Puddlebrook Quarry

Highlights

This is the best known locality for plant fossils from the Visean Drybrook Sandstone, and has yielded four apparently endemic species (Figure 5.34). These include *Muscites plumatus*, which may be the oldest known moss, and *Diplopteridium holdenii*, one of the most completely reconstructed Visean pteridosperms.

Introduction

The Puddlebrook locality consists of a small quarry in the Lower Carboniferous Drybrook Sandstone, just north of Drybrook in the Forest of Dean [SO 647 184] (Figure 5.35). Plant fossils from here were first recorded by Allen (1961), and were the subject of a monographic study by Lele and Walton (1962b). Some of the component species have been reviewed by Thomas (1972) and Thomas and Purdy (1982), but the only comprehensive re-assessment of the assemblage is in an unpublished thesis by Rowe (1986), work done partly in conjunction with the Geological Conservation Review Unit. Certain parts of the latter study have been subsequently published (Rowe, 1988a, b, c, 1992).

Description

Stratigraphy

The geology is described by Rowe (1986), and briefly summarized by Rowe (1988b, c). The exposed strata belong to the Drybrook Sandstone Formation, and palynological evidence suggests an Asbian age. The plant fossils occur in a 1.2 metre thick lens of shale within the sandstone. The lens is interpreted as the infill of an abandoned river channel.

Palaeobotany

The fossils are preserved as adpressions, sometimes with cuticles preserved, or as fusain. The following species have been described to date:

Bryophyta(?):

Muscites plumatus Thomas

Eskdalia variabilis (Lele and Walton) Rowe

E. fimbriophylla Rowe

Lepidostrobophyllum fimbriatum (Kidston) Allen

cf. Stigmaria sp.

Lycopsida:

Selaginellites resimus Rowe

Lagenostomopsida:

Diplopteridium holdenii Lele and Walton

Dichotangium quadrothecum Rowe

Sphenopteris obfalcata Walton

S. cuneolata Lindley and Hutton

Archaeopteridium tschermakii (Stur) Kidston

Telangiopsis sp.

Catpolithus puddlebrookense Thomas and Purdy

Interpretation

Thomas (1972) described a small, leafy shoot from here as *Muscites plumatus*. Although there is no evidence of fertile structures, Thomas argued that it could be a bryophyte, possibly a moss. If so, it would be the oldest known moss, the next oldest being from the Stephanian of France (Renault and Zeiller, 1888). No liverworts have so far been described from Puddlebrook, but Sullivan and Hibbert (1964) reported *Tetrapterites visensis* from another outcrop in the Drybrook Sandstone, which Lacey (1969) has argued might be a spore-bearing body of a liverwort.

The most abundant lycopsid remains here belong to the form-genus *Eskdalia*. The stems were initially described by Lele and Walton (1962b) as *Scutelocladus variabilis* Lele and Walton, who interpreted them as having no leaf cushions, ligule pits or parichnos tissue. Thomas and Purdy (1982) subsequently demonstrated that they had expanded leaf cushions with a lateral wing, basal heel and adaxial ligule pit. They also described grooves in the middle of the leaf cushions as being possibly the surface manifestation of infrafoliar bladders (spongy tissue connected to the parichnos, and thought to be part of an aerating system in certain lycopsids). As a result, they transferred the species to *Tomiodendron*, a form-genus previously only reported from Angaran assemblages of Siberia and the north slope of Alaska (Spicer and Thomas, 1987). Most recently, Rowe (1988c) has investigated fusainized fragments, which indicate that an infrafoliar, aerating bladder was not in fact present in the stems, and so he transferred the species to *Eskdalia*, as interpreted by Thomas and Meyen (1984).

Rowe (1988c) also described several specimens of *E. variabilis* stems with small, terminally-borne strobili (Figure 5.36). The strobili have a slender central axis with spirally-arranged sporophylls with entire margins. Although some evidence of sporangia was found, none yielded spores, and so it is still not possible to place *Eskdalia* in any of the families outlined by Thomas and Brack-Hanes (1984). Nevertheless, these Puddlebrook specimens are of considerable interest as the only known evidence of the fructifications of the shrubby lycopsid *Eskdalia*, although Thomas (1992) has argued that not all species of this stem form-genus may have had the same fructifications. Rooting structures associated with *E. variabilis* were described by Lele and Walton (1962b) as cf.

