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# Rhynie

## Highlights

Rhynie is probably the most important palaeobotanical site in Britain, yielding the oldest known vascular plant fossils with well-preserved anatomical details (Figure 4.22). The 22 species of plant fossil (including fungi) are unique to this locality, and include the 'type-genus' of the Rhyniophytina (*Rhynia* — the best-known early land plant), the earliest well-documented lycopsid (*Asteroxylon*), and a variety of enigmatic species evidently representing early experiments in adaptation to a terrestrial environment. It is also the oldest known example of an *in situ* fossilized terrestrial ecosystem.

## Introduction

This famous locality lies beneath a field near the village of Rhynie, 14 km south of Huntly, in the Grampian Region of Scotland [NJ 495 264]. Probably no other single site has had such an impact on the development of palaeobotany. Walton (1959) described it as 'the most dramatic and important palaeobotanical discovery of the century'. Prior to its discovery, the structure and taxonomic affinities of Lower Devonian plant fossils (until then almost exclusively known as adpressions) were still a matter of debate, and many scientists argued that they were either algal or indeterminate fragments of 'advanced' vascular plants. The petrifications discovered at Rhynie confirmed that vascular plants did exist during the Early Devonian and that they were truly 'primitive'. This has had a major impact on evolutionary ideas and the classification of the Plant Kingdom.

The general background to the Rhynie Chert locality and its fossilized biota is summarized by Chaloner and Macdonald (1980). There is no natural outcrop of the chert, and it was first found as loose blocks in a field and in a drystone wall (Mackie, 1913) (Figure 4.23). Subsequently, however, the Geological Survey excavated a series of trenches through the field, revealing the rock *in situ* and allowing a large quantity of the material to be collected (Horne, 1917; Horne and Mackie, 1917, 1920a, b; Kidston, 1922, 1923e). The specimens were the subject of a series of now classic monographs by Kidston and Lang (1917b, 1920a, b, 1921a, b), in which anatomical details of the plants were described from thin sections of the chert. Pant (1962) argued that Kidston and Lang had been able to determine such fine cellular structure that details of the Rhynie plants were 'nearly as complete as they could be even if the plants were living today'. The method used by Kidston and Lang was, however, not so good at revealing the gross morphology of the plants; their reconstructions (Kidston and Lang, 1921a, pls 1–2) were rather oversimplified. More refined results were only possible when the peel method (Joy *et al.*, 1956) was used, allowing more closely-spaced serial sections to be made. Examples of the use of such techniques are given by Bhutta (1972), Eggert (1974), El-Saadawy and Lacey (1979a, b), Edwards (1980, 1986), Edwards and Lyon (1983), and Lyon and Edwards (1991). Despite being known for over 70 years, new discoveries are still being made at Rhynie (e.g. the vascularized gametophyte by Remy and Remy 1980a, Remy and Hass, 1991a, b, c and Remy, 1991) and there remains considerable potential for further work here.

## Description

### Stratigraphy

The Rhynie Chert is usually included in the Dryden Shale Formation, the highest part of the Rhynie Old Red Sandstone outlier (Trewin and Rice, 1992). Kidston and Lang (1917b, 1921a) regarded the chert as 'not younger than the Middle Division of the Old Red Sandstone'. More recent palynological evidence has, however, suggested an Early Devonian, possibly Siegenian, age (Richardson, 1967; Richardson *in House et al.*, 1977). Banks (1980) included the plant fossils in his *Psilophyton* Zone, indicating a late Siegenian or Emsian age.

The most complete account of the stratigraphy of the Rhynie Chert is by Trewin and Rice (1992). They report it to consist of c. 3.2 metres of alternating chert, mudstone and sandstone (Figure 4.24). It is generally regarded as having been formed by hot siliceous solutions, probably from a volcanic fumerole, impregnating a peat that developed on an alluvial

plain (Kidston and Lang, 1917b, 1921b; Tasch, 1957; Edwards and Lyon, 1983; Edwards, 1986; Trewin and Rice, 1992):

## Palaeobotany

The plant fossils at Rhynie are silica petrifications, preserving very fine anatomical detail (Edwards, 1986). The following taxa have been described to date (see also (Figure 4.25), (Figure 4.28) and (Figure 4.29):

Cyanochloronta:

*Langiella scourfieldii* Croft and George

*Kidstoniella fritschii* Croft and George

*Rhyniella vermiformis* Croft and George

*Rhyniococcus uniformis* Edwards and Lyon

Phaeophycophyta(?):

*Prototaxites taitii* (Kidston and Lang) Pia

*Nematoplexus rhyniense* Lyon

Chlorophycophyta(?):

?*Pachythea* sp.

*Palaeonitella cranii* (Kidston and Lang) Pia

*Archaeothrix oscillatonformis* Kidston and Lang

*A. contexta* Kidston and Lang

*Mackiella rotundata* Edwards and Lyon

*Rhynchertia punctata* Edwards and Lyon

Rhyniopsida:

*Rhynia gwynnevaughanii* Kidston and Lang

*Lyonophyton rhyniensis* Remy and Remy

*Langiophyton mackei* Remy and Hess

Horneophytosida:

*Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah

Zosterophyllopsida:

*Trichopherophyton teuchansii* Lyon and Edwards

Lycopsida:

*Asteroxylon mackei* Kidston and Lang

Fungi:

*Palaeomyces gordonii* Kidston and Lang

*P. agglomerata* Kidston and Lang

*P. asteroxylii* Kidston and Lang

*P. horneae* Kidston and Lang

Affinities uncertain:

*Nothia aphylla* Hoeg

*Aglaophyton major* (Kidston and Lang) Edwards

*Kidstonophyton discoides* Remy and Hess

## Interpretation

*Rhynia gwynnevaughanii* has been widely regarded as the archetypal primitive vascular plant, following the reconstruction given by Kidston and Lang (1921a, pl. 1 fig. 1). They interpreted it as having thin, naked aerial shoots, arising from a prostrate rhizome, and terminated by single sporangia. Branching of the aerial shoots was shown as predominantly dichotomous, but with some subsidiary adventitious branching. Small hemispherical bulges were distributed along the shoots.

Using the peel method, however, Edwards (1980, 1986) has shown that it was a far more complex plant (see (Figure 4.27)a). For instance, the aerial shoots had a much higher proportion of adventitious branching, dichotomies being relatively rare. He also found evidence of an abscission layer at the base of the sporangia, the latter being shed after the release of their spores. An adventitious branch occurs immediately below the site of many of the sporangia.

Although perceptions about the *R. gwynne-vaughanii* gross morphology have changed over the years, Kidston and Lang's (1917a, b) interpretation of the anatomy of the aerial shoots is still generally accepted. The aerial shoots consist of a very slender, terete, centrarch stele, surrounded by a cylinder of phloem, a two-layered cortex and an epidermis (Figure 4.25) and (Figure 4.26). The relative slenderness of the stele has attracted some comment, Filzer (1948) suggesting that it reflects a primitive and inefficient water metabolism control system. Looking at it from another point of view, however, Kevan *et al.* (1975) argued that the relative thickness of the cortex was a strategy to protect the stele from arthropod predation. Speck and Vogellehner (1988a, b) have shown that the stele contributed little to supporting the axes in such early land plants, which was mainly controlled by turgor in the cortex.

Satterthwaite and Schopf (1972) described what they regarded as sieve-like structures in the cylinder of phloem (Satterthwaite and Schopf identified their specimens as '*Rhynia*' *major* Kidston and Lang, but Lemoigne and Zdebska (1980) have argued that they almost certainly belong to *R. gwynnevaughanii*). If correctly interpreted, this remains the oldest unequivocal evidence of phloem tissue in the fossil record.

*R. gwynnevaughanii* sporangia have traditionally been interpreted as lacking a dehiscence structure, a view which was supported by Edwards (1980). However, Remy (1978) has described a band of thin-walled cells, probably lying longitudinally along the sporangium, which may have functioned as a line of weakness to facilitate rupturing (a stomium). No evidence of an annulus was reported, but opposite the stomium was a flexible, so-called joint region, which again may have helped in the dehiscence process. Remy's interpretation has not received universal acceptance (Edwards and Edwards, 1986) but, if proved correct, it will require a significant modification to our view of *Rhynia* as a simple land plant.

