
Whiteadder

Highlights

The Whiteadder has yielded the most diverse Lower Carboniferous plant petrification assemblage in Britain (Figure 5.10). Particularly important is the wide range of early gymnosperm ovules showing details of cell structure, including the morphologically most simple ovule so far found in the fossil record (*Genomosperma*).

Introduction

The Whiteadder River is a tributary of the Tweed, which it joins about 3 km south-west of Berwick-upon-Tweed, Borders Region (Figure 5.11). Finely preserved plant petrifications have been reported from the limestones of the Tournaisian Cementstone Group exposed between Hutton Bridge [NT 921 546] and Cumledge [NT 792 564], and particularly from Edrom [NT 821 560]. Fossils were occasionally recorded from here during the nineteenth century (e.g. Witham, 1830), but it was not until the site was investigated during the early years of the twentieth century by A. Macconochie for the Geological Survey that its real palaeobotanical potential started to be realized. Initially, only adpressions were found, although petrifications were known from homotaxial strata in the Tweed valley and at Langton Burn (Kidston, 1901a), but petrifications were soon also found at the Whiteadder (Kidston, 1902a). Kidston clearly recognized the importance of the Berwickshire petrifications and had numerous thin sections prepared. One paper, intended to be the first of a series, was written in 1912 with Gwynne-Vaughan. However, the project was prematurely terminated, partly because of the death of the latter in 1915, and partly because of the discovery of plant fossils at Rhynie (see Chapter 4), which diverted Kidston's attention. Some of Kidston's Whiteadder slides were described by Solms-Laubach (1910), Gordon (1912) and Calder (1934, 1938), and there was also some interest in the adpressions (Chaloner, 1953). It was not until Long started to re-investigate the fossils from here in 1957, that the significance of the assemblage became evident. In a series of papers published since 1959, Long has described 40 form-species, many of which were new to science. Long's work, which for the first ten years he effectively did as an amateur (Long, 1976c; Andrews, 1980), ranks as one of the most significant contributions to British palaeobotany this century.

Description

Stratigraphy

The strata exposed along this stretch of the Whiteadder belong to the Cementstone Group, and comprise mainly alternating shales and harder bands of calcareous rocks, known as cement-stones. The majority of the cementstones are calcareous mudstones, probably of diagenetic origin. However, they also include lacustrine, shelly limestones, and it is these that contain the plant petrifications (Scott *et al.*, 1984; Scott and Rex, 1987). A measured stratigraphical log for the section has never been published, although general descriptions are given by Scott *et al.* (1984). Miospores obtained from both the shales and the lacustrine limestones at Edrom belong to the CM Biozone, thus indicating a late Tournaisian age. The plant adpressions (see next section) appear to belong to the upper *Triphyllopteris* Biozone, which according to Wagner (1984) indicates an early Viséan age. However, few of the adpressions have been studied in recent years and a revision is necessary to verify their biostratigraphical positions.

Palaeobotany

The following taxa have been described from here as petrifications:

Lycopsida:

Lepidodendron calamopsoides Long

Paralycopodites brevifolius (Williamson) DiMichele

Stigmaria sp.

Oxroadia gracilis Alvin

Mazocarpon pettycurense Benson

Filicopsida:

Cladoxylon kidstonii Solms-Laubach

C. waltonii Long

Hierogramma mysticum Unger

Clepsydropsis antiqua Unger

Protoclepsydropsis kidstonii (Bertrand) Hirmer

Psalixochlaena berwickense Long

Stauropteris berwickensis Long

Lagenostomopsida:

Genomosperma kidstonii (Calder) Long

G. latens Long

Hydrasperma tenuis Long

Stamnostoma huttonense Long

S. bifrons Long

Salpingostoma dasu Gordon

Calathospermum fimbriatum Barnard

Deltasperma fouldenense Long

Eosperma edromense Long

Eccroustosperma langtonense Long

Camptosperma berniciense Long

Telangium sp.

Tristichia ovensii Long

Rhetinangium arberi Gordon

Lyginorachis kidstonii Long

L. arberi Long

L. papilio Long

Pitus primaeva Witham

Calamopityales (*incertae sedis*):

Eurystoma angulare Long

E. burnense Long

Lyrasperma scotica (Calder) Long

Dolichosperma sexangulatum Long

D. pentagonum Long

Alcicornopteris convoluta Kidston

Stenomyelon tuedianum Kidston

S. heterangioides Long

S. primaevum Long

Kalymma tuediana Calder

Uncertain affinities:

Mitrospermum bulbosum Long

Cystosporites devonicus Chaloner and Pettit

Triradioxylon primaevum Barnard and Long

Lyginorachis whitadderensis Barnard and Long

In addition, a number of taxa have been described from impressions found in the shales:

Lycopsida:

Lepidodendron veltheimii Sternberg

L. rhodeanum Sternberg

L. spetsbergense Nathorst

L. nathorstii Kidston

L. berwickense Crookall

Flemingites allantonensis (Chaloner) Brack-Hanes and Thomas

Stigmara ficoides (Sternberg) Brongniart

Lagenostomposida:

?*Sphenopteridium pachyrachis* (Göppert) Schimper

Calamopityales (*incertae sedis*):

Samaropsis bicaudata Kidston

Triphyllopteris collumbiana Schimper

Interpretation

The diversity of Lower Carboniferous petrified plant remains found along the Whiteadder is unrivalled anywhere in the world. However, the significance of the site lies not just in the number of taxa that it yields, but also in the importance of many of the individual species for understanding the evolution of Early Carboniferous plants. In order to assess this, the following discussion will deal separately with each of the classes of plant represented.

Lycopsida

Arborescent lycopsids are amongst the commonest plant remains found along the Whiteadder, but have been relatively ignored. Long (1964c, 1971) briefly described petrified aerial stems of *Lepidodendron calamopsoides* (believed to be equivalent to the adpression species *L. spetsbergense*, *L. nathorstii* and *L. berwickense* — Long 1971) and *Paralycopodites brevifolius*, and stigmarian rooting structures. Long (1971) also described some petrifications of the herbaceous lycopsid *Oxroadia gracilis* from here, providing the first evidence of its rooting structures.

Few lycopsid fructifications have been reported here. Chaloner (1953) described a compression now known as *Flemingites allantonensis* (see also Crookall, 1966), which is very similar in general structure and dimensions to the petrified *Flemingites scottii* (Jongmans) Brack-Hanes and Thomas, the presumed strobilus of *Paralycopodites brevifolius* from Pettycur (see below). Long (1968a) also described two incomplete petrified sporophylls as *Mazocarpon pettycureense*. Little can be determined from these latter specimens, but they are of interest as the oldest known examples of the Sigillariaceae, one of the lycopsid families that came to dominate the equatorial swamp forests later in the Carboniferous.

Cystosporites devonicus was described from here by Long (1968a), who argued that they were megaspores of either lycopsids (e.g. *Lepidocarpon* or *Achlamydocarpon*) or of progymnosperms. Pettitt and Beck (1968) have also linked them with the early gymnosperm *Archaeosperma* (see also comments by Hemsley, 1990b).

Filicopsida

This group of plants is represented here by several taxa. Particularly common are distal parts of vegetative organs, assignable to the artificial form-genera *Hierogramma* and *Clepsydroopsis* (Long, 1967, 1968b).

