Ballanucater Farm

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Highlights

Ballanucater Farm has yielded the best British assemblage of Emsian plant fossils with cuticles. They include the earliest known examples of spines with glandular tips.

Introduction

This small stream section near Callander, Central Region (Scotland — [NN 630 019]) exposes plant-bearing elastic sediments of the Old Red Sandstone. Although plant fossils have been reported from localities in this area since the mid-nineteenth century (history summarized by Henderson, 1932 and Lang, 1932), the earliest records of specimens from Ballanucater Farm appear to be those by Henderson (1932) and Lang (1932). Since then some of the flora has been investigated by Edwards *et al.* (1982) and Rayner (1982, 1983, 1984), particularly with reference to the finely preserved cuticles.

Description

Stratigraphy

The sequence belongs to the Strathmore Group, as defined by Armstrong and Paterson (1970). It includes grey coarse flaggy sandstones and blue-green mudstones. Palynological evidence suggests that they are Emsian in age (Ford, 1974; Richardson *in* Rayner, 1983).

Palaeobotany

Plant fossils have been found in both the sandstones and the mudstones, the former yielding partially pyritized compressions and the latter carbonized compressions with cuticles. The following species have been described to date:

Chlorophycophyta(?):

Pachytheca sp.

Zosterophyllopsida:

Sawdonia ornata (Dawson) Hueber

?Margophyton goldschmidtii (Halle) Zacharova

Lycopsida:

Drepanophycus spinaeformis Göppert

Trimerophytopsida: *Dawsonites* sp.

Discussion

Henderson (1932), Lang (1932), Edwards *et al.* (1982) and Rayner (1984) have all described specimens of *Drepanophycus spinaeformis* from here (Figure 4.19). Although there are older known examples of this form-genus, such as the Siegenian specimens from Craig-y-Fro (p. 71), these are the oldest yet found with cuticles preserved. The plant is

lycopsid-like, with broad, leafy axes up to 30 mm wide, but with a comparatively narrow vascular strand, generally no more than 3 mm wide. No sporangia have been found at Ballanucater Farm but some excellent cuticle preparations show the arrangement of epidermal cells around the stomatal pore (Lang, 1932; Edwards *et al.,* 1982; Rayner, 1984). The twin guard cells are completely enclosed by two reni-form subsidiary cells. These are the oldest compression fossils of land plants from which paired guard cells and paracytic subsidiary cells have been described. Comparable cuticles of *Drepanophycus* have been described from the Eifelian of North America (Stubblefield and Banks, 1978).

The most common constituent of the assemblage is *Sawdonia ornata* (syn. *Psilophyton princeps* var. *ornatum* Dawson), a spiny zosterophyll (*sensu* Banks, 1968). It was briefly described from here as part of the form-genus *Psilophyton* by Henderson (1932) and Lang (1932), but a fuller account is provided by Rayner (1983). The axes are up to 6.5 mm wide and divide pseudomono-podially. They are covered with black-tipped, multicellular spines (or trichomes), up to 3 mm long, which are believed to have been secretory. Cuticle preparations from here (Edwards *et al.,* 1982; Rayner, 1983) indicate the papillate nature of the epidermis, details of the 'hair bases' (*sensu* Edwards, 1924), and the structure of the stomata. The 'hair bases' consist of elongate, papillate epidermal cells around a central, isodiametric cell with a thin or incomplete cuticle cover. They have been termed 'rosettes' by Rayner (1983), but their function remains unknown. The stomata are round to elongate, and consist of a pore enclosed by a guard cell area. There is no evidence of the intercellular flanges in this area, which would have suggested that a pair of guard cells was present, and compare with the stomata of *Zosterophyllum myretonianum* Penhallow (Lele and Walton, 1962a; Edwards *et al.,* 1982). Nevertheless, Rayner (1983) interpreted the *Sawdonia* stomata as originally having had a pair of guard cells, and that the intercellular flanges were just not present in life. The guard cells lay at the bottom of a shallow stomatal pit, formed by cuticular thickenings between the subsidiary and guard cells (see also Zdebska, 1972; Chaloner *et al.,* 1978).