Another contentious issue surrounding *R. gwynnevaughanii* is its possible status as a vascularized gametophyte. Considering the fine preservation in the chert, the apparent absence of readily identifiable gametophytes of the Rhynie

plants had puzzled palaeobotanists (e.g. Chaloner, 1960; Pant, 1962). Merker (1958, 1959, 1961) argued that perhaps some of the prostrate axes of *R. gwynnevaughanii* were gametophytes, from which the sporophytic aerial shoots arose. Pant (1962) went further, suggesting that the *R. gwynnevaughanii* plant as a whole was a vascularized gametophyte, and Lemoigne (1968a) has argued that it was the gametophyte of the plant then known as *Rhynia major* Kidston and Lang (now included in the form-genus *Aglaophyton* — see p. 89). The argument was based largely on structures on *R. gwynnevaughanii* axes, which were interpreted by Pant and Lemoigne as archegonia and antheridia (see also Lemoigne, 1968b, c, 1969a, b, 1970, 1975, 1981). However, the photographic record of these structures is not entirely convincing, and Bhutta (1969) has argued that the 'archegonia' are merely stomata damaged by fungal attack. Edwards (1980) made an extensive search for similar structures in his specimens of *R. gwynnevaughanii*, without success, and further more found unequivocal evidence that at least the aerial shoots of the plant were sporophytic. Edwards (1979b) argued that the gametophytes of the primitive vascular plants were fast growing and quick to mature, and thus had a very low preservational potential. Alternatively, Edwards (1986) suggested that gametophytes of these plants only developed under relatively rare and favourable conditions, and that they normally spread by the development of extensive growth of the sporophytic generation. Whatever the true explanation, the nature of the *R. gwynnevaughanii* gametophytes is unknown.

Based mainly on Kidston and Lang's observations, *Rhynia* has been used as the effective type of the most primitive class of vascular plants — the Rhyniopsida (Banks, 1975b). In this role, it has tended to be central to any discussion on the early evolution of vascular plants. However, the new evidence provided by Edwards (1980) has required the concept of the Rhyniopsida to be modified and enlarged (Edwards and Edwards, 1986). It still probably represents the most primitive class of vascular plants, but now includes forms such as *Renalia* showing a wider diversity of morphologies, particularly in the branching of the axes.

*R. gwynnevaughanii* has also played a key role in understanding the early evolution of the stele and leaves. It had been argued that the stele first evolved in leaves, and only later developed in stems by the coalescence of the leaf traces (for example see comments by Arber, 1921). The evidence from *Rhynia* clearly indicates that the primitive condition is a simple protostele in the stem (Scott, 1924a). Zimmermann's (1926) discovery that the stomata are associated mainly with the hemispherical bulges on the aerial shoots suggests that these bulges may represent the early phases in the development of non-vascularized, leaf-like emergences, similar to those of *Asteroxylon* (see below). Further aspects of the epidermal structure of *Rhynia* are discussed by Edwards *et al.* (1982).

Another primitive vascular plant found at Rhynie was described as *Hornea lignieri* Kidston and Lang (later re-named *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah, 1938). It has been reconstructed, with thin, dichotomous axes arising from a corm-like rhizome (Kidston and Lang, 1921a; Eggert, 1974) (Figure 4.27)B, C and (Figure 4.28). The axes have a very irregular surface, which Eggert (1974) argued to be a taphonomic effect, but which El-Saadawy and Lacey (1979b) interpreted as being due to small emergences, as in *Nothia* (p. 89). The anatomy of the aerial shoots is essentially similar to that of *Rhynia*, except that the terete, centrarch stele is rather thicker. The nature of the transverse breaks in the protostele observed by Kidston and Lang (1920a) has never been properly established, but might be a preservational feature. The limited available evidence of the cuticles of *Horneophyton* is discussed by Edwards *et al.* (1982).

In addition to its corm-like rhizome, *Horneophyton* is distinctive because of the structure of its apical sporangia. These are little more than cavities in the apical parts of the aerial shoots, into which extends the vascular tissue, forming a columella-like structure (Eggert, 1974, fig. 28). These fertile shoot-terminations are often branched, resulting in lobed sporangia. Kidston and Lang (1920a) failed to recognize any dehiscence structures, but an apical slit has since been reported in the apex of each sporangial lobe (Bhutta, 1972; Eggert, 1974; El-Saadawy and Lacey, 1979b). Considerable variation in the size and ornamentation of the spores was found by Bhutta (1973a), which he suggested might represent incipient heterospory. Alternatively, however, the smaller spores may merely be immature.

The taxonomic position of *Horneophyton* has never been firmly established. Similarities with the bryophytes have been noted (Bower, 1920; Scott, 1924a, 1928; Church, 1926), and Smith (1955) has argued that it provides an evolutionary link between the bryophytes and the more 'advanced' vascular plants. However, it is normally regarded as a true vascular plant and is often included in the Rhyniaceae, because of its elongate sporangia and centrarch stele (Banks, 1968). As

pointed out by Edwards and Edwards (1986), however, its lobed sporangia with apical dehiscence structures are not really compatible with it belonging to the Rhyniopsida. Eames (1936) placed it in its own family, the Horneaceae, whereas Meyen (1978, 1987) included it in a monotypic class, the Horneophytopsida. The latter view has been followed here.

Lemoigne (1966) has described a possible spore-producing capsule of a bryophyte from Rhynie. It contains spores of only about half the size, but is otherwise indistinguishable from a *Horneophyton* sporangium. Its bryophytic affinities must remain in doubt until more complete specimens are found.

For many years, the zosterophylloids appeared to be notable by their absence from Rhynie. Recently, however, some fragments described by Lyon and Edwards (1991) as *Trichopherophyton teuchansii*, clearly belong to that class (they had earlier been mentioned by Lyon in Lindley (1968) and Gensel *et al.* (1975)). Particularly distinctive features are their spiny axes with a terete, exarch stele, circinately-tipped shoots, and marginally dehiscent sporangia. The main difficulty with interpreting the fossils was that many features of the gross-morphology could not be determined, in particular the configuration of the sporangia on the axes; most other zosterophylloids are identified on such features of gross morphology. However, that the spines on the axes are unicellular structures seems to be unique in the class; the emergences found in the other genera such as *Sawdonia* and *Crenaticaulis* are multicellular. The more or less terete stele also contrasts with that present in most other members of the class, in which it tends to be oval in cross-section. These factors alone are enough to justify placing this Rhynie species in a separate form-genus. However, much more information on its gross morphology will be needed before its detailed taxonomic position within the Zosterophylloids can be established.

The most 'advanced'-looking of the Rhynie plants is *Asteroxylon mackei*, which in many ways resembles a lycopsid ((Figure 4.4)a). Like *Rhynia*, it has a prostrate, creeping rhizome, but the aerial shoots are clothed in microphyll-like leaves. The xylem in the aerial shoots is fluted, giving a stellate cross-section, and is mesarch with annular tracheids (Kidston and Lang, 1920b; Lang, 1952; (Figure 4.29)). Such an actinostele was probably a more efficient water-conducting structure than the simple protostele of the rhyniopsids, but apparently gave little extra support to the plant (Speck and Vogellehner, 1988a, b). The actinostele has spirally arranged leaf traces, but they only enter the very base of the leaves, which are thus not the same as true lycopsid microphylls. Two types of leaves were recognized by Edwards *et al.* (1982), those with a smooth surface, and those with an undulate surface caused by epidermal cells with a strongly convex outer wall.

Kidston and Lang (1921a) reconstructed *Asteroxylon* with naked, dichotomous axes attached to the 'leafy' aerial shoots, on which were borne terminal sporangia. This was based on the frequent association of such naked shoots with the more typical *Asteroxylon* axes. Subsequently, however, Lyon (1964) and Bhutta (1969) found examples of *Asteroxylon* with zosterophyll-like reniform sporangia attached laterally to the leafy shoots (the naked axes with sporangia have since been assigned to a separate species *Nothia aphylla* Hoeg — see below).

