Loch Humphrey Burn

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Highlights

Loch Humphrey Burn has yielded two pivotal assemblages of Lower Carboniferous plant petrifactions, the lower reputedly of Tournaisian and the upper of Visean age (Figure 5.30). The lower is dominated by filicopsids, unlike most Tournaisian petrifaction assemblages; it includes the earliest possible examples of tedeleacean, corynepteridacean and marattialean ferns. The upper assemblage includes the only known fertile specimens of the progymnosperm order Protopityales. It has also provided invaluable information on the anatomy of the early sphenopsid *Protocalamites* and several evolutionarily significant pteridosperms such as *Calathospermum.* Finally, it is one of the few Lower Carboniferous localities that yields both petrifactions and adpressions, thereby offering the potential for correlating features of anatomy and gross morphology. It is a site of outstanding palaeobotanical importance.

Introduction

This locality straddles a small tributary of Loch Humphrey Burn [NS 467 753] (Figure 5.31). It is one of two classic palaeobotanical localities in the Kilpatrick Hills, near Glasgow (the other, Glenarbuck, is described in the next section). Lower Carboniferous plant fossils were probably first discovered at Loch Humphrey Burn in about 1870 by the Geological Survey, but the earliest documentary evidence is a letter that accompanied specimens sent by James Bennie to Robert Kidston in 1886 (Smith, 1960; Scott *et al.,* 1984). Kidston published many descriptions of the adpressions from here in his classic 1923–1925 monograph, but passed the petrifactions to D.H. Scott for description (Scott, 1899, 1902, 1918, 1920–23, 1924b). The next phase of collecting was undertaken during the early 1930s by Robert Brown, Jessie Wilson and John Walton, who amassed a considerable quantity of material. This formed the basis for a series of studies by Calder (1935), Walton (1940, 1949a, b, c, 1957), Lacey (1953), Smith (1959, 1960, 1962a, b, 1964b) and Chaphekar (1965) (see also Walton *et al, 1938*). Most recently Scott and Bateman have clarified the stratigraphy and sedimentology at the site. Although Scott *et al.* (1984, 1985) reviewed some of the fossils discovered during their 1982 excavations, there have been only two detailed descriptions published to date (Meyer-Berthaud and Galtier, 1986b; Bateman, 1991).

Description

Stratigraphy

The geology of this site is briefly described by Scott *et al.* (1984, 1985), whose work was in turn amended by Bateman (unpublished) following re-excavation of the most important exposure. The sequence is in the lower part of the Clyde Plateau Volcanic Formation (Hall, 1978). The plant-bearing strata immediately underlie the lowermost of several lava flows and represent a fluviodeltaic complex rich in volcanigenic sediments (Figure 5.32). Detailed logging of the section has resulted in a revised classification of the sequence into five lithostratigraphical units, which will be described fully elsewhere (Bateman, in prep., see summary in (Table 5.1)). Comparison with palynological evidence summarized by Scott *et al* (1984, 1985) suggests that Units 1 and 2 are in the CM Zone (upper Tournaisian), Unit 3 in the lower Pu Zone (Chadian, lower Visean) and Units 4 and 5 in the uppermost Pu Zone (Holkerian, middle Visean). Scott *et al.* (1984) postulated a depositional break approximating the Unit 2–3 boundary to explain this apparently long period of time relative to the thickness of the strata.

Lithostrati- graphical Unit	Main Lithologies	Environmental Interpretation	Bed Numbers of Scott *et al.* (1984, fig. 8)	Fossil Plant Assemblages

Unit 5	Siltstones and fine sandstones with intercalated coarse sandstones, thin shales, coals and rooted palaeosols	Extensive flood plain	21–33	Compressions of rhizomorphic lycopsid rootlets, with rare rhizomorph and aerial axis fragments
Unit 4	Medium to coarse, gritty sandstones, with a few thin shales	Fluvial channel	13–20	Nodular petrifactions of many organs representing a wide range of higher taxa (Bed 17); also compressions, especially of pteridosperm and putative progymnosperm foliage
Unit 3	Thinly laminated shales and an impure limestone	Flood plain/ lacustrine	9–12	Compressions, especially pteridosperm and putative progymnosperm foliage
Unit 2	Siltstones and fine sandstones	Flood plain	6–8	Nodular petrifactions of fragmentary filicopsids, sphenopsids and pteridosperms, especially reproductive organs (Bed 6)
Unit 1	Poorly sorted, coarse sandstones and conglomerates, rich in volcanic ash and clasts	?Channel/ flood plain	1–5	Large, partially petrified pteridosperm axes (Bed 1)