Stigmaria sp. Very similar structures are known from Moel Hiraddug (see below), where they are associated with Lepidodendron' perforatum Lacey, a species that may belong to Eskdalia (Rowe, 1988c).

A second species of *Eskdalia* from Puddlebrook has been described by Rowe (1988c) as *E. fimbriophylla*. Isolated leaves were originally identified by Lele and Walton (1962b) as *Lepidophyllum* cf. *fimbriatum*, but no evidence was found of attached sporangia, as would be expected if they were sporophylls. Rowe demonstrated that they were leaves attached to *Eskdalia*-like stems, although they are wider and have larger leaf cushions than *E. variabilis* stems. *E. fimbriophylla* has not been identified from any other locality; however, there is a possible comparison with the leaf *Lepidophylloides fisheri* Crookall, described by Crookall (1966) from the more or less coeval Scremerston Coal Group of Northumberland.

Allen (1961) described abundant, isolated lycopsid sporophylls from here as *Lepidostrobophyllum fimbriatum* (Kidston) Allen. They have a clearly fimbriate margin, and thus differ from the entire-margined sporophylls of the *Eskdalia variabilis* strobili. It is tempting instead to speculate a connection with *E. fimbriophylla*, whose leaves are also fimbriate, but direct evidence of attachment is so far lacking.

A third type of lycopsid found at Puddlebrook is a small herbaceous plant known as *Selaginellites resimus* Rowe, 1988a. Although only represented by fragmentary material, Rowe was able to reconstruct it as having mainly recumbent, rambling stems, which produced vertical, dichotomous shoots. Some of these vertical shoots bore what Rowe interpreted as terminal strobili, which included sporangia containing megaspores. It .thus appears to be a typical example of the Selaginellaceae, one of the most conservative families of vascular plants, which has remained essentially unaltered since the Late Devonian (Fairon-Demaret, 1977).

The most completely understood pteridosperm from Puddlebrook is *Diplopteridium holdenii* (Figure 5.37). The basic features of the foliage were described by Lele and Walton (1962b), but a more comprehensive study by Rowe (1988b) has enabled him to provide a reconstruction of most of the plant, including some details of the fructifications (Figure 5.7). It appears to have been herbaceous, with an upright stem bearing a crown of fronds. As in most pteridosperms, the fronds have an essentially bipartite architecture, the main rachis dichotomizing near the base to produce bipinnate branches. In fertile fronds, however, there is a trichotomy, the third branch bearing the fructifications. Rowe was able to demonstrate organic connection between the fertile branches of the *D. holdenii* frond and cupulate seed/ovule-bearing structures, that Lele and Walton (1962b) had earlier named as *Calathiops* sp. This is only the second known species of *Diplopteridium*; the other being *D. teilianum* Walton from Teilia (p. 178), from which it differs in having narrower pinnule segments.

Rowe (1988b) also described a synangiate organ associated with *D. holdenii*, which Lele and Walton (1962b) had initially identified as *Telangium* sp. Although Rowe presented considerable circumstantial evidence that it was the pollen organ of *D. holdenii*, in the absence of direct evidence of attachment he assigned it a separate name, *Dichotangium quadrothecum*. Rowe (1986) described other sporangial structures from Puddlebrook, including one that he compared with *Telangiopsis*. However, the results of this work have yet to be published.

Other pteridosperm fronds from Puddlebrook, were identified by Lele and Walton (1962b) as *Sphenopteris obfalcata* and *S. cuneolata*. The former is only otherwise known from Teilia (p. 179), and there is as yet inadequate knowledge of its frond architecture or fructifications for its taxonomic position to be firmly established.