More diagnostic are the main stems of these plants. The Whiteadder has yielded two species of cladoxylids, both of which are unique. The best known is *Cladoxylon waltonii*, 35 specimens of which were described by Long (1968b), demonstrating a range of forms. They fall into two groups: radially symmetrical stems, 8–12 mm in diameter, with a slightly dorsiventral actinostele; and dorsiventral stems, 2–7 mm in diameter, with a IP-shaped stele. It is far from certain that they all in fact belonged to the same species, but Long united them in the absence of evidence to the contrary. If they are, then they provide a valuable insight into the anatomical variability of this unusual group of plants, particularly with reference to the anastomosis and dissection of the stele.

Cladoxylon kidstonii is only known from a single imperfect specimen, and is inadequately understood (Solms-Laubach, 1910; Seward, 1917; Scott, 1920–1923).

A single species of zygopterid (Coenopteridopsida) stem has been described — *Protoclepsydroopsis kidstonii*. The fragmentary holotype originated from Langton Burn near Gavinton (Bertrand, 1911a, b; Hirmer, 1927), but all other specimens have come from the Whiteadder (Long, 1967). It has been interpreted as a creeping, herbaceous plant with a deeply dissected stele that produced *Clepsydroopsis* petioles in a 2/5 phyllotaxy. The anatomy of the stele and the petioles is somewhat similar to *Cladoxylon*, which Long (1967) used as evidence for the close affinity between the Cladoxylopsida and the Coenopteridopsida.

A second type of coenopterid found at the Whiteadder is *Stauropteris berwickense* Long (1966). It has similar vegetative structures to *Stauropteris burntislandica* Bertrand from Pettycur (p.147), except for having a more symmetrical vascular cross-section, but it does not have the significant swelling of parenchymatous tissue at the base of the sporangium. Long (1966) argued that these two features point to *S. berwickense* being less specialized and more primitive than both the Pettycur species and *Stauropteris oldbamia* Binney from the Westphalian.

The only possible true fern described to date from the Whiteadder is *Psalixochlaena berwickense* Long (1976b). It is based on 21 slender stem fragments (although Long suggested that some might be parts of the same stem) and some isolated petioles. In the absence of fructifications or of evidence as to the orientation of the petioles in relation to the stems, its generic position is provisional (contrast the situation with the Westphalian species *P. cylindrica* (Williamson) Holden Holmes, 1981). However, a point of interest is the possible presence of trifurcate branching of the petioles, produced by a foreshortened double dichotomy, which Taylor (1981) has compared with similar branching in the trimerophytes.

Lagenostomopsida

About two thirds of the form-species described from the Whiteadder belong to the group of gymnosperms with large, divided leaves, known informally as the pteridosperms. The 28 form-species probably originated from 15 whole-plant species, belonging to two classes: the Lagenostomopsida, and a so-far unnamed class that includes the Calamopityles. They are, scientifically, probably the most significant components of the Whiteadder flora. This is not so much because they were dominant in the life assemblage (lycopsids were probably dominant — Long, 1964c), but instead probably reflects a combination of greater species diversity in a group occupying less stable habitats and the greater attention that they have received from palaeobotanists. Although the earliest known ovules originated from the Upper Devonian of the USA (Gillespie *et al.*, 1981; Rothwell and Scheckler, 1988; Rothwell *et al.*, 1989), the Whiteadder has yielded the greatest variety of different primitive types showing details of their anatomy. The site has also yielded key information in relating them to whole-plant reconstructions (e.g. Retallack and Dilcher, 1988). It has thus been central to the development of ideas about early gymnosperm taxonomy and evolution.

The Lagenostomopsida includes pteridosperms with protostelic or siphonostelic stems (e.g. *Heterangium*, *Rbetinangium*, *Lyginopteris*). Long (1975) characterized the ovules by a number of features, but this has to be modified as he included within the Lagenostomales ovules now thought to belong to the Calamopityales and the enigmatic Eospermaceae. The ovules of this order appear now to be characterized as follows: integument free from nucellus at least above the plinth; a single set of vascular bundles in the integument; no vascular tissue in the nucellus; and radial symmetry. The male reproductive organs are of the *Telangium/Telangioopsis* type.

Until recently, the Lower Carboniferous lagenostomalean species were only known from isolated organs, which made it difficult to classify the group. However, studies by Long, based mainly on Whiteadder material, have gone a long way towards relating the various organs to one another and it is now possible to think more in terms of whole plants. It must be emphasized that the proposed reconstructions are based mainly on histological similarities of the various organs, and have not been confirmed by organic connection between them (cf. comments under Oxroad Bay see p. 134). They nevertheless provide a starting point from which to consider these early lagenostomaleans as whole plants.

The most completely known is that which bore the *Stannostoma* ovules (Long, 1979a; Retallack and Dilcher, 1988). Retallack and Dilcher state that the Foulden site is the main locality for developing this reconstruction, but nearly half the specimens on which Long (1960a, 1962, 1963, 1979a) based his primary studies in fact originated from the Whiteadder. The plant is interpreted as arborescent, over 25 metres tall, with a trunk about one metre in diameter, and of a habit similar to that of the extant Scots pine (*Pinus sylvestris* L.) (see (Figure 5.6)). The trunk is believed to be of the type commonly described as *Pitus primaeva* Witham (Long, 1963, 1979a). The fronds were bipartite, with at least two pairs of sub-opposite pinnae attached below the dichotomy, and *Lyginorachis papilio* Kidston petioles. There has been disagreement as to the form of these leaves and what they would be called if preserved as impressions. Long (1963) argued that they would be called *Sphenopteris affinis* Lindley and Hutton, but such fronds are in fact quadripinnate. Based on evidence of association at Foulden (Scott and Meyer-Berthaud, 1985), Retallack and Dilcher (1988) argue that they were *Aneimites acadica* Dawson; but fronds with such flabellate pinnules were probably from calamopityalean

plants. Since the details of the *Aneimites* frond architecture are unknown, it is unwise to link it with the *Stamnostoma*-bearing plant. A more convincing link is with the bipartite adpression fronds known as *Sphenopteridium pachyrrachis* (Göppert) Schimper, which are of a similar size and have pinnae attached below the dichotomy (Kidston, 1923b).

The fertile organs of this plant are borne on an axillary branch attached to the dichotomy of some fronds. Such fertile branches differ from the vegetative part of the frond in having a radial symmetry, and were identified with axes described by Long (1962, 1963) as *Tristichia ovensii*. Scott and Meyer-Berthaud (1985) have argued that *Tristichia* was part of a quite different plant with non-cupulate ovules (see also Galtier, 1977), but Long's description of the fertile axillary branch of the *Stamnostoma*-bearing plant nevertheless remains valid. In the female fronds, the fertile branches are terminated by clusters of *Calathiops*-like campanulate cupules (microcupules *sensu* Long, 1977a), which are formed from a sheaf of dichotomously branched, terete telomes. Each cupule contains four *Stamnostoma* ovules. No direct evidence of the male fronds has been reported, but Long (1979a) noted the frequent association of *Telangium* synangia bearing pre-pollen.

