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# 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 844 323], and has yielded plant fossils of Ludlow and also possibly Pridoli 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).

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 (Doming *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 Pridoli (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).

## 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 leaflike 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 rhy-niophytoid 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.

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.

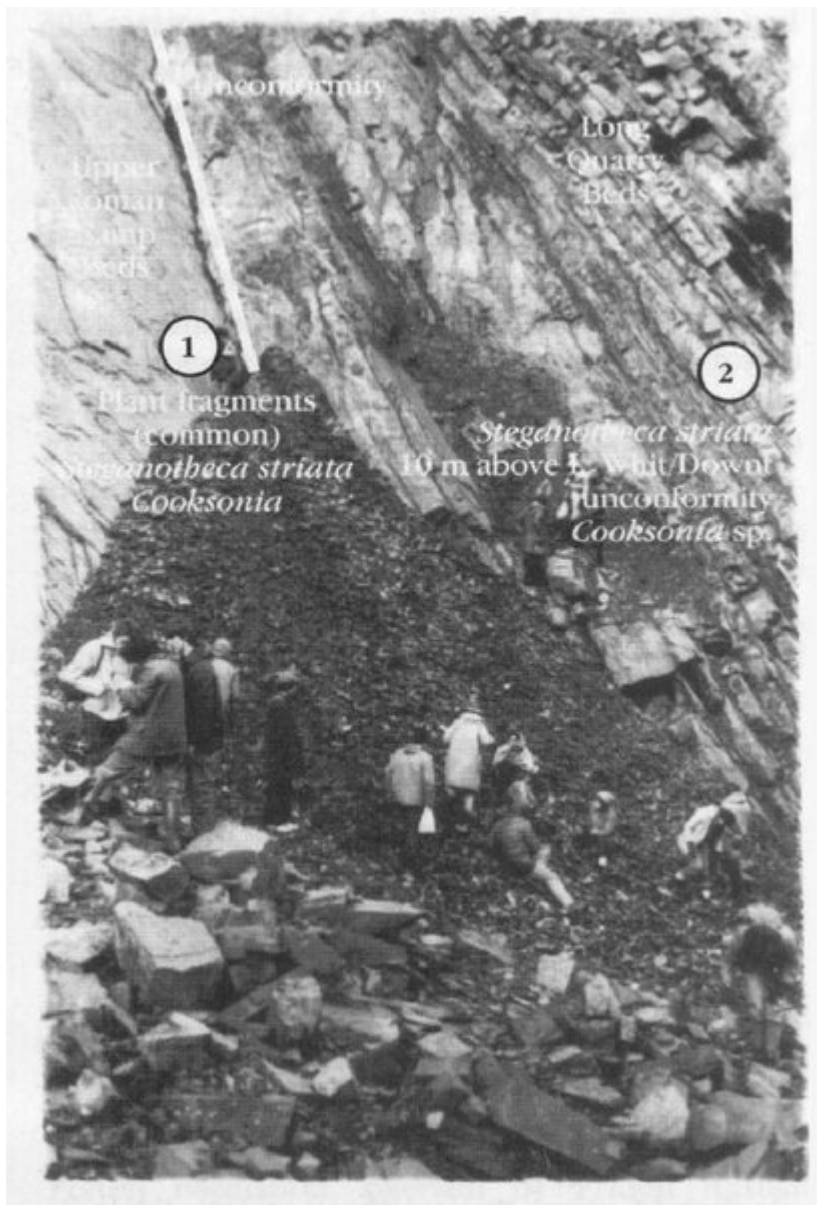
## Conclusion

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.

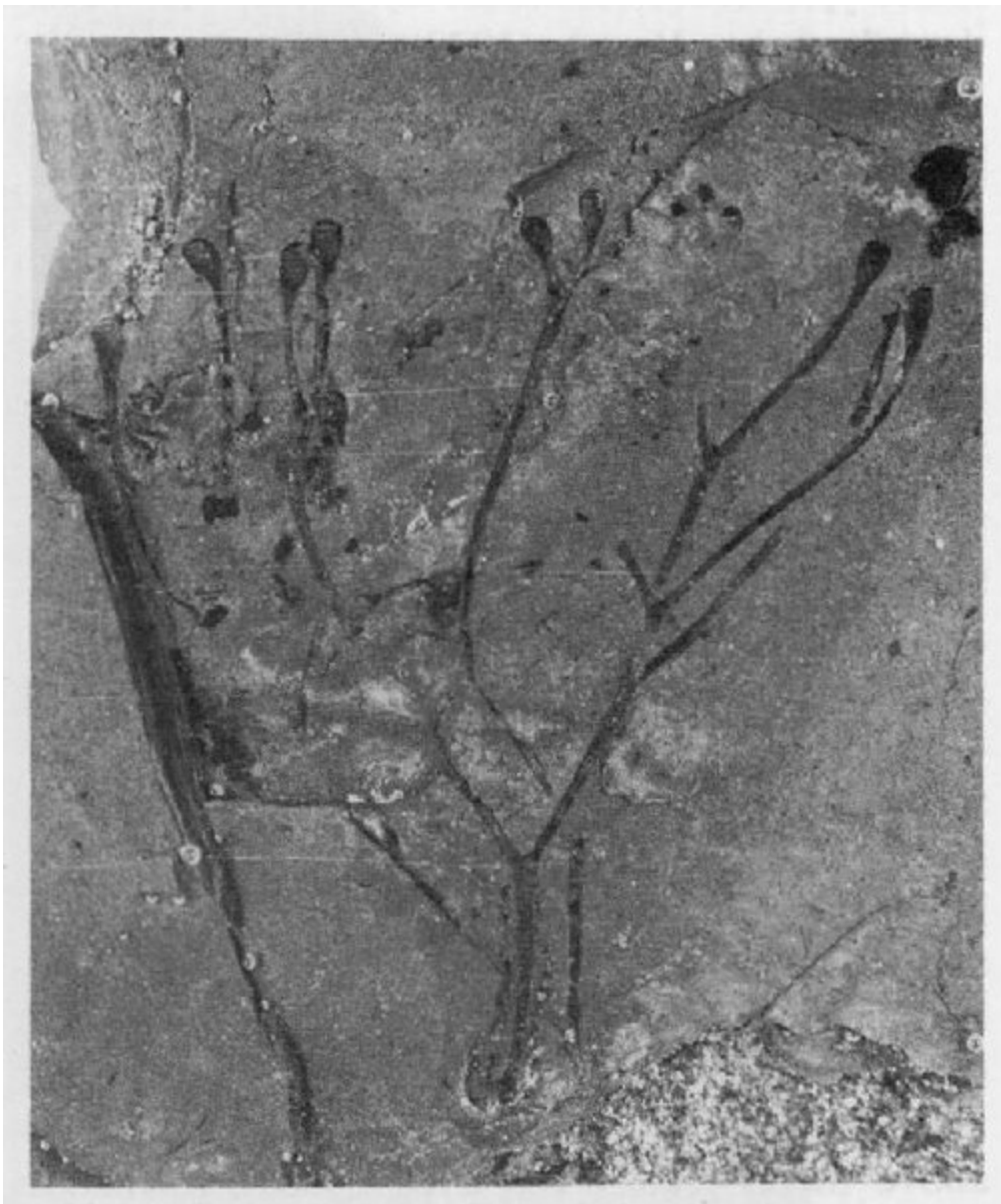
## References



(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 Pridoli beds of the Long Quarry Formation. (Photo: C.J. Cleal.)



(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.)



(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. x 1.5. (Photo: Photographic Studio, National Museum of Wales.)