Palaeobotany

Petrified, fusainized and adpression plant fossils have been found here. The anatomically-preserved fossils occur at three discrete horizons: (1) towards the bottom of Unit 1, (2) towards the bottom of Unit 2 (both reputedly lower Tournaisian) and (3) in the middle part of Unit 4 (middle Visean). The following list notes the distribution of each species among the numbered lithostratigraphical units, and deviates from the senior author's preferred classification for higher taxa:

Equisetopsida:

Protocalamites goeppertii (Solms-Laubach) Bateman (2, 4)

Protocalamostachys arranensis Walton (2, 4)

P. cf. *farringtonii* (*Bateman*)(2)

Filicopsida:

Cladoxylon cf. *taeniatum* Bertrand (2)

Hierogramma sp. (2)

Syncardia sp. (2)

Clepsydropsis sp. (2)

Metaclepsydropsis sp. (2)

Botryopteris cf. *antiqua* Kidston (2)

cf. *Senftenbergia* sp. (2)

cf. *Musatea* sp. (2)

Burnitheca pusilla Meyer-Berthaud and Galtier (2)

Etapteris tubicaulis Göppert (4)

Progymnospermopsida:

Protopitys scotica Walton (4)

Gymnospermopsida

Lagenostomales:

Eristophyton fasciculare (Scott) Zalessky (?4)

E. waltonii Lacey (4)

Bilignea resinosa Kidston (?4)

Lyginorachis trinervis Calder (4)

Lyginorachis spp. several (2, 4)

Calathospermum scoticum Walton (4)

Geminitheca scotica Smith (4)

cf. *Pullaritheca* sp. (4)

Calamopityales:

'*Calamopitys*' *radiata* Scott (?1)

Kalymma cf. *tuediana* Long (2)

Kalymma sp. (4)

Alcicornopteris hallei Walton (4)

Gymnosperms (*incertae sedis*)*:*

Amyelon sp. (2)

The best preserved adpressions occur in the middle Visean part of the sequence (units 3 and 4). The following taxa have been identified:

Lycopsida:

Lepidophloios cf. *kilpatrickensis* Smith

Stigmaria ficoides (Sternberg) Brongniart

Equisetopsida:

Archaeocalamites radiatus (Brongniart) Stur

Pothocites grantoni Paterson

Filicopsida (?):

Rhodeopteridium sp.

Progymnospermopsida (?):

Rhacopteris lindsaeformis Sunbury.

R. inaequilaterata Göppert

R. robusta Kidston

R. petiolata Göppert

Gymnospermopsida

Lagenostomales:

Sphenopteridium pachyrrachis (Göppert) Schimper

S. crassum (Lindley and Hutton) Kidston

Sphenopteris affinis Lindley and Hutton

S. bifida Lindley and Hutton

Calathiops trisperma Smith

Calamopityales:

Spathulopteris ettingshausenii (Feistmantel) Kidston

S. obovata (Lindley and Hutton) Kidston

Staphylotheca kilpatrickensis Smith

Alcicornopteris convoluta Kidston

A. zeilleri Kidston

Interpretation

Lycopsida

Although lycopsids are considered to be very poorly represented at Loch Humphrey Burn (Smith, 1964b), one of us (RMB) has found in Unit 5 frequent, poorly preserved *Stigmaria* and an axial compression that compares with the outer surface of the petrified *Lepidophloios kilpatrickensis* Smith from nearby Glenarbuck (see below).

Equisetopsida

Protocalamites goeppertii occurs in both petrifaction assemblages here, and its adpression/cast analogue (*Archaeocalamites radiatus*) is frequent in the Visean part of the section. The anatomical details of the stem nodes described by Walton (1949b) prompted Chaphekar (1963) to unify *Archaeocalamites* with *Protocalamites* (the two principal form-genera for Lower Carboniferous sphenophytes), but this action was subject to detailed criticism by Bateman (1991).