The lagenostomean plant that bore *Genomosperma* ovules was probably rather different. Although the sort of detailed reconstruction outlined above has not been achieved for this plant, there is enough circumstantial evidence to suggest that it was significantly smaller, perhaps only one metre or so high (Long, 1959b, 1964b). The main stem is probably of a type known as *Rhetinangium*, which is only about 20 mm wide, and the longest known example is 260 mm long (Gordon, 1912). Based on association, Long (1964b) argued that the stem bore *Lyginorachis arberi* (syn. *L. cf. trinervis* Calder of Long, 1959b) petioles and *Genomosperma latens* ovules. The overall form of the fronds is unknown, but they were probably bipartite, as in many other lagenostomeans. Again based partly on association, Long (1964b) suggested that a second species of ovule (*Genomosperma kidstonii*) was borne on fronds with *Lyginorachis kidstonii* (syn. *Lyginorachis* sp. Crookall, 1931a) petioles. In all likelihood, these were also probably borne on *Rhetinangium* stems, although supporting evidence has yet to be forthcoming.

Another well-known Lower Carboniferous lagenostomean plant was that which bore *Salpingostoma dasu* ovules in *Calathospermum fimbriatum* cupules (Retallack and Dilcher, 1988). However, the reconstruction described by Retallack and Dilcher is based mainly on material from Oxroad Bay (p. 134), and the Whiteadder has provided little additional information.

Isolated ovules from the Whiteadder have been described by Long (1961b) as *Hydrasperma tenuis*. However, such ovules have been described from other localities in two quite distinct types of cupules, which have been named *Kerryia* and *Pullaritheca* (Rothwell and Wight, 1989) and it is impossible to be certain which (if either) contained the Whiteadder ovules. Long (1975) included *Hydrasperma* in his new family the Eurystomaceae, most of whose member species probably belong to the Calamopityales (see below). However, *Hydrasperma* does not have the characteristic broad, barrel-shaped lagenostome (or salpinx) of most of the other Eurystomaceae ovules, and is more comparable to the lagenostomean *Stamnostoma*. Furthermore, *Pullaritheca longii* from Oxroad Bay (see below) was borne on *Sphenopteris bifida* fronds, which is probably lagenostomean (Long, 1979b).

One of the most significant aspects of the lagenostomeans from the Whiteadder is the primitive form of the ovules, particularly in the form of the integument (Figure 5.12). The following levels of development of the integumentary sheaf can be recognized.

1. *Genomosperma kidstonii*. The integument comprises a tubiform sheaf of eight more or less terete lobes, which are only attached to the nucellus at the chalaza (Long, 1959b). Niklas (1981) has argued that this in fact is better termed a 'pre-integumentary truss', although most palaeontologists continue to refer to it as a true integument.
2. *Genomosperma latens*. The integumentary telomes are fused to one another in the proximal part of the ovule, and converge at the distal end of the ovule to form a canopy over the lagenostome.
3. *Hydrasperma* and *Salpingostoma*. The integumentary telomes are even more fused, forming a sheath around the entire ovule below the plinth.

4. *Stamnostoma*. The integument is a completely fused sheath forming an open collar around the lagenostome. Long (1975) interpreted the latter as a micropyle but, as it does not cover the lagenostome fully, it cannot have had the same pollen-capturing function as the micropyles of later lagenostomean ovules. It may nevertheless represent an early stage in the evolution of the micropyle.

Most of the lagenostomean ovules from the Whiteadder belong either to the families Genomospermaceae or Elkinsiaceae (Cleat 1993). However, there is a third group consisting of *Eosperma*, *Deltasperma*, *Eccroustosperma* and *Camptosperma* (Long, 1961a, b, 1966, 1975). There is no evidence as to which plant-type bore them, or even if they were contained in cupules. However, they are all platyspermic and show the same type of short, distally-tapered lagenostome, containing a conical central plug (Figure 5.13) The most distinctive aspect of the group is the variation in curvature of the ovules: *Eosperma* is flat, *Deltasperma* slightly curved, *Eccroustosperma* 'S'-shaped and *Camptosperma* fully campylotropous (i.e. the chalaza and lagenostome are on the same side of the ovule). The latter is particularly unexpected, as it is a condition most usually associated with angiosperms. Long (1961a) argued that it might indicate that the *Camptosperma* ovules were attached directly to a dorsiventral frond, and was to assist in the better exposure of the lagenostome (and presumed pollen drop) for pollination. Long (1975) assigned these ovules to a separate family within the Lagenostomales, the Eospermaceae (see also comments by Barnard, 1959). This is still widely accepted (e.g. Cleat, 1993), although no other lagenostomean ovule is known to be platy-spermic, and there are also differences in the structure of the lagenostome.

The Whiteadder lagenostomean ovules thus provide strong support to the telomic hypothesis for early ovule evolution, whereby a sporangium containing a single viable megaspore becomes surrounded by a sheath of fused lobes, that eventually fuse to become the integument (Walton, 1940, 1954, 1964b; Smith, 1959; Long, 1960a; Andrews, 1961). However, it is less certain from the available evidence whether the surrounding telomes were originally all fertile (Benson, 1904) or were sterile.

This is the most diverse known assemblage of lagenostomean ovules showing the primitive hydrasperman reproductive mechanism, in which pollen-capture prior to fertilization is achieved by the nucellus, rather than by the integument and micropyle as in most other gymnosperms (Rothwell, 1986). Pollen was probably wind transported (Niklas, 1981), and pollen capture achieved by a pollen-drop secreted by the lagenostome. There is little evidence that arthropods played a part in this process.

Calamopityales

This major order of Lower Carboniferous pteridosperms is also well represented in the Whiteadder assemblage. The best known reconstructed plant from here is that known as the *Lyrasperma scotica* plant of Retallack and Dilcher (1988; see also Long, 1960b, 1964a) (Figure 5.8). It is thought to have been up to about 1.5 metres high, with a succulent trunk. Isolated stems are identified as *Stenomyelon tuedianum* and have a distinctive protostele, which is divided into three strands by radiating bands of parenchyma. Long (1964a) described petioles known as *Kalymma tuediana* attached to such stems. The overall form of the fronds borne by this plant has caused some difficulties. Retallack and Dilcher state that they probably correspond to foliage known as *Sphenopteridium pachyrrachis* (Göppert) Schimper when preserved as adpressions, but, as correctly pointed out by Long (1964a), there are serious discrepancies in the frond architecture, especially in the absence of pinnae attached to the primary rachis below the main dichotomy. The report by Long (1964a) of *S. pachyrrachis* pinnules associated with *Stenomyelon/Kalymma* at nearby Foulden was probably coincidental, the former being more likely to have lagenostomean affinities (see above). Other types of calamopityalean have been shown to have fronds with rounded, non-digitate pinnules (Sebby and Matten, 1969; Skog and Gensel, 1980). In the Scottish Cementstone Group, foliage with similar pinnules belong to *Aneimites acadica* Dawson and it is thus more likely that this is the adpression form of the foliage in the *Lyrasperma scotica*-bearing plant.

Retallack and Dilcher state that ovules of this plant have been found with pre-pollen of the *Colatisporites*-type in the pollen chamber. However, there is no evidence of the pre-pollen-bearing organs themselves. The *Lyrasperma scotica* ovules are platyspermic and slightly curved, with prominent apical horns on either side of the exposed salpinx (Calder, 1938; Long, 1960b). The integument is fused to most of the nucellus, being free only above the plinth. They probably correspond to the ovules known as *Samaropsis bicaudata* Kidston when preserved as adpressions (Kidston, 1901a,

1902a, 1902b), in which the megaspore has been found to show a prominent trilete mark, a feature generally regarded as primitive.