An interesting feature of this locality is the presence of small bodies (diameter 901um or less) inside many of the macerated *Sawdonia* spines. Lang (1932) described them as fungal vesicles, under the name *Palaeomyces* sp., whereas Rayner (1983) interpreted them as possibly the spore resting stage of a fungus.

Within the sandstones, there are many spiny axes that appear to conform to Halle's (1916) description of *Psilophyton goldschmidtii* Halle, and were identified as such by Lang (1932). Halle erected the species to describe sterile, spiny axes with a distinctive branching pattern, found in Norway. The specimens from Ballanucater Farm are also sterile and look very similar to those illustrated by Halle. The main axes are up to 5 mm wide and divide pseudomonopodially, in contrast to the much narrower lateral branches which fork dichotomously. There is a continuous line on the axes running parallel to the edges. There are also oval regions filled with matrix at the point of divergence of the lateral branches, which may correspond to axillary tubercles. This species has since been transferred to the genus *Margophyton* by Zakharova (1981), who regarded it as a zosterophyll (see also Edwards *et al.,* 1989). However, in the absence of fertile organs, it is impossible to be certain whether or not the Ballanucater specimens also belong here.

Clusters of fusiform sporangia are found both as fossils on the rock surfaces, and in maceration residues. They are best assigned to the form-genus *Dawsonites* as, although they are sometimes connected to quite extensive dichotomously branching axes, they lack any distinguishing features which would allow identification with any species of *Psilophyton.* The fusiform sporangia are elongate, 4–6 mm long, pendulous, and borne terminally on dichotomizing axes. They occur in pairs, the individuals of which are often twisted around one another. They dehisce longitudinally, and contain trilete spores averaging 60 pm in diameter. The spores are almost completely enclosed by a finely sculptured outer exine, which shows a tendency to break away from mature individuals.

The presence of *Dawsonites* in the Ballanucater assemblage indicates that it belongs to the *Psilophyton* Zone (Banks, 1980; Edwards and Berry *in* Cleal, 1991). Similar assemblages have been reported from a series of localities in the Callander area (Jack and Etheridge, 1877; Henderson, 1932; Lang, 1932), but Ballanucater Farm has yielded easily the best preserved and most abundant specimens. A similar assemblage has also been reported from Auchensail Quarry near Cardross (p. 78), but no evidence of cuticles has been found there.

Raymond *et al.* (1985) place this assemblage in their American phytogeographic subunit of the equatorial and low latitude floras. The only other British *Psilophyton* Zone assemblage belonging to this subunit was found in Emsian beds in a borehole in Oxfordshire (Chaloner *et al.,* 1978). Those from the Siegenian Senni Beds of south-east Wales, such as

from Craig-y-Fro and Llanover (pp. 67–75), belong to the European subunit of Raymond *et al.* (1985) and differ from the Strathmore Group assemblages in their more diverse composition. From outside of Britain, assemblages with a more comparable, restricted composition have been reported from Rorangen, Norway (Halle, 1916), Matringhem, France (Danzé-Corsin, 1955) and James Bay, Canada (Hueber, 1964). However, none of these places has yielded such well-preserved cuticles as found at Ballanucater. This gives Ballanucater a unique significance in Lower Devonian palaeobotany, especially for work on early epidermal structures (e.g. stomata, trichomes), whose evolution was a key factor in allowing plants to overcome the problems of desiccation inherent in living in a terrestrial environment.

Conclusion

Ballanucater Farm has yielded an important assemblage of fossils representing plants of 390 Ma. The fossils are particularly important as they still preserve the outer, protective skin of the plant (known as the cuticle), in which details of the microscopic breathing pores (stomata) and hairs can be seen. They are some of the oldest known examples of modern-looking stomata, in which the pore is surrounded by two specialized cells (guard cells) that control the size of the opening. This was an important development for helping plants adapt to the land environment, allowing greater control over water-loss and gas-exchange with the atmosphere. A similar assemblage of fossils occurs at Auchensail Quarry (p. 78), as well as at localities in Norway, Belgium and Canada, but none has yielded such well-preserved cuticles as found at Ballanucater.

References

(Figure 4.19) Drepanophycus spinaeformis Göppert. Leafy shoot; Natural History Museum, London, specimen V.58185. Strathmore Group (Emsian), Ballanucater Farm. x 1. (Photo: Photographic Studio, Natural History Museum, London.)