Chaphekar (1965) identified adpressions from here as *Pothocites grantonii,* and showed that it was probably the fertile organ of *Archaeocalamites.* Bateman (1991) has demonstrated that a new specimen of petrified *Protocalamostachys arranensis* from Unit 4 is the anatomically-preserved analogue of *Pothocites grantonii. Protocalamostachys arranensis,* which was previously only known from a single fragment from Laggan (see above), provides a valuable comparison with the smaller *P. farringtonii* Bateman; fragments from both cone species were recorded in Unit 2 by Scott *et al.* (1985; see also Bateman, 1991; Hemsley *et al.,* in press).

Filicopsida

Only one petrified fern, the zygopterid phyllophore *Etapteris tubicaulis,* has been reported from the upper assemblage (Walton *et al., 1938;* Scott *et al.,* 1984). It has not been described in detail, even though Loch Humphrey Burn is the only known British locality for this species.

The Tournaisian assemblage described below is much richer in anatomically-preserved ferns (Scott *et al.,* 1985). The Cladoxylales is represented by the stem *Cladoxylon* cf. *taeniatum* (*its* only British record) and its branches *Hierogramma* and *Syncardia.* No demonstrably cladoxylalean fructifications have yet been found.

The zygopterids are represented by the phyllophores *Clepsydropsis* and *Metaclepsydropsis,* this being regarded as the lowest recorded stratigraph-ical occurrence of the latter (Scott and Galtier, 1985). Scott *et al.* (1985) also recorded sporangia similar to *Musatea,* which is generally regarded as the fertile organ of *Metaclepsydropsis.* Another sporangial type recorded by Scott *et al.* (1985) appears to be a precursor of the more familiar genus *Corynepteris,* a relatively common fern in the Upper Carboniferous.

Scott *et al.* (1985) identified axes with a simple xylem anatomy as *Botryopteris* cf. *antiqua,* again the oldest known examples of this species. Associated isolated annulate sporangia are similar in general form to those known from *B. antiqua* (Galtier, 1967) but differ in the details of the annulus. Another coenopteridalean fructification was compared by Scott *et al.* (1985) with the tedelea-cean form-genus *Senftenbergia,* which again would represent an oldest known record.

The only sporangium so far described in detail from Unit 2 is *Burnitheca pusilla* Meyer-Berthaud and Galtier (1986b). It consists of a bilaterally symmetrical cluster of eight sporangia, fused basally around a central column. Although it broadly resembles lagenostomalean microsporangiate organs such *as Telangium,* the form of the tapetum and the spores that it contains suggest affinities with the marattialean ferns. If this interpretation is correct, *Burnitheca is* the oldest known example of this extant order. Two further types of sporangia, possibly belonging to ferns, are mentioned by Scott *et al.* (1985) as 'Fructifications G and H'.

The evidence from Loch Humphrey Burn documents the rapid diversification of the ferns in the Early Carboniferous. The supposedly upper Tournaisian Unit 2 contains a remarkable number of first recorded occurrences of fern species, genera and even families, and its taxonomic composition is more consistent with the mid-Visean age attributed to the overlying units at Loch Humphrey Burn. Many of these early ferns lacked fully planated fronds, but possessed fructifications characteristic of recognized fern taxa. By the early Late Carboniferous, more modern-looking ferns had developed, especially in the palaeoequatorial areas. The fossils found at Loch Humphrey Burn, although fragmentary, are thus of considerable value in recording this group of plants at a key stage in its evolutionary history.

Progymnospermopsida

Loch Humphrey Burn is one of the most important localities for Lower Carboniferous progymnosperms. They are thought to have been widespread in the equatorial and northern-temperate palaeolatitudes. However, progymnosperms are difficult to identify with confidence since this requires demonstrating the absence of ovules, and anatomically-preserved fertile material is rare. Loch Humphrey Burn has yielded the only known fertile specimens of the order Protopityales (Walton, 1957; Smith, 1962b). Stems from Loch Humphrey Burn share many anatomical features with *Protopitys buchiana* Solms-Laubach from Yorkshire and Falkenberg (Solms-Laubach, 1893; Walton, 1957, 1969); both have oval siphono-steles emitting distichous leaf-traces, features that characterize the Protopityales. However, the Loch Humphrey specimens have less extensive primary wood, no high biseriate rays, and secondary wood with multiseriate pitting, and so were placed in a new species, *Protopitys scotica* by Walton (1957).

Sporangia attached to these stems were described by Walton (1957) and Smith (1962b). This was the first recorded example of a plant that had both gymnospermous wood and pteridophy-tic reproductive organs.