Although direct evidence is not available, Long (1969) argued that the *Lyrasperma* ovules were probably borne in multiovular cupules, of the type known as *Alcicornopteris*. Such cupules contain a group of ovules surrounded by a sheaf of terete telomes, which in turn is enclosed by a second sheaf, made up of more laminar elements. These are quite different from the single-layered lagenostomean cupules, such as bore *Stamnostoma* (see above). This lends support to the view of Smith (1964a) that cupules evolved independently in more than one group of gymnosperms. It remains uncertain as to where the cupules were borne on the plant. However, if the outer sheaf of the cupule is the laminate part of a fertile frond (i.e. the structure is a megacupule *sensu* Long, 1977a), then it would probably have been attached directly to the main stem, perhaps near the top of the plant. There is no direct evidence that they were attached to the fronds near the dichotomy of the main rachis, as suggested by Retallack and Dilcher (1988).

A distinctive aspect of *Lyrasperma* ovules is the squat, barrel-shaped lagenostome, with a thin, biconcave central plug at the base, quite different from the more elongate lagenostome, and thicker central plug of the lagenostomean ovules. Almost identical lagenostomes have also been described in *Eurystoma angulare*, *E. burnense* (syn. *Anasperma burnense* Long), *Dolichosperma pentagonum* and *D. sexangulatum* (Long, 1960b, 1961b, 1965, 1966, 1969, 1975) (Figure 5.14). These are also presumably calamo-pityalean ovules, although there is no evidence of their attachment to identifiable stems/petioles. They are of particular interest in the great variation that they show in symmetry, varying from bilateral (in *Lyrasperma*) to six-fold (in *D. sexangulatum*). Ovule symmetry, which is controlled largely by the number of vascular bundles entering the integument at the chalaza, has been given considerable weight in certain phylogenetic analyses (e.g. Meyen, 1984; Crane, 1985). The results from the Whiteadder calamopityalean ovules, however, clearly indicate that the feature has to be used in this context with caution (Rothwell, 1986).

In addition to *S. tuedianum*, two other types of calamopityalean stem have been described from the Whiteadder by Long (1964a): *Stenomyelon beterangioides* and *S. primaevum*.

They are distinguished mainly by the distribution of parenchyma in the stele, although it is possible that it merely represents variation in structure at different positions in the plant. A fourth type of stem reported from here, *Stenomyelon tripartum*, Kidston is now regarded simply as a form of *S. tuedianum* (Calder, 1938).

Problematic gymnosperms

Triradioxylon prlmaevum has a progymnosperm-like, trilobed protostele and secondary wood; but the sclerotic nests and sparganum structure in the cortex, and the dorsiventral symmetry of the 'fronds', suggest possible affinities with the early pteridosperms. Barnard and Long (1975) placed this and the stem *Buteoxylon* in the *incertae sedis* family Buteoxylonaceae, and Taylor (1981) suggested that it might be intermediate between the progymnosperms and pteridosperms. Recent research (e.g. Rothwell and Erwin, 1987), however, suggests that the Buteoxylonaceae may not be a 'natural' group, and *Triradioxylon* may have affinities with the lagenostomeans.

An ovule from here which stands out from the rest was described by Long (1977c) as *Mitrospermum bulbosum* (Figure 5.15). Like *Lyrasperma* it is platyspermic with prominent apical horns, but it is not curved, has no basal plug in the lagenostome, and has a free nucellus. Long (1977c) argued that it has many features normally associated with the Cordaitales. Other evidence of cordaites in the Lower Carboniferous is equivocal. Crookall (1970, pl. 155 figs 6–7) figures some possible leaves from the Lower Carboniferous of Scotland, but their identity is far from certain. Lacey (1953) and Barnard (1962) have described some petrified stems and roots from elsewhere in Scotland (Oxroad Bay, Glenarbuch, Loch Humphrey Burn — see p. 135) as having possible cordaite affinities, but they have since been interpreted as probably pteridospermous (Long, 1987; Bateman and Rothwell, 1990). The Whiteadder ovules appear to be the best available evidence of Early Carboniferous cordaites, but on their own cannot be used to dismiss Rothwell's (1986) argument that the group probably did not appear before the Westphalian.

Angiosperm origins

Long (1966, 1975, 1977b, 1985) has used the evidence from the Whiteadder to argue that angiosperms may have evolved from Carboniferous pteridosperms, particularly by the development of carpels from cupules (see also Delevoryas, 1962; Andrews, 1963). This view has not met with widespread acceptance (e.g. Stewart, 1983; Crane, 1985), although one of the often mentioned objections to it (the long stratigraphical gap between the Lower Carboniferous and where angiosperms appear in the fossil record) may have to be re-assessed in the light of recent work on DNA sequencing in extant angiosperms (Martin *et al.*, 1989; Cleal, 1989).

General remarks

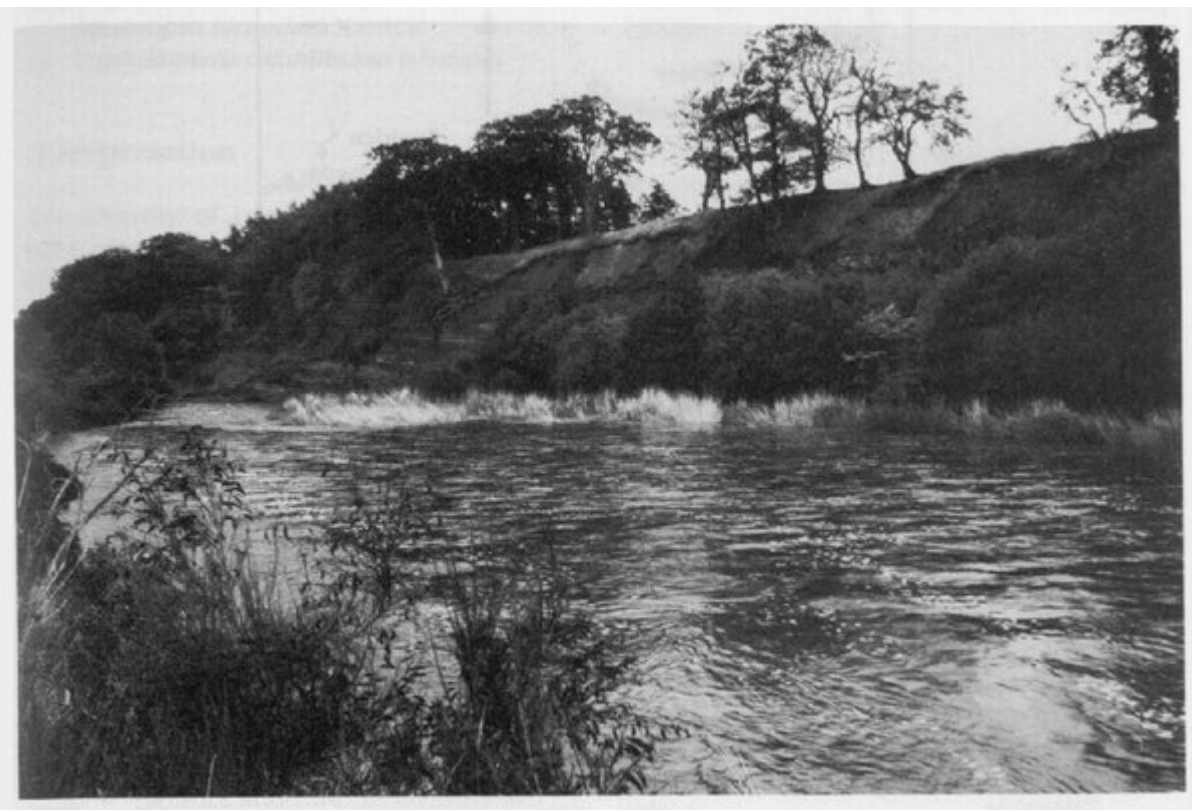
This is by far the best locality for plant fossils in the Lower Carboniferous Cementstone Group. It has yielded 44 petrification form-species, including lycopsids, ferns, progymnosperms and pteridosperms, which is far more than any other site. Of the other Cementstone Group localities, the most comparable are Langton Burn and Cove, which have yielded 20 and 11 form-species respectively (Scott *et al.*, 1984), but neither has yielded taxa not found in the Whiteadder. The Oxroad Bay (see below) assemblage has some taxa in common with the Whiteadder, but there are also significant differences. The other major Lower Carboniferous petrification sites in Britain, such as Pettycur (p. 144), Loch Humphrey Burn (p. 155) and Glenarbuck (p. 164), yield quite distinct assemblages from Whiteadder, a function of differences of both environment and age.