Kidston and Lang (1920b) regarded *Asteroxylon* as being a possible link between the simple rhyniopsids and the lycopsids, a view which is still broadly held today (Hueber, 1992; Gensel, 1992). The discoveries by Lyon and Bhutta of attached sporangia have further refined this view. Kidston and Lang argued that it should be regarded as an advanced member of what they called the psilophytes (essentially equivalent to the class Rhyniopsida of Banks, 1968, 1975b), placing it in a family Asteroxylaceae. Other authors have, however, regarded it as a primitive lycopsid, including it in the Protolpidodendrales (e.g. Taylor, 1981). A third solution has been to assign it to a separate taxon, intermediate between the zosterophylls and lycopsids, such as the class Drepanophycopsida of Rayner (1984). Whatever solution is found to the problem of classifying this plant, it holds a key position in helping us to understand the origins and early evolution of the lycopsids.

As stated above, the fertile axes originally assigned to *Asteroxylon* by Kidston and Lang, are now recognized to belong to a quite separate plant. Lyon (1964) introduced the name *Nothia aphylla* for it, but this remained a *nomen nudum* until Hoeg (in Boureau *et al.*, 1967) provided the first validly published diagnosis. Only the terminal parts of the plant are known; these consist of slender, dichotomous axes, covered with small, tuberous emergences. Stomata are usually situated on these emergences but, unlike those of *Rhynia* and *Horneophyton*, have distinctive broad guard cells

(Edwards *et al.*, 1982). Lyon (1964) originally regarded it as rhyniophytoid. Subsequent work by El-Saadawy and Lacey (1979a) has shown, however, that it has what appear to be a combination of rhyniopsid characters (thin dichotomous axes and a centrarch 'stele') and zosterophyll characters (rhizomes with 'H'-type branching, aerial shoots with circinate curved tips, oval cross-section to the 'stele', and reniform sporangia with a dehiscence slit). There are also certain characters which place it outside either of these taxa, such as the mixture of both terminally and laterally borne sporangia, and the absence of thickening of the sporangial wall near the dehiscence slit. Perhaps most significantly, however, El-Saadawy and Lacey failed to find any evidence of thickenings or pitting on the cells in the so-called xylem, calling into question the status of *Nothia* as a true vascular plant (Edwards and Edwards, 1986). The taxonomic position of this curious plant must thus remain in doubt.

Some similarity has been noted between *Nothia* and the adpression species *Sartilmania jabachensis* (Kräusel and Weyland), both in the structure and the position of attachment of the sporangia (Fairon-Demaret, 1986b). The *Sartilmania* sporangia are more elongate and attached to longer lateral branches, and have never been found terminally attached, as sometimes occurs in *Nothia*. These differences, as well as those of the preservation, make it unwise to assign them to the same form-genus. As pointed out by Fairon-Demaret, however, they may both represent a group of Early Devonian plants in the process of diversifying to form the major taxonomic groups more clearly recognizable in later floras.

Another Rhynie species whose status as a vascular plant has recently been questioned is *Aglaophyton major*. Kidston and Lang (1920a) regarded it as a second species of *Rhynia*, and they reconstructed it as looking similar to *R. gwynnevaughanii* except that it was larger (more than half a metre high), and had aerial shoots with no adventitious branching or hemispherical bulges. They noted the absence of any clear thickenings on the cells in the central conducting tissue of the aerial shoots, but put this down largely to taphonomy. However, Edwards (1986) regarded this as unlikely, considering the fine preservation of other tissues in this plant, and concluded that the central conducting tissue was not composed of tracheids, but of tissue similar to the hydroids of certain bryophytes. As pointed out by Speck and Vogellehner (1988a, b), the central conducting strand in the early land plants provided little strength to the axes, and so the development of thickenings on the tracheids' would give them little immediate advantage. Edwards also reconstructed the plant rather differently, giving it an essentially decumbent habit, with vertical shoots attaining a height of no more than 0.18 metres (less than one third of the height suggested by Kidston and Lang) and with a much wider angle of branching (Figure 4.30). Germinating spores of *Aglaophyton* showing immature gametophytes have been described by Lyon (1957) and Bhutta (1973b).

It is difficult at present to classify non-vascular rhyniophytoids such as *Aglaophyton* and *Nothia*, there being no established high-ranked taxa to receive them. Edwards suggested that shoots (similar to *Horneophyton*) but with a non-vascular conducting strand (similar to *Aglaophyton*), and terminated by discoidal gametangia with archegonia and antheridia. The fact that in its vegetative form it is probably isomorphous with the sporophytic generation gives this oldest unequivocal gametophyte particular significance. It provides a possible stem-condition from which both the bryophytic and more typical pteridophytic heteromorphic generations could be derived (Remy, 1980a). It has also given added impetus to the search for the missing *Rhynia* gametophyte, discussed above.

Other non-vascular plants represented at Rhynie include the so-called nematophytes. The best documented to date is *Prototaxites taitii* (Kidston and Lang, 1921b). The species was originally based on two fragments, one of which shows the typical pseudoparenchymatous tissue with smooth-walled thick tubes normally associated

*Aglaophyton* might represent a group of primitive land plants, ancestral to both bryophytes and vascular plants, but he was reluctant to propose a formal taxon (which would have to be at the rank of division at least) in the absence of any other definite members of the group (he did not regard *Nothia* as part of it). Whatever formal classification is eventually adopted, however, these taxa will play an important role in helping unravel the early evolutionary history of land plants, and perhaps the relationship between the vascular plants and the bryophytes (the earliest unequivocal bryophyte fossil is from the Middle Devonian of Podolia — Ishchenko and Shlyakov, 1979).

Some of the more remarkable discoveries in recent years at Rhynie have been vascularized gametophytes, which were named *Lyonophyton rhyniensis*, *Langiophyton mackei* and *Kidstonophyton discoides* (Remy and Remy, 1980a, b; Remy, 1991; Remy and Hass, 1991a, b, c). The former was thought to be probably the gametophyte of either *Horneophyton* or

*Aglaophyton*, with which it was found closely associated ((Figure 4.31)A). Germinating spores of *Horneophyton* showing immature gametophytes had been earlier described by Bhutta (1973a), but the specimens described by Remy and Remy are clearly in a mature condition. They have dichotomous aerial with the form-genus, but the second has thick tubes with spiral thickenings (further material has been described by Lyon, 1962). Burgess and Edwards (1988) have suggested that if Kidston and Lang's two specimens represent the same species, they might not be true *Prototaxites*, but belong to their new form-genus *Nematasketum*. Another type of nematophyte from Rhynie was described as *Nematoplexus* by Lyon (1962). This also has tubes with spiral or occasionally annular thickenings, but which are characterized by localized areas of branching known as 'branch knots'. An unpublished thesis by D.S. Edwards (1973) provides the most extensive account of this group from Rhynie, and this makes it evident that other species occur here. He also demonstrated possible evidence of the anatomy of the outer parts of these prototaxitoid axes (also mentioned by Kidston and Lang, 1921b) and of appendages (?rhizomorphs) to a holdfast. It is clear that Rhynie may hold the key to establishing the true nature of these enigmatic plants, although considerably more work is required.

D.S. Edwards (1973) described from Rhynie a poorly preserved spherical object, with a structure reminiscent of *Pachytheca*. Lang (1945) also recorded *Pachytheca* from the Rhynie outlier, but did not state if it came from the chert.

Examples of fine, septate filaments with distinctive nodal structures have been described by Kidston and Lang (1921b) and Edwards and Lyon (1983) as *Palaeonitella cranii* (Kidston and Lang). They have been interpreted as probably the vegetative parts of a charophyte, but no reproductive organs have yet been found.

A variety of other green and blue-green algae have been described from here (Kidston and Lang, 1921b; Croft and George, 1959; Edwards and Lyon, 1983), including filamentous, palmeloid and unicellular forms. It is by far the most diverse, non-marine algal assemblage to be described to date from the Devonian, but there remains little information on their reproductive structures and thus their taxonomic positions.