Together with the correlation of *Callixylon* wood and *Archaeopteris* foliage by Beck (1960), this was one of the main arguments for recognizing the class Progymnospermopsida as a precursor to the pteridosperms (and arguably the conifers: Beck, 1970, 1971). The spores of *P. scotica* show little variation within sporangia, but considerable variation among adjacent sporangia, and the overall size distribution determined by Smith (1962b) is weakly bimodal. Thus, it is unclear whether the plant was heterosporous (Bateman and DiMichele, in press).

Archangelsky and Arrondo (1966) and Beck (1976) suggested that the adpression foliage *Rhacopteris* is progymnospermous, based on its similarity to *Archaeopteris.* The co-occurrence at Loch Humphrey Burn of adpressed *Rhacopteris* and petrified *Protopitys* lends some support to this argument, though the former is abundant and the latter rare.

Pteridosperms

Seed plants dominate the assemblages in Units 3 and 4, but Scott *et al.* (1985) reported that they are subordinate in Unit 2. Both the Lagenostomales and Calamopityales are represented.

Lagenostomopsida

Petrified stems of *Eristophyton* and *Bilignea* were probably found in the Visean part of the section, although their precise origin was not stated. They include the type and one of only two known specimens of *Eristophyton fasciculare* Scott (1899, 1902, 1918), and the only known specimen of *E. waltonii* Lacey (1953). The latter differs from *E. fasciculare* in having a larger parenchymatous pith with sclerotic nests, smaller primary xylem strands emitting undivided leaf traces, and in its ability to develop larger wood rays. *Bilignea resinosa* Scott (1924b) is similarly known from only a single specimen. It resembles *Eristophyton* in many characters, but has a large core of pitted tracheids interspersed with large resin sacs, rather than a parenchymatous pith. Although affinities with the cordaites (Scott, 1899, 1924b; Andrews, 1940; Lacey, 1953) and the calamopityales (Read, 1937) have been suggested for these genera, Long (1987, pers. comm. 1988) and Bateman and Rothwell (1990) have shown that they are lagenostomalean.

Abundant and diverse *Lyginorachis* petioles occur at Loch Humphrey Burn, mainly in the upper part of the section. Of these, only *L. trinervis* Calder (1935) has been formally described. Its unusual tripartite stele and rapid decrease in diameter along its 2 mm length suggest that it is the basal portion of a petiole. Similar petioles have recently been identified from approximately coeval deposits at Kingswood (see above). Another well-preserved petiole from Loch Humphrey Burn resembles *Lyginorachis waltonii,* first described from Laggan on the Isle of Arran (see above). Long (1987) has reported similar axes attached to *Eristophyton beinertianum* stems at Oxroad Bay (see above).

Loch Humphrey Burn is the only known locality for the petrified lagenostomalean cupules *Calathospermum scoticum* Walton (1949a) and *Geminitheca scotica* Smith (1959). *C. scoticum* is the type species of *Calathospermum,* a genus of large, multi-ovular 'megacupules' that also includes *C. fimbriatum* Barnard from Oxroad Bay (see above). These 'megacupules' have been interpreted as entire reduced fronds and are assumed to have been borne directly on the stem (Long, 1977b); in contrast, 'microcupules' are thought to have been only a distal part of a fertile frond that otherwise resembled conspecific sterile fronds. Clusters of microcupules were thus attached to foliage (usually in the fork of a vegetatively bipartite frond) rather than directly to the stem.

Many of the several known specimens of *C. scoticum* are barren, the ovules having been released; the few ovulate cupules are either immature or mature but unfertilized. The ovules resemble *Salpingostoma dasu* Gordon, as found in *C. fimbriatum* Barnard, but are smaller and have more integumental lobes (Walton, 1949a; Barnard, 1960b). *C. scoticum* probably bore a greater number of ovules (*c.* 48 according to Matten and Lacey, 1981) than C *fimbriatum,* but had only six undissected lobes. Furthermore, Matten and Lacey (1981) suggested that the *C. fimbriatum* cupule is characterized by an initial dichotomy followed by monopodial or pseudo-monopodial divisions, but that *C. scoticum* has basally-fused cupular lobes. Some enigmatic structures in one *C. scoticum* cupule were interpreted by Walton (1949a) as microsporangia, who thus believed that these cupules were bisexual.