From outside Britain, the best known Tournaisian petrification assemblages are from the New Albany Shales of the USA (Cross and Hoskins, 1951) and the Lydienne Formation in the Montagne Noire, France (Galtier, 1970). Both have yielded a wide variety of taxa, but mainly of stems and rachides; neither has such a variety of pteridosperm ovules as the Whiteadder. Also similar to the Montagne Noire assemblage is that from Saalfeld (Bertrand, 1935), but as no modern study has been undertaken its flora is relatively poorly understood and a full comparison with the Whiteadder is difficult. The basal Tournaisian (topmost Devonian) assemblage from Kerry Head, Irish Republic (Matten *et al.*, 1975, 1980; Bridge *et al.*, 1980) has some taxa in common with the Whiteadder, but is of far more restricted composition. The Whiteadder assemblage clearly stands out as the most significant Tournaisian plant petrification site in the world.

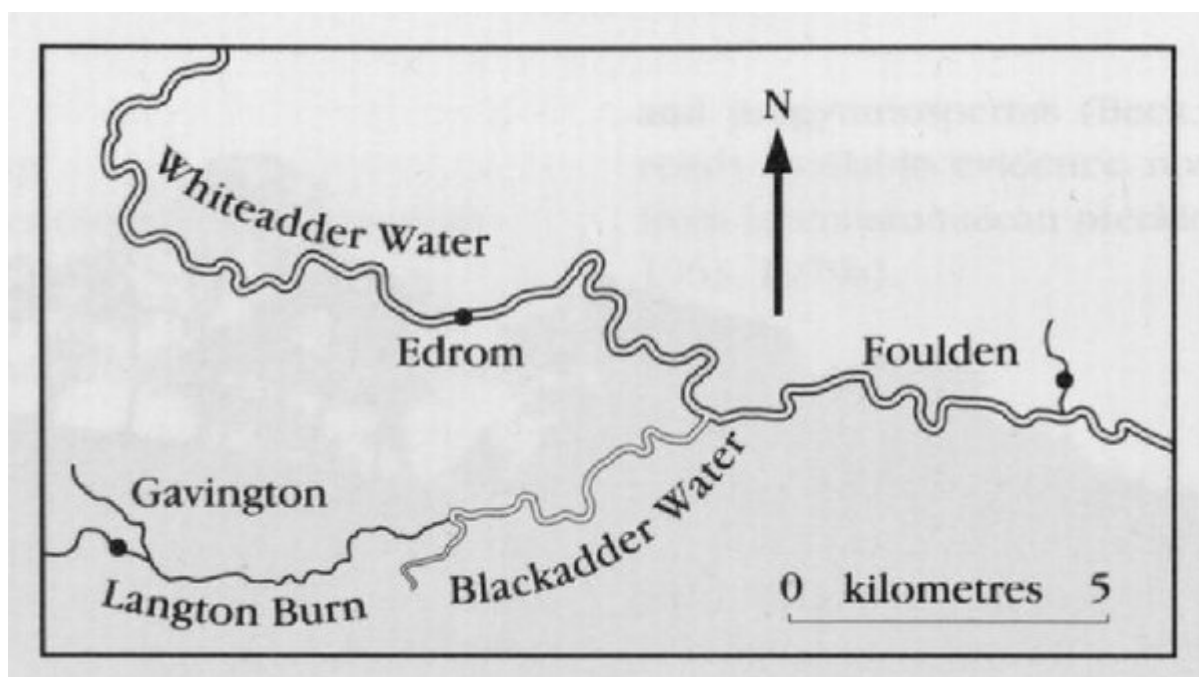
Conclusion

The Whiteadder section is one of a series of sites in basal Carboniferous rocks in southern Scotland yielding anatomically-preserved plant fossils, about 350 million years old. Nowhere else in the world has so many sites of this age yielding such well preserved fossils. Of the Scottish sites, the Whiteadder has yielded the most diverse assemblage, with 44 species having been described in the literature. Particularly important is the wide range of 'seeds' of early higher (seed-bearing) plants, whose anatomy has been studied in great detail, revealing features such as their unusual and distinctive pollination structures (later replaced by the micropyle in modern 'seeds'). They include the most morphologically primitive 'seed' so far found in the fossil record (*Genomosperma*). They are marginally pre-dated by the earliest known 'seeds' from West Virginia, USA, but the latter are not preserved in such fine detail. Also, the American site yields just one type of 'seed', whereas the Whiteadder contains 16 distinct types belonging to at least two major plant groups (lagenostomaleans and calamopityaleans). This site is thus of outstanding significance for understanding the early evolution of the seed plants, and thus the origin of most modern groups of plants (including flowering plants).