Also abundant in the Rhynie Chert are mycelia, vesicles and resting spores of fungi (Kidston and Lang, 1921b; Harvey *et al.*, 1969; Boullard and Lemoigne, 1971; Taylor *et al.*, 1992a, b). In the absence of detailed information on their reproductive organs, they have been assigned to the generalized form-genus *Palaeomyces*. *P. gordonii* and *P. agglomerata* were found throughout the chert and were undoubtedly saprophytic. Others, however, occur only in the rhizomes of particular vascular plants, such as *P. asteroxylii* in *Asteroxylon* and *P. horneae* in *Horneophyton*. Boullard and Lemoigne argued that these were mycorrhizal and, if this is correct, they represent the oldest known examples of such a symbiosis. It has been suggested that symbiosis between vascular plants and mycorrhizal fungi was essential to the early colonization of the land, allowing the vascular plants to obtain sufficient nutrients from a relatively impoverished environment (Pirozynski and Malloch, 1975; Pirozynski, 1981). Most recently, Taylor *et al.* (1992a, b) have argued that, at least in some cases (e.g. the putative charophyte *Palaeonitella*), the fungi were parasitic, resulting in a reaction by the host plant.

None of the vascular plant fossil species from Rhynie has been found anywhere else in the world. Even at the rank of form-genus, the plants are unique. Two other species were included for a time in *Asteroxylon*: *A. elberfeldense* Kräusel and Weyland, 1926, from the Middle Devonian of Germany (see also Scott, 1926); and *A. setchellii* Read and Campbell, 1939, from the Mississippian of the USA. However, the former has been transferred to *Thursophyton* because of its medullated stele and scalariform tracheids (Lyon, 1964; Hoeg *in* Boureau *et al.*, 1967); and the latter is now included in the ?pteridosperm form-genus *Stenokoleos* (Hoskins and Cross, 1951, 1952). A possible correlation between *Lyonophyton* and the adpression form-genus *Sciadophyton* ((Figure 4.31)B) has been suggested (Remy *et al.*, 1980a), but the limited anatomical detail preserved in the latter makes it difficult to confirm this. A possible correlation between *Rhynia* and *Salopella* has also been suggested (e.g. Edwards and Richardson, 1974; Taylor, 1981) but again the preservation of the latter is a problem.

In addition to the significance of its individual plant fossil taxa, the Rhynie Chert is important as a preserved *in situ* ecosystem (Edwards, 1986), the oldest of its kind discovered to date (Figure 4.32). The palaeoecology of the chert has been discussed by Kidston and Lang (1917b, 1921b), Tasch (1957), Kevan *et al.* (1975) and Trewin and Rice (1992). Of particular interest is the evidence

that it provides of the triangular interaction between the 'vascular' plants, the fungi and an arthropod fauna. The relationship between the 'vascular' plants and the fungi has already been mentioned, but it is also worth noting that the arthropods may have been a significant dispersal vector for the fungi (Kevan *et al.*, 1975). There is considerable evidence, particularly in the aerial shoots of *Rhynia*, of lesions possibly produced by sap-sucking animals. There is also some evidence that the smaller arachnids occupied empty sporangia and cavities in the aerial shoots of *Rhynia*, which may have represented a more equable micro-environment than conditions outside. There is considerable potential for further elucidating the structure of this early terrestrial ecosystem, particularly if observations on the *in situ* chert become possible.

## Conclusion

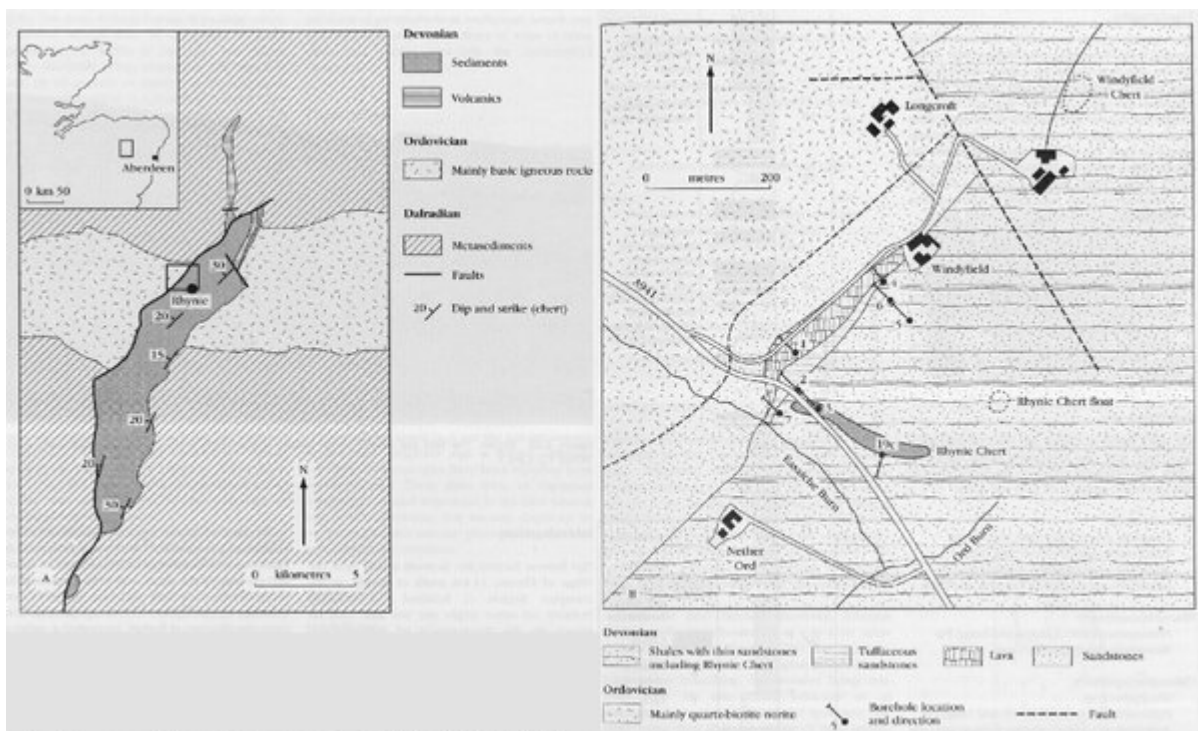
Rhynie is the most important single Devonian palaeobotanical site, and one of the most important of any age in the world. It yields the oldest examples of land plants, c. 390 million years old, in which anatomical details are still largely preserved intact. It provided the first indisputable evidence that Devonian plants were truly primitive, and not just badly preserved remains of more advanced groups seen in younger rocks. Its discovery just before the First World War catalysed the search for other Devonian (and subsequently Silurian) plant fossils throughout the world, and has resulted in the model for the early evolution of land plants that is accepted today (summarized in Chapter 3). Practically all that is known about the early evolution of land plants is a direct consequence of the discoveries at Rhynie, and this in turn provided a focus for the rest of palaeobotanical research. The 22 species of plant fossil (including fungi) are unique to this locality, and include what is widely regarded as the archetypal early land plant (*Rhynia*), the earliest club-moss for which a detailed anatomy has been described (*Asteroxylon*), and a variety of enigmatic species evidently representing early experiments in adapting to a terrestrial environment. Rhynie is also important as the oldest known example of an entire terrestrial ecosystem preserved in place, showing how plants and animals interacted with each other and with the abiotic environment at this early stage in the development of life on land.