In contrast, *Geminitheca scotica is* a micro-cupule containing only two ovules. A specimen recently discovered by Scott shows *c.* 15 cupules borne on a repeatedly dichotomizing fertile frond. Like *Calathospermum scoticum,* it has up to six cupular lobes, but according to Matten and Lacey (1981) shows monopodial branching. Its ovules are also unusual in having an integument that is joined to the nucellus only at the base. This primitive characteristic is shared with *Genomosperma* from the Whiteadder (see earlier in this chapter). However, a salpinx with a central column and a vascular strand extending to the base of the nucel-lus, characters typical of *Genomosperma,* have not been reported for *Geminitheca,* which has also been correlated with different spores.

Smith (1959, 1960) reported *Telangium*-like sporangia associated with *Geminitheca.* Sincethey contained similar spores to those found within the lagenostome of *G. scotica,* he argued that they probably belonged to the same plant.

A compressed ovulate cupule was described by Smith (1962b) as *Calathiops trisperma.* It resembles *Geminitheca,* but is smaller and supposedly contains three ovules. The apparently ubiquitous development of ovulate cupules by repeated dichotomies (cf. Matten and Lacey, 1981) renders triovulate cupules uncommon, though the condition has been reported in some specimens of *Stamnostoma oliveri* from Oxroad Bay (see above). *Calathiops trisperma* may be an immature form of *G. scotica.*

A third type of lagenostomalean cupules has been found by one of us (RMB) at Loch Humphrey Burn. Like *Geminitheca,* it is a small cupule pair, but unlike that genus it has numerous cupular lobes and ovules with about ten integumental lobes. It may have affinities with *Pullaritheca longii* from Oxroad Bay (see above).

There is thus evidence of at least three lagenostomalean plants preserved as petrifactions in the upper assemblages of Loch Humphrey Burn. Their foliage presumably occurs in the diverse fern-like foliage preserved here as adpressions. Perhaps the best candidate is *Sphenopteridium,* which has pinnules attached below the main dichotomy, and racheis with transverse bars. Two form-species have been recorded here, *S. pachyrrachis* and *S. crassum,* although there is a morphological continuum between them and they may be conspecific. Other probable lagenostomalean fronds recorded by Walton (1957) and Smith (1964b) were *Sphenopteris affinis, S. bifida* and *Rhodeopteridium* sp.

Calamopityales

The only known specimen of the stem '*Calamopitys*' *radiata* Scott (1924b) originated from an unspecified horizon at Loch Humphrey Burn; its poor state of preservation suggests that it was from Unit 1, recently rediscovered at the base of the sequence. It is characterized by wide rays and probable exarch primary wood, but may be more appropriately segregated from *Calamopitys.* Scott *et al.* (1985) also illustrate, from the lower part of the section (Unit 2), a specimen of *Kalymma* cf. *tuediana,* which is probably part of a calamopityalean frond.

The upper part of the Loch Humphrey Burn section has yielded some of the best preserved examples of calamopityalean reproductive organs, *Alcicornopteris ballei.* These appear to be exclusively microsporangiate (Walton, 1949c; Smith, 1962a), in contrast to the apparently ovulate *Alcicornopteris* described from the Cementstone Group of Berwickshire

(Long, 1969). Thus, this genus can encompass both male and female reproductive organs.

The affinities of a second sporangial cluster found at Loch Humphrey Burn are far less certain. The compression *Staphylotheca kilpatrickensis* Smith (1962b) consists of infrequently dichotomizing racheis with clusters of linear organs that bear sporangia. Smith tentatively assigned it to the pteridosperms on the basis of its tracheidal pitting, but its spores are enigmatically dimorphic: Type A is large, round and thin-walled and Type B is small, subtriangular and thick-walled. Smith argued that this morphological discontinuity between the two spore types is rather extreme to represent a contrast between viable and abortive spores. If so, this would imply the presence of heterospory and possible assignment of *Staphylotheca* to the progymnosperms.

The most likely calamopityalean foliage at Loch Humphrey Burn is *Spathulopteris.* Characteristics of these fronds include the thick-limbed, spathulate pinnules, longitudinal striae on the racheis but no transverse markings, and the absence of pinnae attached to the petiole below the initial dichotomy of the petiole. The two form-species described from Loch Humphrey Burn (*S. ettingshausenii* and *S. obovata*) probably represent ontogenetic variations of a single biological species.