The holotype of *S. cuneolata*, from the Oil Shale Group of Scotland, was poorly illustrated and Kidston (1923b, p. 156) reported that it was lost. Kidston (1923b, pl. 214) illustrated a second specimen under this name, but Lele and Walton (1962b) note that it differs markedly from Lindley and Hutton's specimen in its nervation and the outline of the pinnules. Lele and Walton therefore nominated one of the Puddlebrook specimens as lectotype' (in fact a neotype), but it is far from clear that it is conspecific with Lindley and Hutton's original concept of the species.

Thomas and Purdy (1982) describe some apparently radiospermic (i.e. radially symmetrical) seeds or ovules as *Carpolithus puddlebrookense*. They had an integument fused to the nucellus except at the apex, where it formed four apical lobes. The nearest comparison seems to be with the Tournaisian petrified seeds/ovules *Eurystoma angulare* Long from the Whiteadder (p. 124). However, *Eurystoma* was borne in *Alcicornopteris* cupulate structures, of a type not so far reported from Puddlebrook. Furthermore, *Eurystoma* is thought to have calamopityalean affinities, and none of the foliage found at Puddlebrook is of a type normally associated with that order (e.g. *Triphyllopteris*, *Spathulopteris*).

Two fragmentary Puddlebrook specimens were identified by Lele and Walton (1962b) as *Archaeopteridium tschermakii*. Better specimens have been since described by Rowe (1992), who also found pre-pollen organs which confirm that the species belongs to the pteridospermous class Lagenostomopsida. Although generally rare, this is a widely occurring species, having been reported from several localities in Scotland, Germany and Poland. The Puddlebrook specimens are the only examples known from England or Wales.

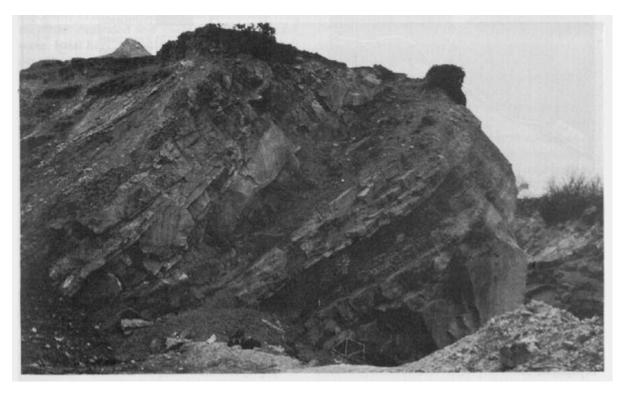
Although plant fossils have been reported from elsewhere in the Drybrook Sandstone (e.g. Cleal, 1986a), this is by far the most diverse assemblage from the formation. Five of the taxa listed at the beginning of this section have been reported only from the Drybrook Sandstone, and four of these only from Puddlebrook. There is some overlap in composition with other British Visean assemblages, particularly those from North Wales (Teilia and Mod Hiraddug — see p. 175). However, the overall balance of species separates Puddlebrook from most other palaeobotanical sites of this age. This presumably represents its spatial isolation, being separated from these other, more northerly localities by the

Wales-Brabant 'landmass'.