## References

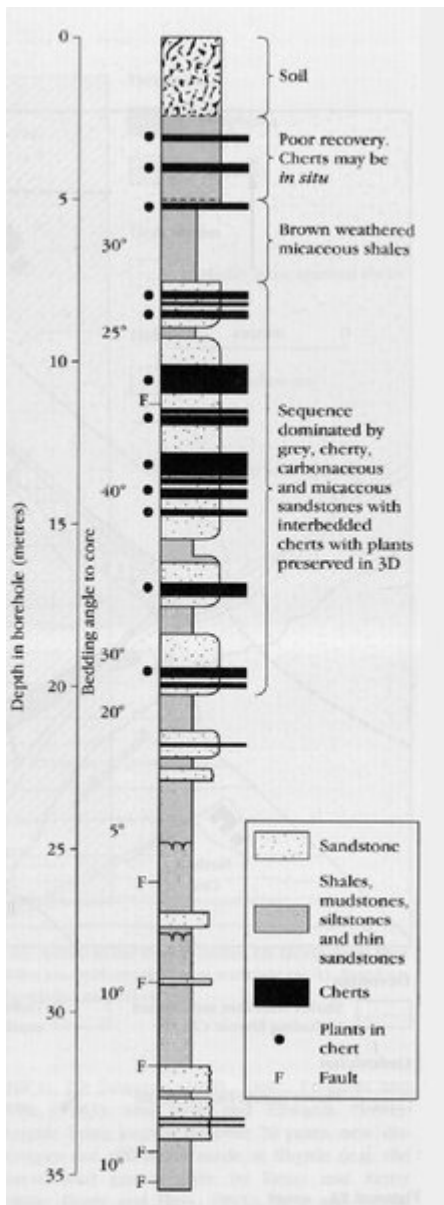


(Figure 4.22) Rhynie. The field just outside of the village, under which lies the Siegenian fossiliferous chert. (Photo: C.J. Cleal.)

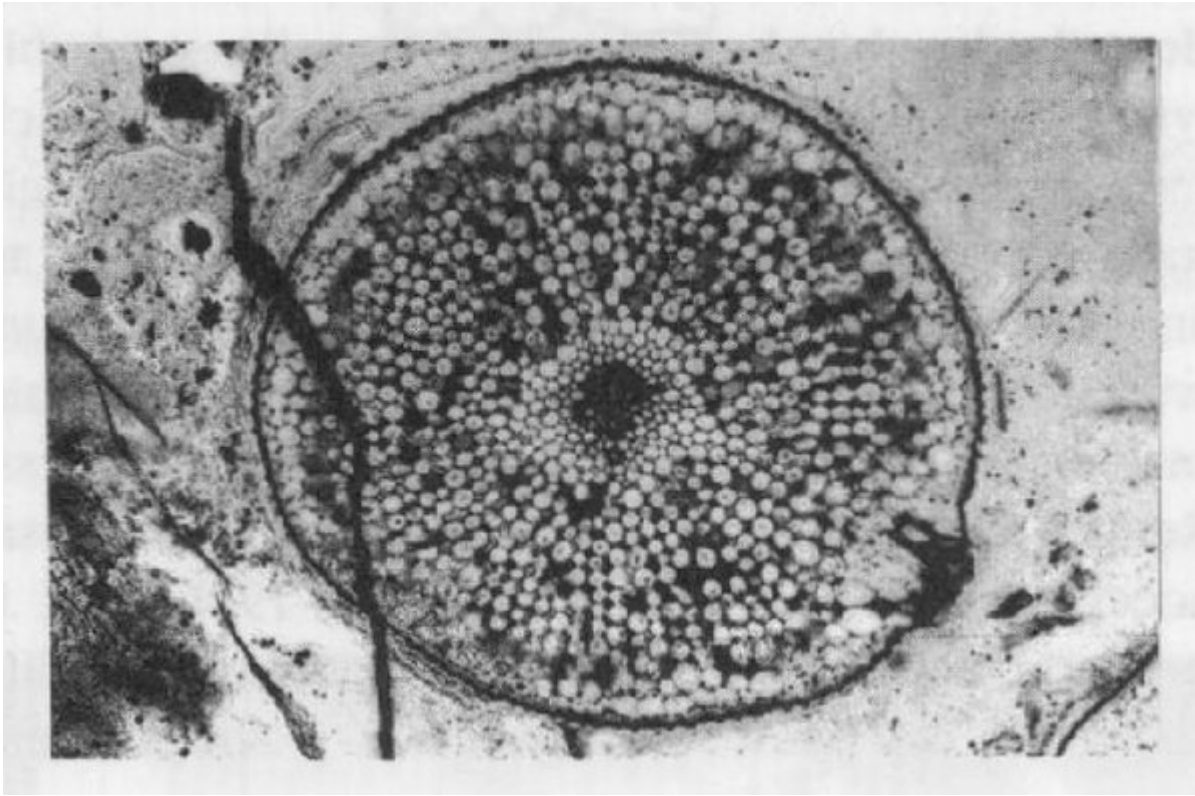




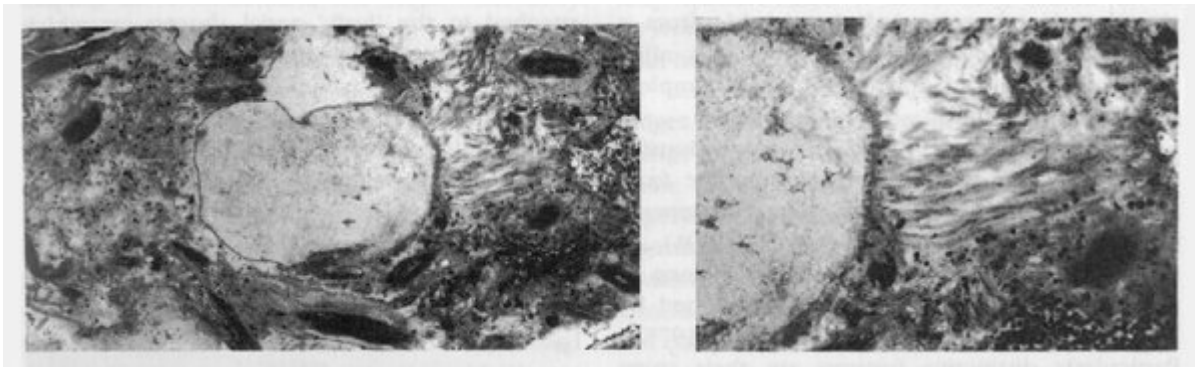
(Figure 4.23) Geology of the Rhynie area. (A) Map showing the outline of the Rhynie outlier. (B, facing page) Map showing detail of that part of the outlier containing the fossiliferous chert (marked by a rectangle on A). Based on Trewin and Rice (1992, figure 1), who provide details of the boreholes marked on (B).



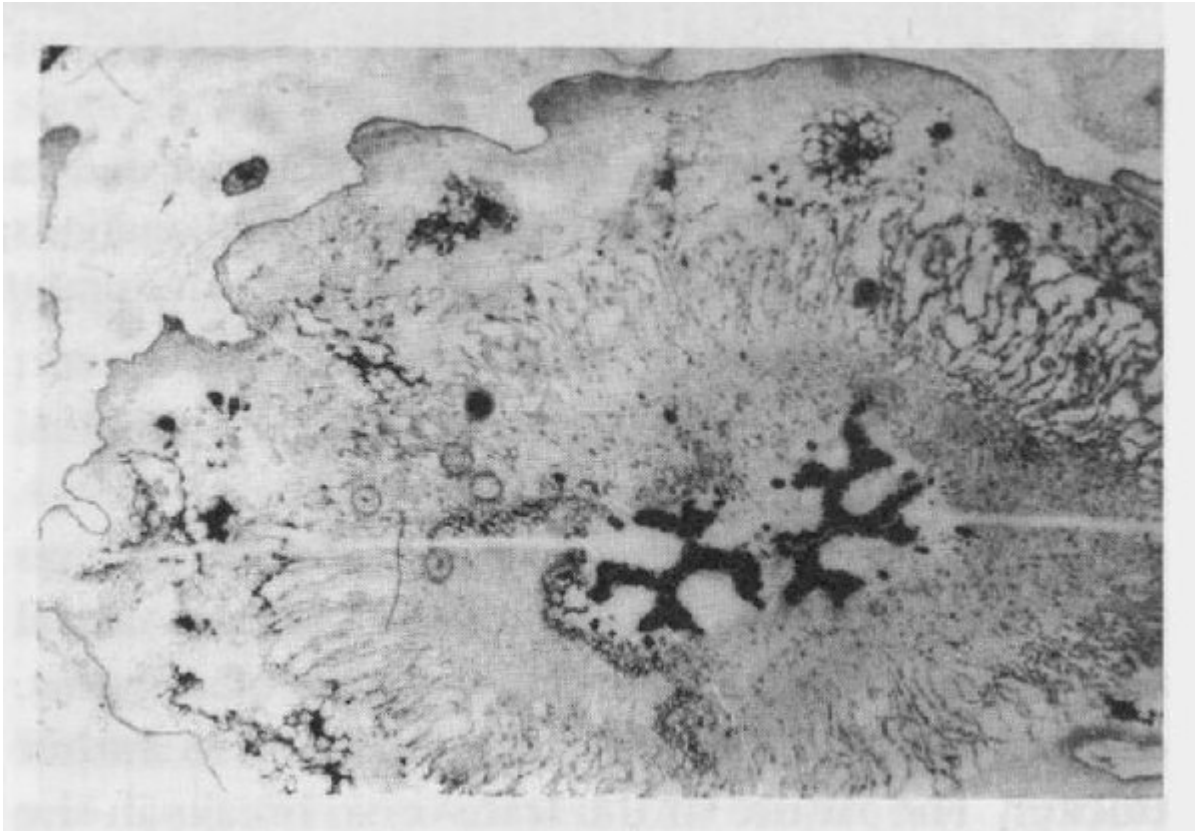
(Figure 4.24) Composite log through Rhyrie Chert showing distribution of plant-bearing horizons. Based on Trewin (1989, p. 11).