General remarks

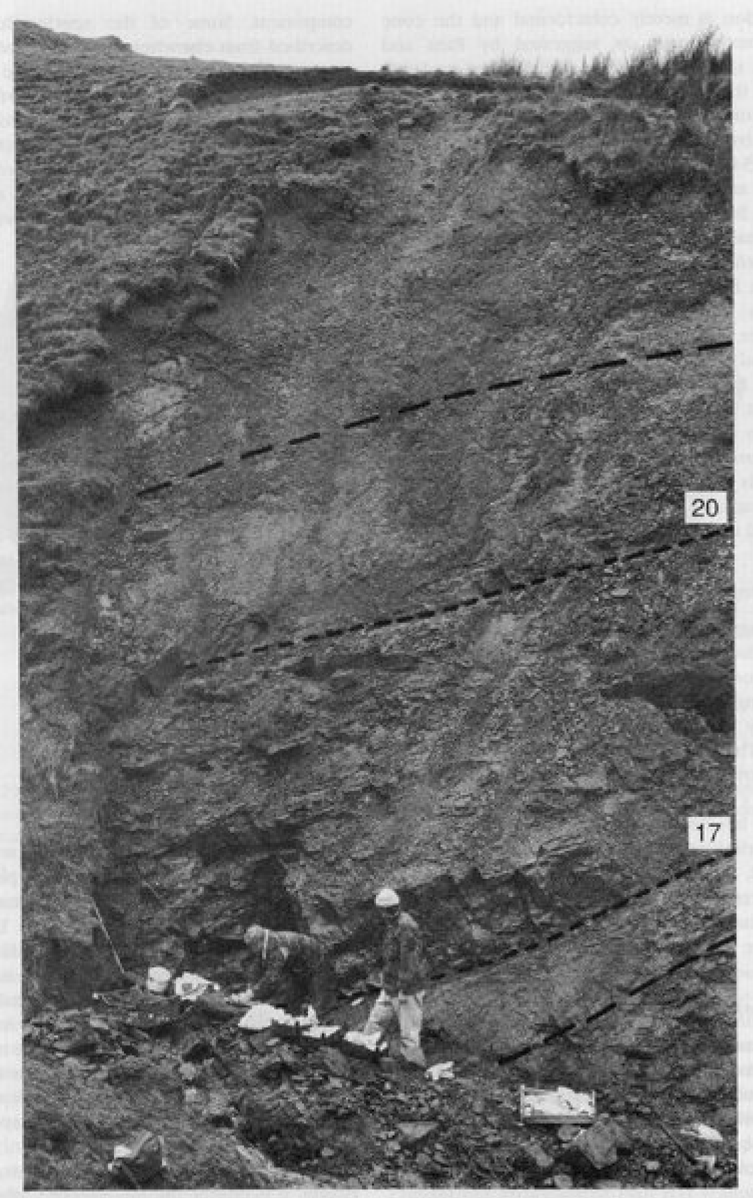
Loch Humphrey Burn is of special interest in that it contains two speciose assemblages of anatomically-preserved plant fossils that are taxonomically, stratigraphically and (supposedly) temporally distinct. Fossils in the older assemblages (summarized by Scott *et al.,* 1985) are fragmentary and thus difficult to interpret, both taxonomically and palaeobiologically. Many of its diverse ferns are potential first occurrences of genera or families (e.g. Marattiaceae, Tedeleaceae), but this interpretation requires acceptance of the upper Tournaisian age attributed to the assemblage on palynological evidence; the megafloras and lithostratigraphy are more consistent with the mid-Visean age of the overlying petrifaction assemblages.

The better known upper assemblages are dominated by pteridosperms and putative progymnosperms, many of the species being endemic. It is quite different in general aspect to the other well-known Visean petrifaction site in Britain at Pettycur (see above), where the assemblage is dominated by ferns and lycopsids. Lycopsids also dominate the more restricted petrifaction assemblage from nearby Glenarbuck (discussed in the next section). Overall, the plant fragments would reconstruct to yield at least eight whole-plant species in the lower assemblage and seven in the upper assemblage. Loch Humphrey Burn is the most significant Visean site in Europe for understanding the evolutionary history of the early gymnosperms and late progymnosperms.