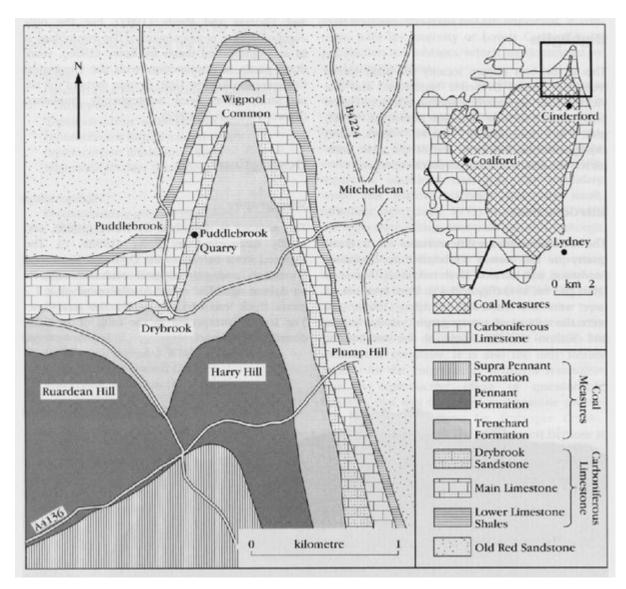
Conclusion

This is the best site for Lower Carboniferous plant fossils in southern Britain. They represent the vegetation growing here about 330 million years ago, which consisted mainly of shrubby club-mosses and primitive seed plants. They include fossils that demonstrate the connection between vegetative and reproductive structures, which allows some of the species to be viewed more as whole, living plants, rather than just as disarticulated organs. Several of the species are unique to this locality, including *Diplopteridium holdenii* Lele and Walton, one of the most completely reconstructed early seed plants.

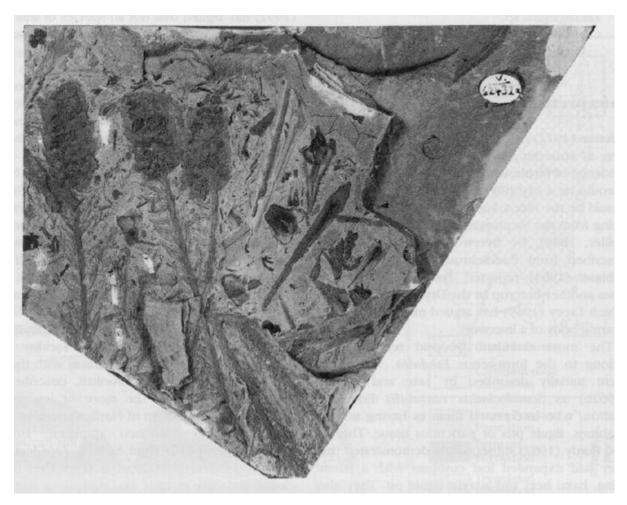
References



(Figure 5.34) Puddlebrook. Asbian fluvial deposits of the Drybrook Sandstone, prior to the 1982 excavations at the site. (Photo: C.J. Cleal.)



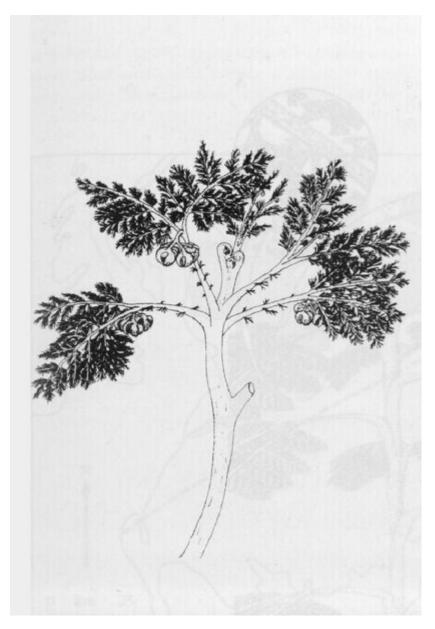
(Figure 5.35) Geological map of the northern part of the Forest of Dean, showing the location of Puddlebrook Quarry. Based on Sullivan (1964, text-figure 1).



(Figure 5.36) Eskdalia variabilis (Lele and Walton) Rowe. Leafy lycopsid shoots bearing terminal fructifications; Natural History Museum, London, specimen V.62432a. Drybrook Sandstone (Asbian), Puddlebrook Quarry. x 1. (Photo: Photographic Studio, Natural History Museum, London.)



(Figure 5.37) Diplopteridium holdenii Lele and Walton. Pteridosperm frond with fructifications; Natural History Museum, London, specimen V.62331a. Drybrook Sandstone (Asbian), Puddlebrook Quarry. x 0.5. (Photo: Photographic Studio, Natural History Museum, London.)



(Figure 5.7) Reconstruction of the Early Carboniferous lagenostomalean pteridosperm Diplopteridium. Based on Rowe (1988b, figure 35).