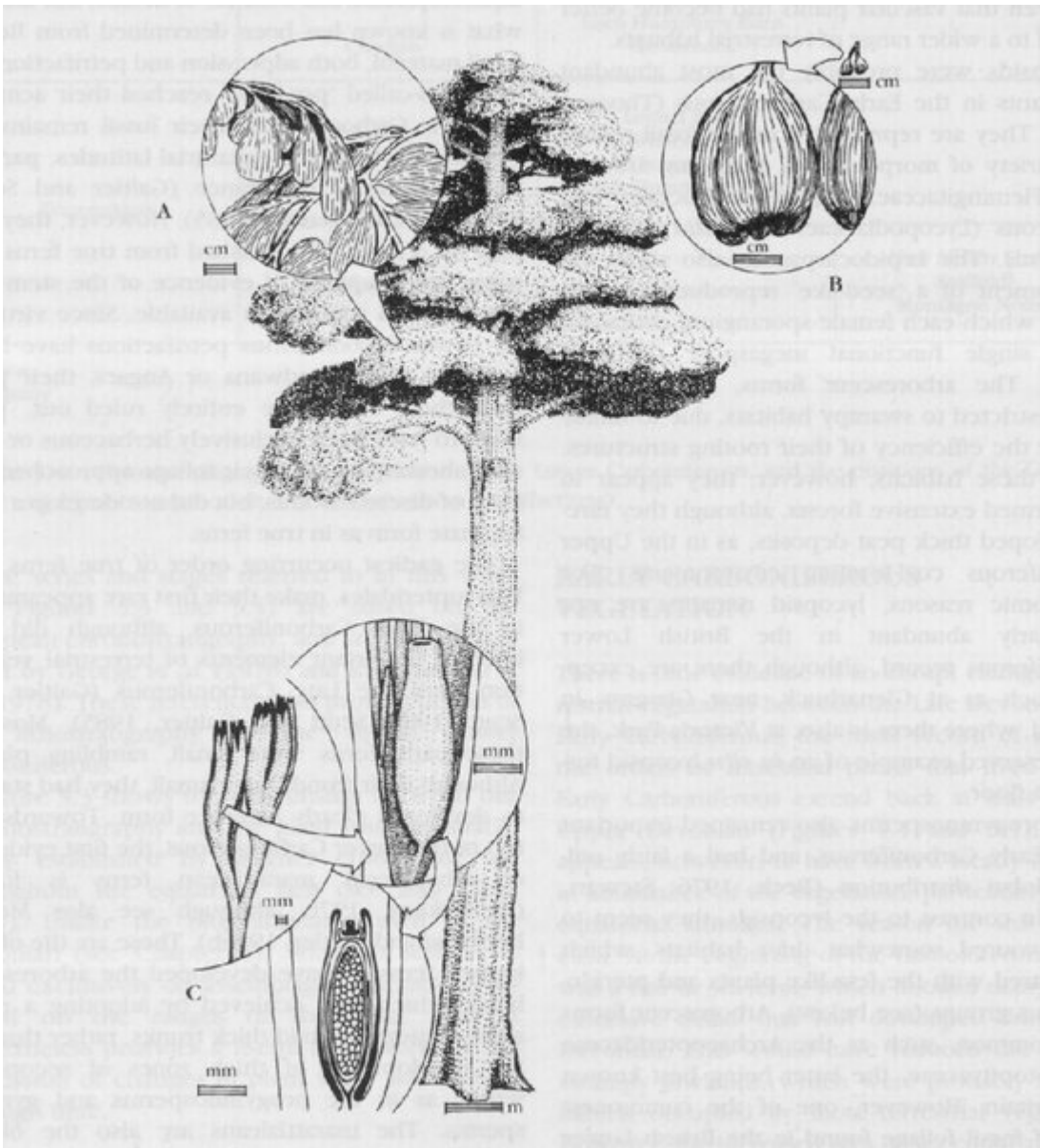
[References](#)



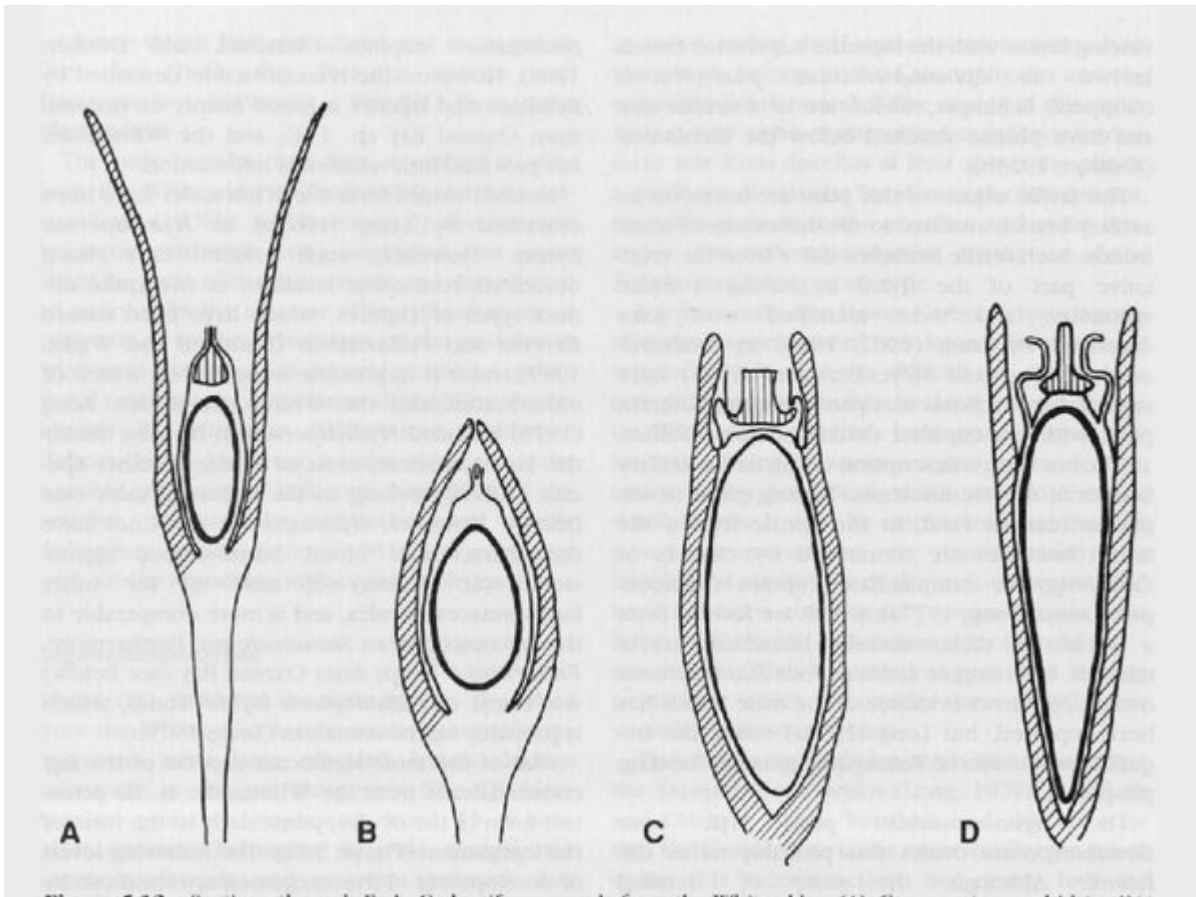
(Figure 5.10) Edrom, Whiteadder River. Shales and cemented mudstones of the upper Tournaisian Cementstone Group. The main plant bed is in the bed of the river. (Photo: C.J. Cleal.)