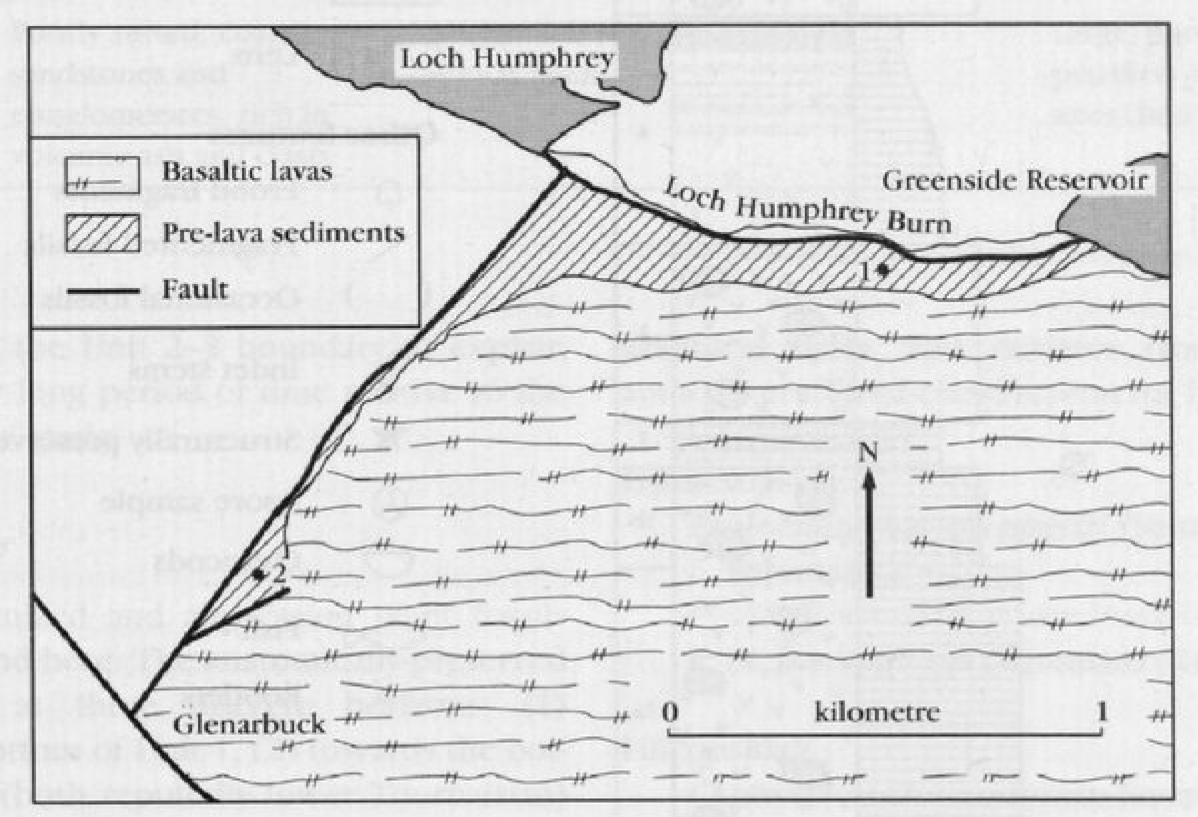
Conclusion

Loch Humphrey Burn has yielded exceptionally well-preserved plant fossils that reputedly range in age from 340 to 350 Ma. Early ferns predominate in the lower part of the succession and, if correctly dated, include the oldest examples known from anywhere in the world of two families which were common in the Late Carboniferous (Tedeleaceae and Corynepteridaceae), and the earliest known example from anywhere in the world of the extant fern order Marattiales. It has also provided invaluable information on the morphology and anatomy of early sphenophytes ('horsetails') and seed plants, especially reproductive structures such as the 'megacupule' *Calathospermum.* Loch Humphrey Burn is one of the few localities of this age to yield both anatomically-preserved and compressed plant fossils. Although these are not in organic connection, further work may allow correlation by indirect methods, thereby combining features of anatomy and gross morphology. Stratigraphical and palaeoecological investigations have proved fruitful and will continue.