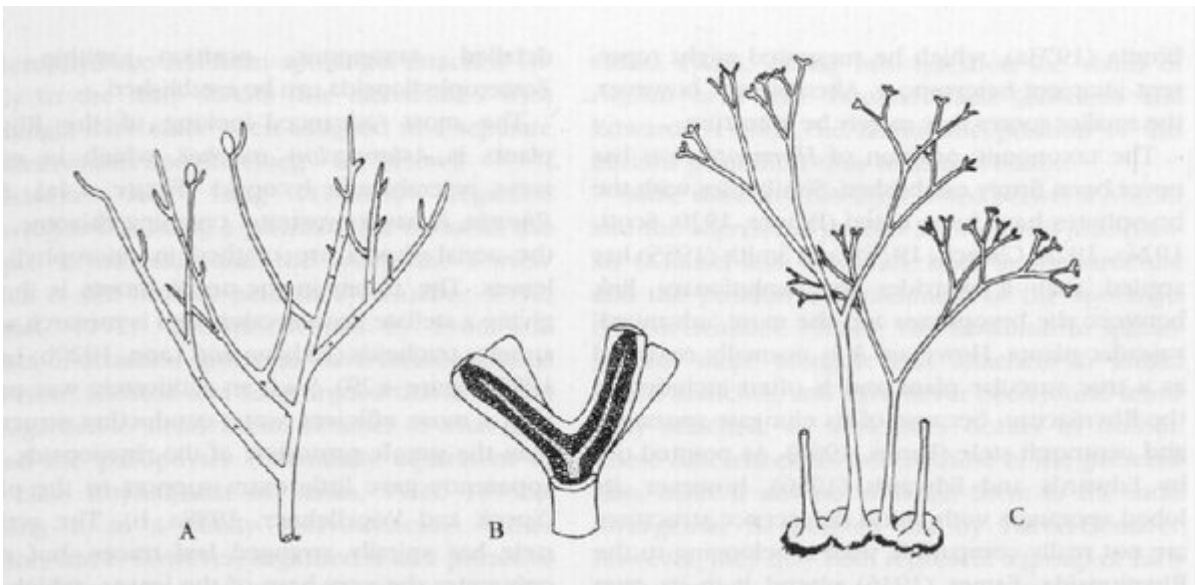
(Figure 4.25) *Rhynia gwynnevaughanii* Kidston and Lang. Transverse section through stem showing central vascular strand; Natural History Museum, London, specimen SC.3132. Rhynie Chert (Siegenian), Rhynie. x 25. (Photo: Photographic Studio, Natural History Museum, London.)



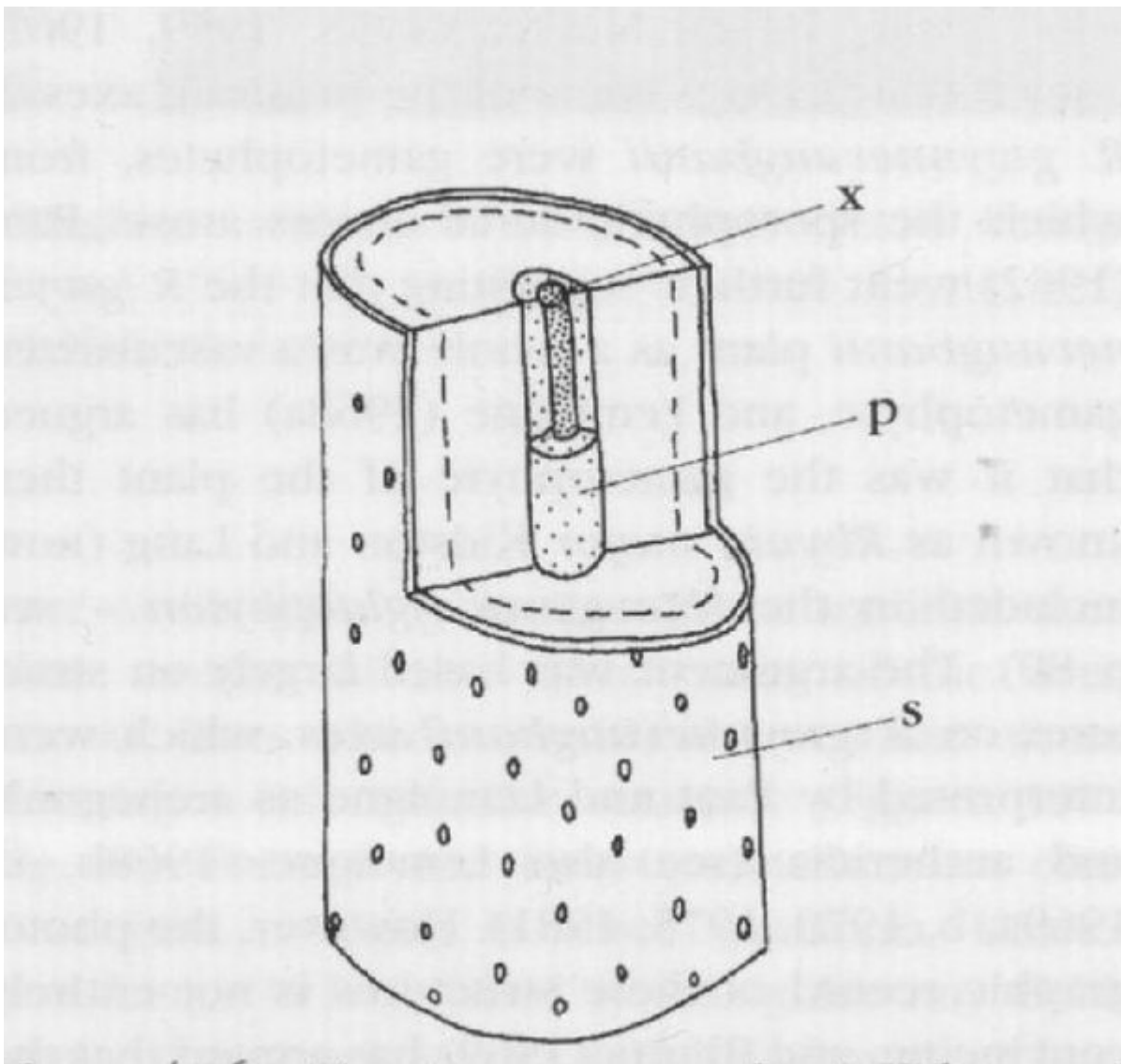
(Figure 4.28) *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah. Longitudinal sections through corm-like rhizome; Natural History Museum, London, specimen V.15648. Rhynie Chert (Siegenian), Rhynie. (left) x 8, (right) x 5. (Photos: Photographic Studio, Natural History Museum, London.)