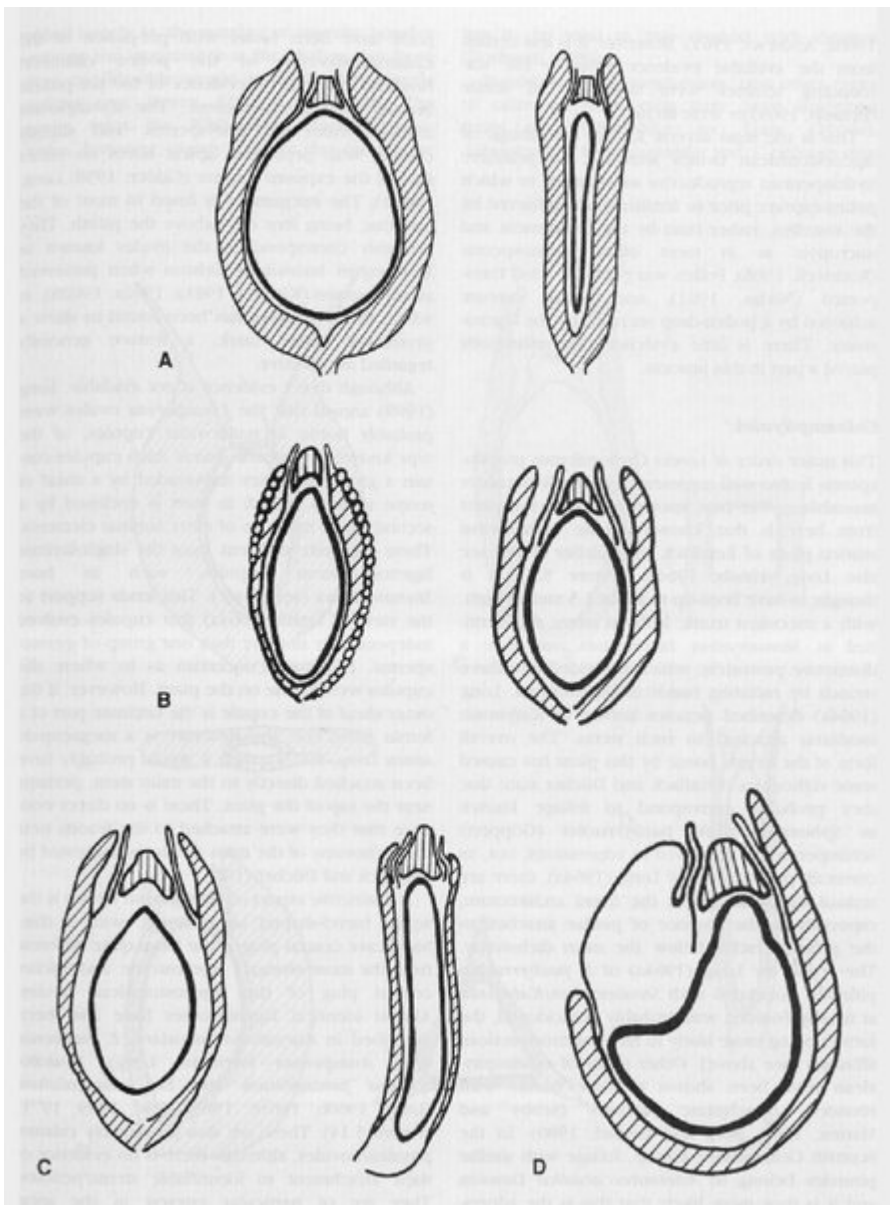
(Figure 5.11) Location map for the Whiteadder GCR palaeobotany site. Based on Scott et al. (1984, figure 14).



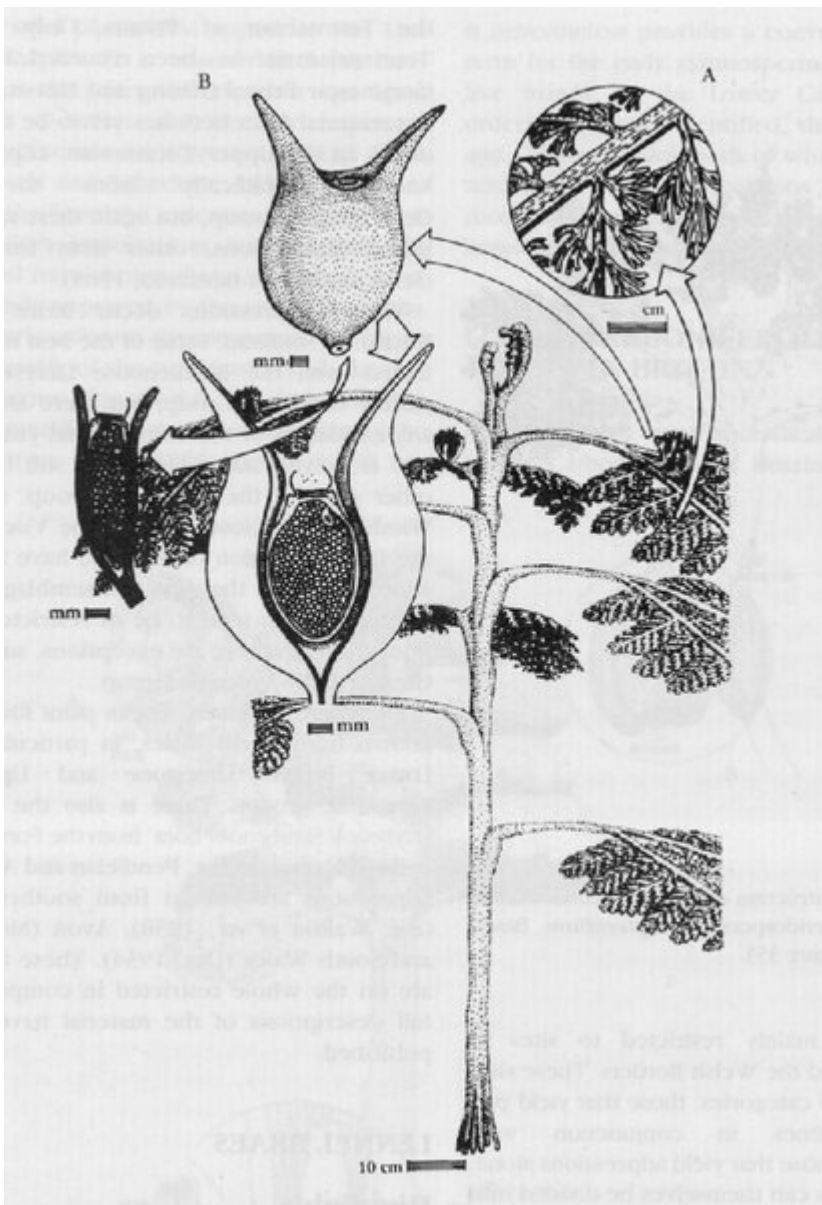
(Figure 5.6) Reconstruction of the Early Carboniferous lagenostomalean pteridosperm tree *Stamnostoma*, with insets showing details of foliage (A), pollen organs (B) and seeds (C). Based on Retallack and Dilcher (1988).



