehole in Oxfordshire (Chaloner *et al.,* 1978) and in the Strathmore Group of Scotland, such as at Auchensail Quarry and Ballanucater (pp. 75–80). Raymond *et al.* (1985) assigned these to the American phytogeographic subunit and they differ markedly from the Llanover assemblage, being much less rich in species and dominated by *Pachytheca, Sawdonia, Dawsonites* and (in the Strathmore Group) *Drepanophycus.* However, this may be a function of the Llanover assemblage being marginally older than the Oxfordshire and Scottish fossils. The Llanover fossils provide a clearer reflection of the general diversity of the Siegenian vegetation of Laurussia, and are thus of considerable significance for studying the early phases of the diversification of vascular plants.

Conclusion

Llanover Quarry has yielded one of the most diverse flora in Britain from the Siegenian Stage, and is about 400 million years old. It is particularly important for our understanding of the group of plants known as the zosterophylls, which were the ancestors of the club-mosses that dominated much of the land vegetation later in the Palaeozoic, particularly the Late Carboniferous equatorial coal swamps (see Chapter 6). Not only is this one of the most diverse assemblages of zosterophylls (*Gosslingia, Deheubarthia,* and three species of *Zosterophyllum*), but much important information has been discovered from here about their anatomy, which has been vital for understanding the evolutionary significance of the group. The club-mosses themselves are represented by *Drepanophycus* stems bearing reproductive organs, which are the second oldest fertile club-mosses known from anywhere in the world. Also present is one of the world's earliest examples of a trimerophyte (*Dawsonites*), which is the group thought to be ancestral to the seed plants (and thus also of flowering plants). The fossils are very similar to those found at Craig-y-Fro (see below), but are not preserved differently and thus show different aspects of the anatomy. Similar assemblages have been reported from Belgium, Moldavia and Ukraine but, except for the first of these, they have not been studied in such detail, and do not yield such well-preserved anatomical detail.

References

(Figure 4.14) Zosterophyllum llanoveranum Croft and Lang. A group of fertile spikes probably originating from a single plant; Natural History Museum, London, specimen V.26516a. Brownstone Group (Siegenian), Llanover Quarry. x 1.5. (Photo: Photographic Studio, Natural History Museum, London.)

(Figure 4.15) Dawsonites arcuatus Halle. Terminal part of fertile truss; Natural History Museum, London, specimen V.26492. Brownstone Group (Siegenian), Llanover Quarry. x 2. (Photo: Photographic Studio, Natural History Museum, London.)