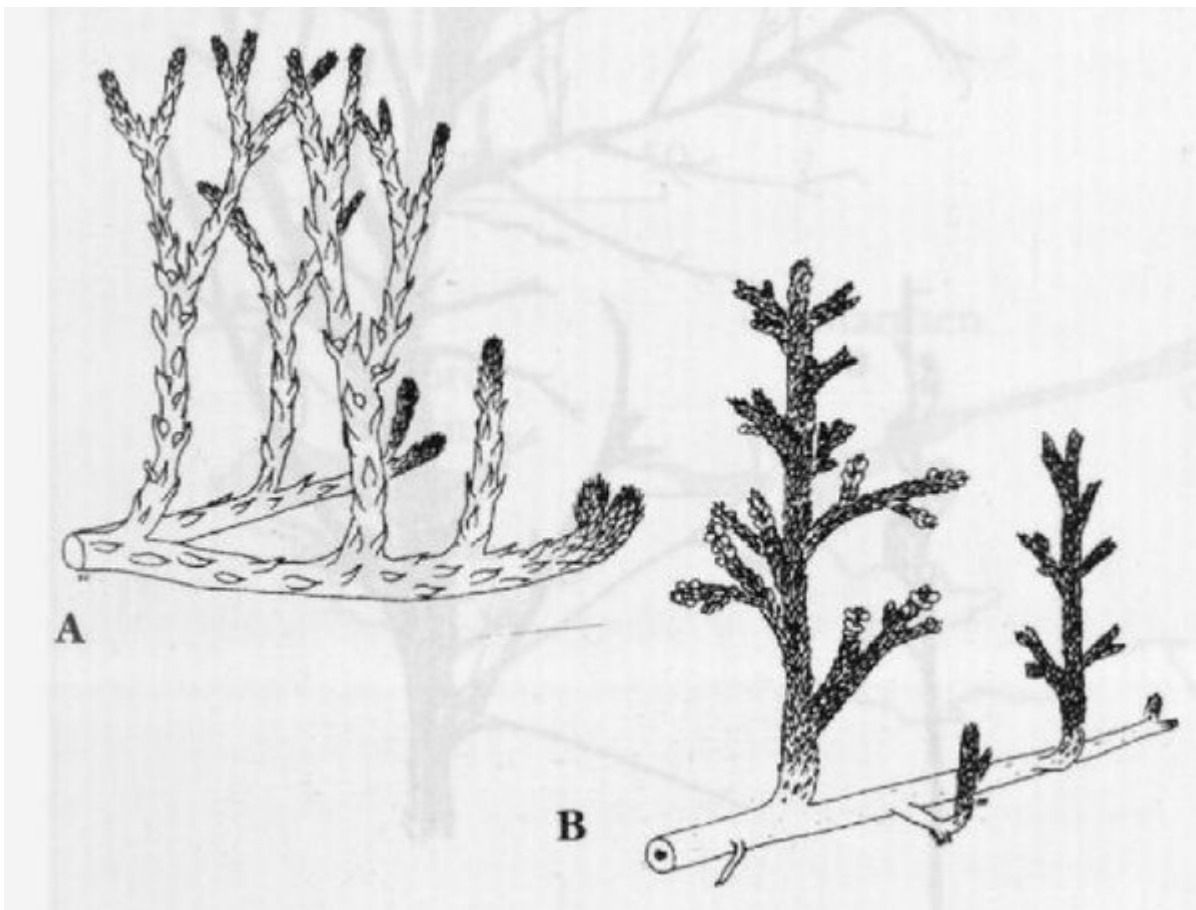
(Figure 4.29) *Asteroxylon niackei* Kidston and Lang. Transverse section through dichotomizing stem, showing two vascular traces with the characteristic stellar cross-section; Natural History Museum, London, specimen V.15643. Rhynie Chert (Siegenian), Rhynie. x 6.66. (Photo: Photographic Studio, Natural History Museum, London.)



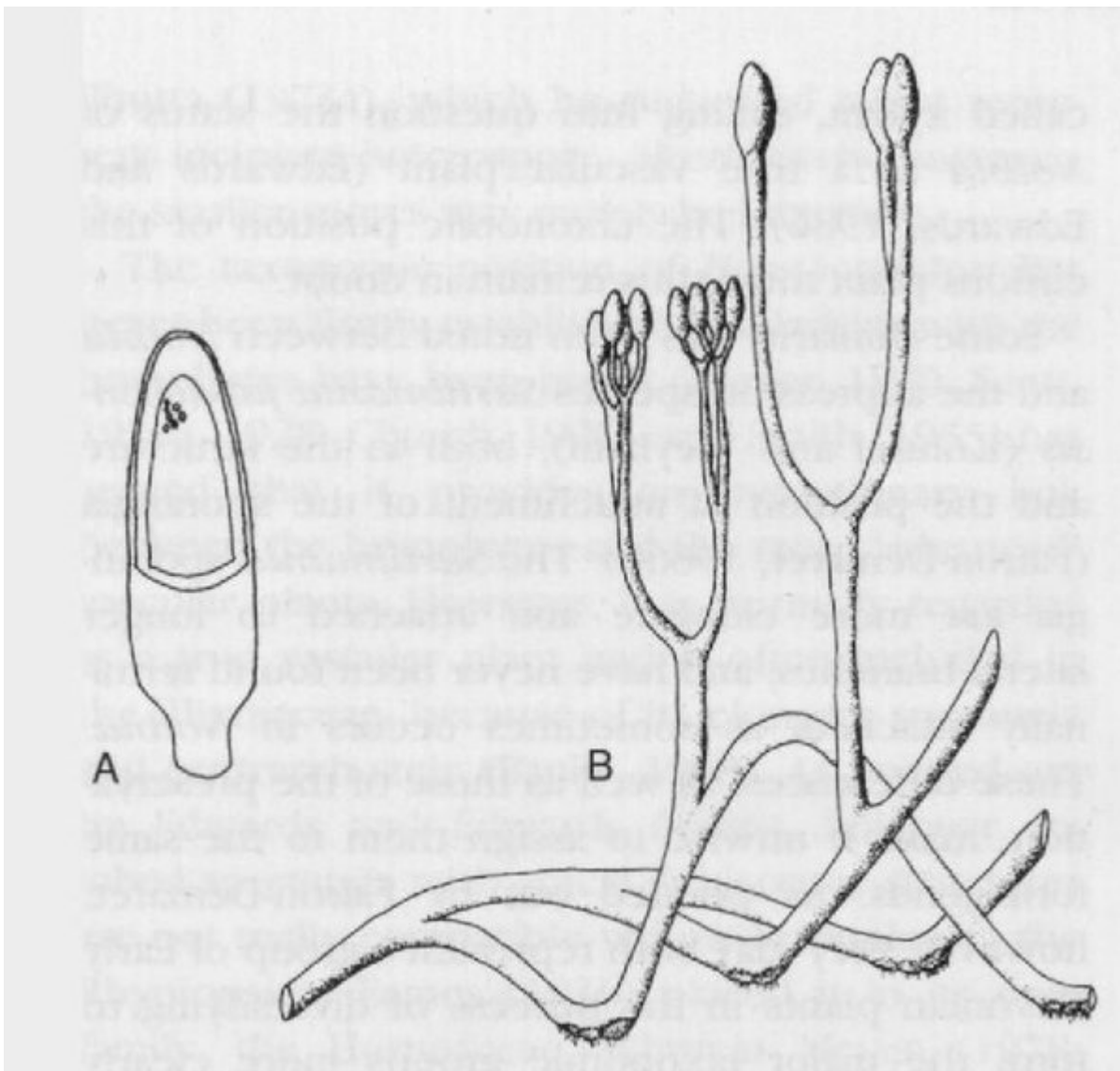
(Figure 4.27) (A) *Rhynia gwynnevaughanii* Kidston and Lang; reconstruction of aerial parts of plant including terminal sporangia. (B-C) *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah; (B) cut-away reconstruction of dichotomizing sporangia showing the central columella; (C) reconstruction of whole plant. From Thomas and Spicer (1987, figure 3.2C, E, and F; after Eggert and D.S. Edwards).