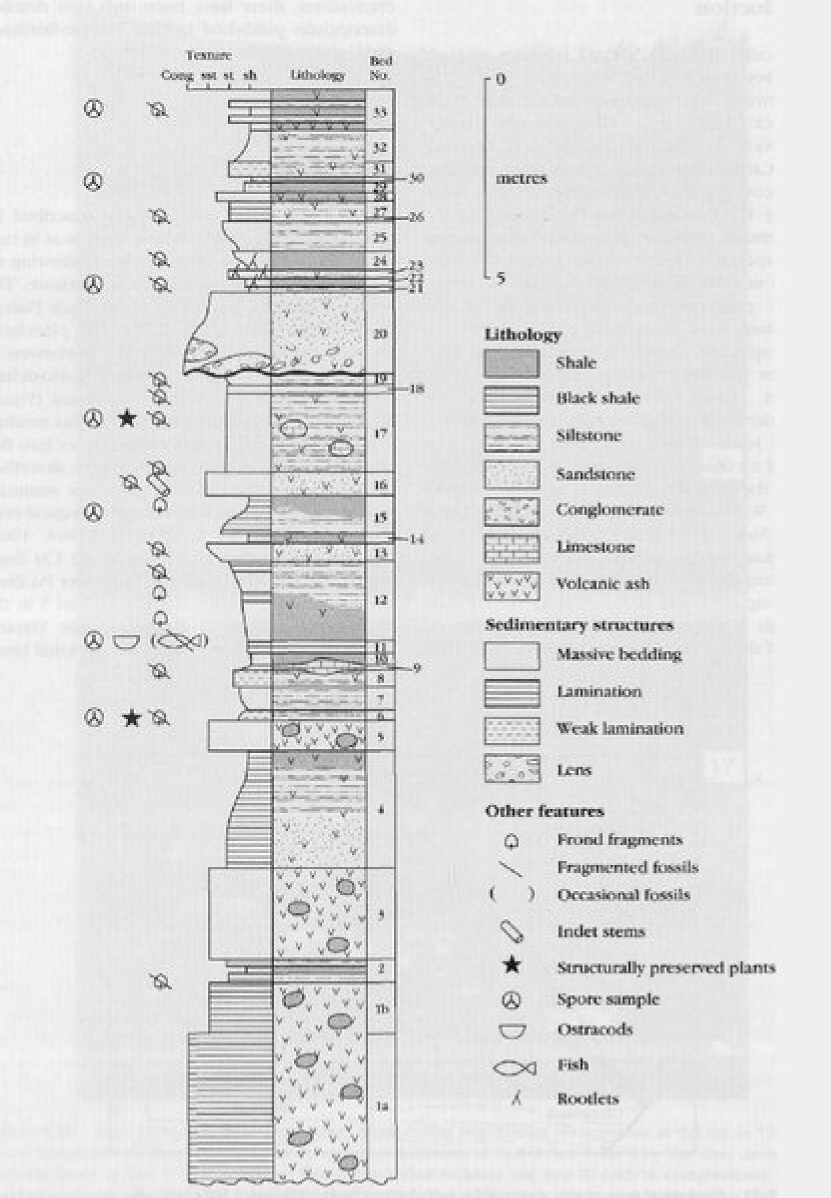
References



(Figure 5.30) Loch Humphrey Burn. Photograph taken during NCC-funded re-excavation of the site in 1985. The coarse dashed lines delimit the plant-rich volcanigenic sediments of Unit 4 (see (Table 5.1)). The finer dashed lines mark the bases of Bed 17 (the source of Walton's petrified nodules) and Bed 20 (rich in compressions, notably Pothocites cones). The overlying Unit 5 includes thin coals and represents a clastic swamp containing giant lycopsids; this correlates with the nearby Glenarbuck site. (Photo: R.M. Bateman.)



(Figure 5.31) Geological map of area south of Loch Humphrey in the Kilpatrick Hills, showing positions of Loch Humphrey Burn (1) and Glenarbuck (2) sites. Based on Scott et al. (1984, figure 5).



(Figure 5.32) Sedimentological log at Loch Humphrey Burn. Based on Scott et al (1984, figure 8).

Lithostratigraphical Unit	Main Lithologies	Environmental Interpretation	Bed Numbers of Scott *et al.* (1984, fig. 8)	Fossil Plant Assemblages
Unit 5	Siltstones and fine sandstones with intercalated coarse sandstones, thin shales, coals and rooted palaeosols	Extensive flood plain	21–33	Compressions of rhizomorphic lycopsid rootlets, with rare rhizomorph and aerial axis fragments
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Unit 1	Poorly sorted, coarse sandstones and conglomerates, rich in volcanic ash and clasts	?Channel/ flood plain	1–5	Large, partially petrified pteridosperm axes (Bed 1)

(Table 5.1) Lithostratigraphy of Loch Humphrey Burn (R.M. Bateman, unpublished)