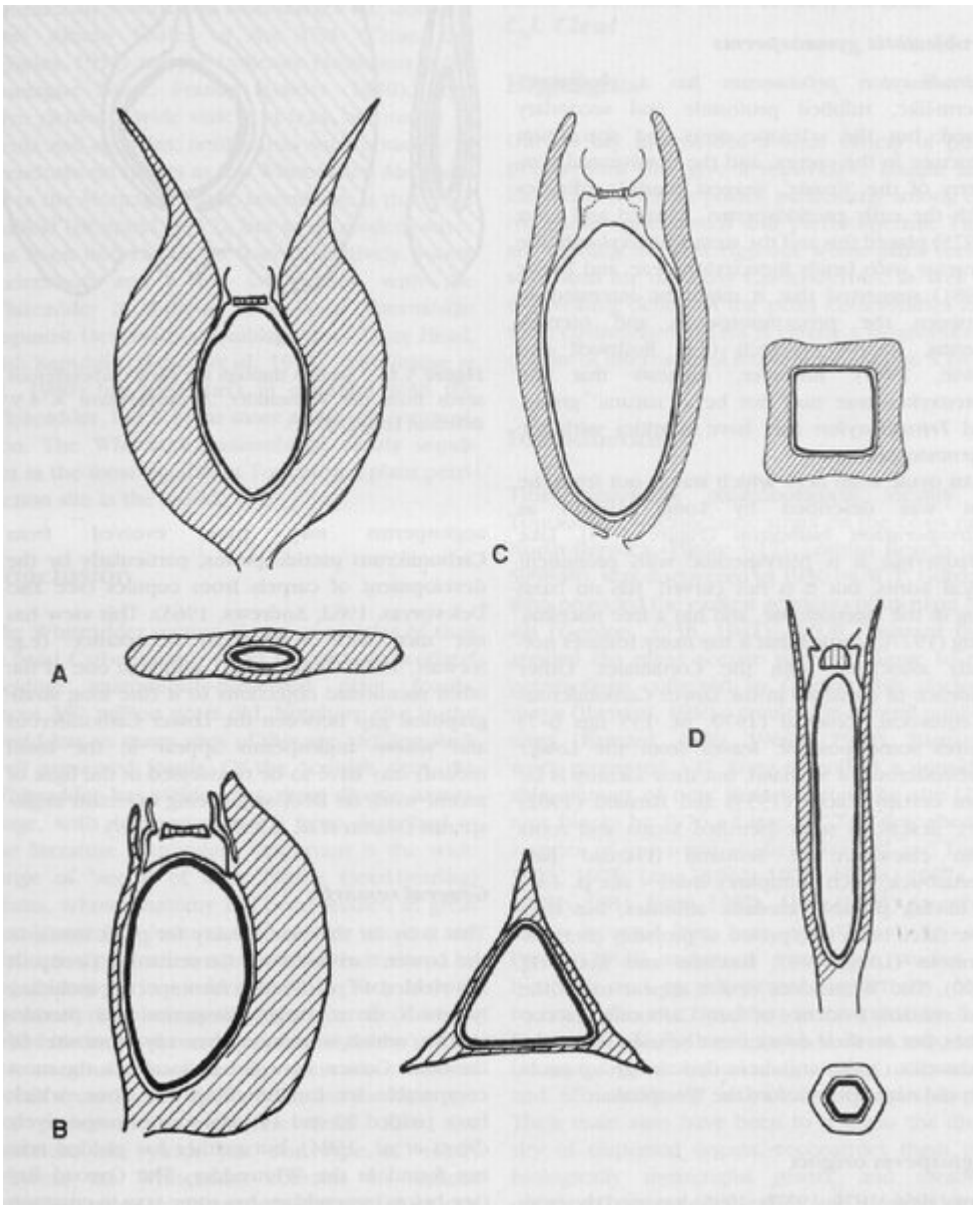
(Figure 5.12) Sections through Early Carboniferous seeds from the Whiteadder. (A) *Genomosperma kidstonti* x 5. (B) *G. latens* x 5. (C) *Stamnostoma buttonense* x 20. (D) *Hydrasperma tenuis* x 20. Based on Long (1959b, 1960a, 1961b).



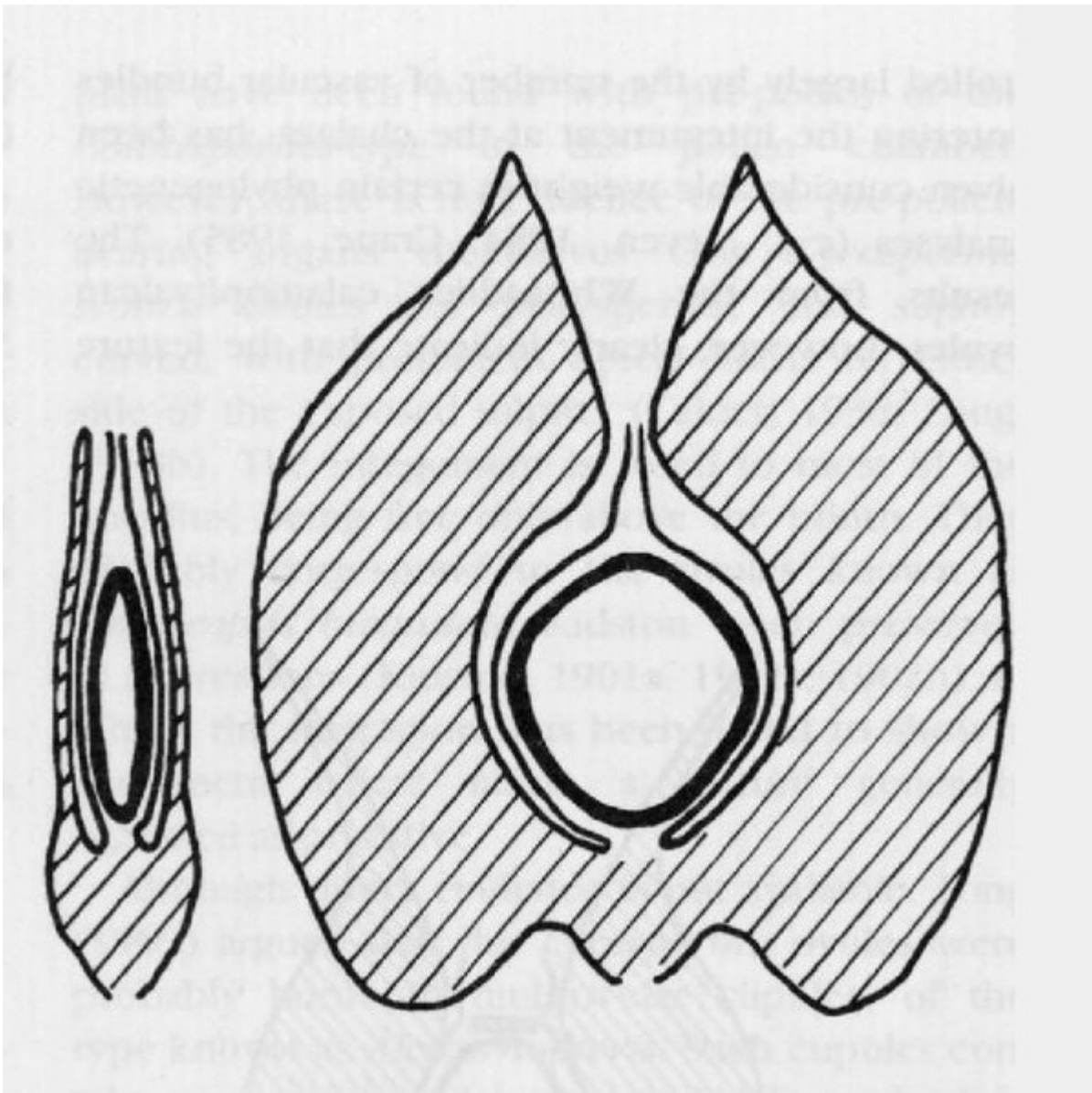
(Figure 5.13) Sections through Early Carboniferous seeds from the Whiteadder (*Eospermaceae*). (A) *Eosperma edromense*. (B) *Deltasperma fouldenense*. (C) *Eccroustosperma langtonense*. (D) *Camptosperma berniciense*. All x 18. Based on Long (1961a, b, 1966).



(Figure 5.8) Reconstruction of the Early Carboniferous calamopityalean pteridosperm *Lyrasperma*, with insets showing details of foliage (A) and seeds (B). Based on Retallack and Dilcher (1988).



(Figure 5.14) Sections through Early Carboniferous seeds from the Whiteadder (Calamopityales). (A) *Lyrasperma scotica* x 4.5. (B) *Eurystoma trigona* x 13.5. (C) *E. angulare* x 9. (D) *Dolichosperma sexangualtum* x 4.5. Based on Long (1960b, 1961b, 1969).



(Figure 5.15) Section through the Early Carboniferous seeds from the Whiteadder, *Mitrospermum* x 4.5. Based on Long (1977c).