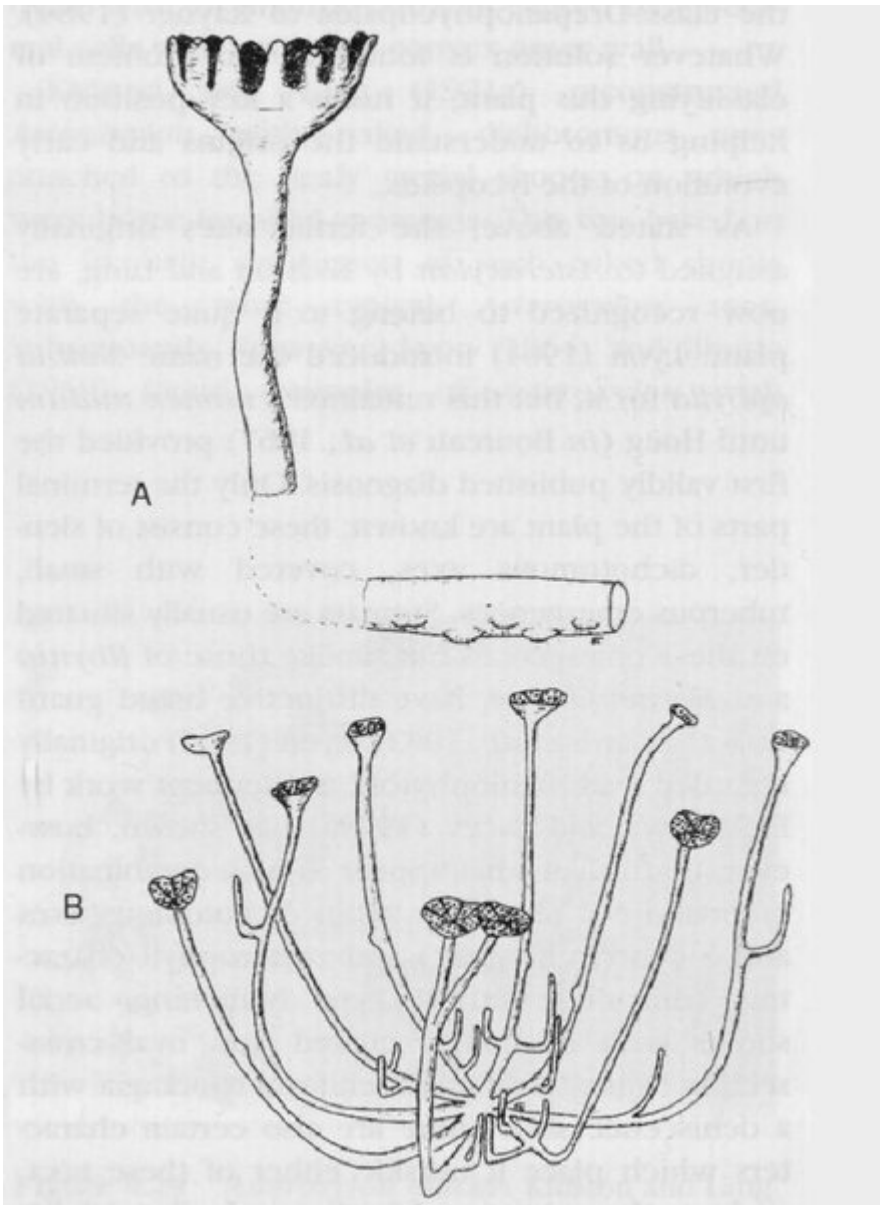
(Figure 4.26) *Rhynea gwynnevaughanii* Kidston and Lang. Cut-away reconstruction of stem showing cylindrical protostele of xylem (x), phloem (p), and stomata on the stem surface (s). From Thomas and Spicer (1987, figure 3.2D; after Chaloner and Macdonald).



(Figure 4.4) Reconstructions of Early Devonian lycopsids. (A) *Asteroxylon*. (B) *Drepanophycus*. From Thomas and Spicer (1987, figure 3.6; after Kräusel and Weyland, and Kidston and Lang).

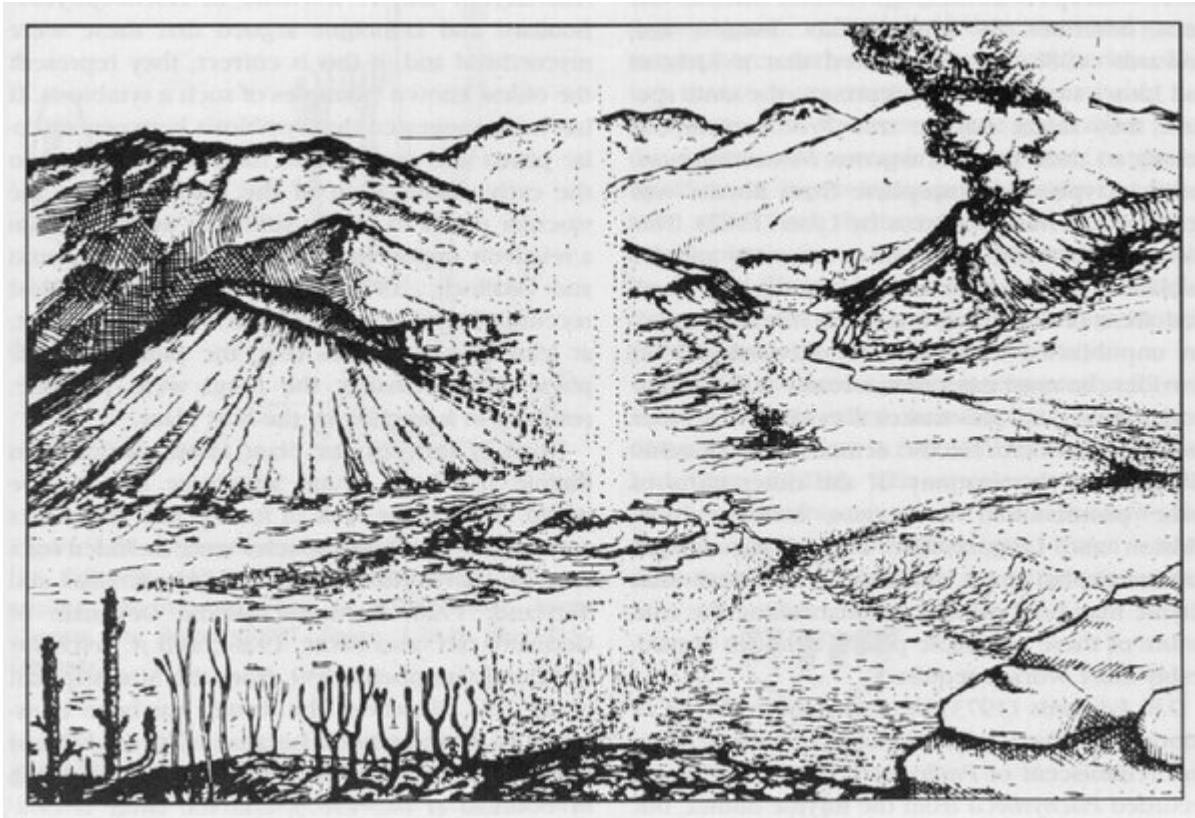


(Figure 4.30) *Aglaophyton major* (Kidston and Lang) D.S. Edwards. (A) cut-away reconstruction of sporangium. (B) reconstruction of whole plant. From Thomas and Spicer (1987, figure 3.2A-B; after D.S. Edwards).



(Figure 4.31) Putative Devonian gametophytes. (A) *Lyonophyton rhyntensis* Remy and Remy, based on Rhyntie fossils. (B) *Sciadophyton steinmannii* Kräusel and Weyland, based on Lower Devonian fossils from Germany. From Thomas and Spicer (1987, figure 3.9; after W. Remy and R. Remy).





(Figure 4.32) Reconstruction of the Early Devonian vegetation at Rhynie. Based on Trewin (1989, p. 12).