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History of research on the geology and palaeontology of the Rhynie area, Aberdeenshire, Scotland

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ABSTRACT: Geological and palaeontological research in the Rhynie area, Aberdeenshire, Scotland, has progressed in several stages. Following early surveys in the nineteenth century, Dr William Mackie mapped the western margin of the basin in 1910–1913, and discovered the plant-bearing chert. Following trenching of the chert in 1913, Kidston & Lang described the plant fossils between 1917 and 1921 and Scourfield, Hirst and Maulik the arthropods in the 1920s. Following a 'dark age' of some 30 years, Geoffrey Lyon awakened interest in the late 1950s. Trenching in 1963–1971 provided Lyon and his co-workers with new material, and resulted in finds of new plants and reinterpretations of earlier work. The next phase was initiated by Winfried Remy's discovery of gametophytes in material given to him by Lyon. Since 1980, the Münster school has continued to make exciting discoveries. Aberdeen University involvement began in 1987 with geochemical work confirming a hot spring origin for the chert. Drill cores taken in 1988 and 1997, and further trenching have allowed structural, sedimentological and stratigraphic reappraisals, and resulted in the discovery of a new biota in the Windyfield chert. Long-term collaborative international research continues to advance interpretation of this unique Early Devonian hot spring system, and the remarkably diverse freshwater and terrestrial biota of the cherts.

KEY WORDS: chert, hot-spring, Kidston, Lang, Lyon, Mackie, Remy.

This contribution records the history of geological research on the Rhynie outlier of the Old Red Sandstone (ORS) in Aberdeenshire, Scotland, particularly documenting investigations of the fossiliferous Rhynie and Windyfield cherts. The main periods of investigation into both the geology and palaeontology of the area are discussed, together with the people who have played pivotal roles in the investigations. The scientific advances which have resulted from study of the biota of the Rhynie chert have been discussed elsewhere. Edwards (2004), Kerp *et al.* (2004) and Cleal & Thomas (1995) have noted the impact of the publications of Kidston & Lang (1917, 1920a, b, 1921a, b) on palaeobotany. The known arthropod fauna (Anderson & Trewin 2003; Dunlop *et al.* 2004; Fayers & Trewin 2004) has significantly increased since the discussions by Kevan *et al.* (1975) and Rolfe (1980) on the roles of the Rhynie arthropods as part of an early terrestrial ecosystem.

There have been several phases of exploration and mapping of the Rhynie outlier (Wilson & Hinxman 1890; Read 1923; BGS 1993; Rice *et al.* 2002; Rice & Ashcroft 2004). These papers document the changing interpretations of the stratigraphy and structure of the area. In particular, the depiction of the structure as a simple half graben faulted on its western side has been radically changed following extensive drilling and excavation (Rice *et al.* 2002; Rice & Ashcroft 2004). Investigations of the hydrothermal system (Rice & Trewin 1988; Rice *et al.* 1995) have advanced the inspired interpretation of Mackie (1913) that the cherts originated as hot-spring deposits.

With the increased intensity of investigations at Rhynie, it is timely to record the phases of site investigation, and consolidate locality details for the various phases of trenching and drilling. It is the intention that this information will be of value in planning future investigations of this important site. The sources of information used comprise published accounts, Ph.D. theses (El-Saadawy 1966; Bhutta 1969; Edwards 1973; Powell 1994; Fayers 2003) and the manuscript notes of Dr A. G. Lyon held by the Department of Geology and Petroleum Geology, Aberdeen University, Aberdeen.

The two fields beneath which the Rhynie chert was first located were declared a Site of Special Scientific Interest (SSSI) in 1956 under the National Parks and Countryside Act of 1949, and the site was re-designated in 1986 under the 1981 Wildlife and Countryside Act. The site was purchased by Lyon in 1963, and gifted by him to Scottish Natural Heritage (SNH) in 1992.

1. Historical notes

The fertile valley underlain by the ORS of the Rhynie outlier (Fig. 1) has been inhabited from early times. The most notable remaining monuments are the vitrified iron age fort on Tap o' Noth, the Pictish symbol stones that can be seen at Rhynie churchyard, and the ruins of Kildrummy Castle that dates from thirteenth century and fell into ruin following the 1715 uprising. The castle was a ruin at the time it was illustrated by Cordiner (1780), who records that quarries for freestone and millstones were situated at the top of a hill overlooking the Bogie, presumably Quarry Hill.

There is a persistent story still current in the Rhynie area that Tap o' Noth is an extinct volcano. This theory is supported by an account by an unnamed 'gentleman' quoted by Cordiner (1780). This gentleman found it impossible to believe that men could have built the large ramparts, or that they could have been vitrified by 'any artificial or incidental fires'. He also supposed that an opening, now considered to have been a well, was the latest crater of the volcano. He did concede that the structure had later been utilised by man for defence.

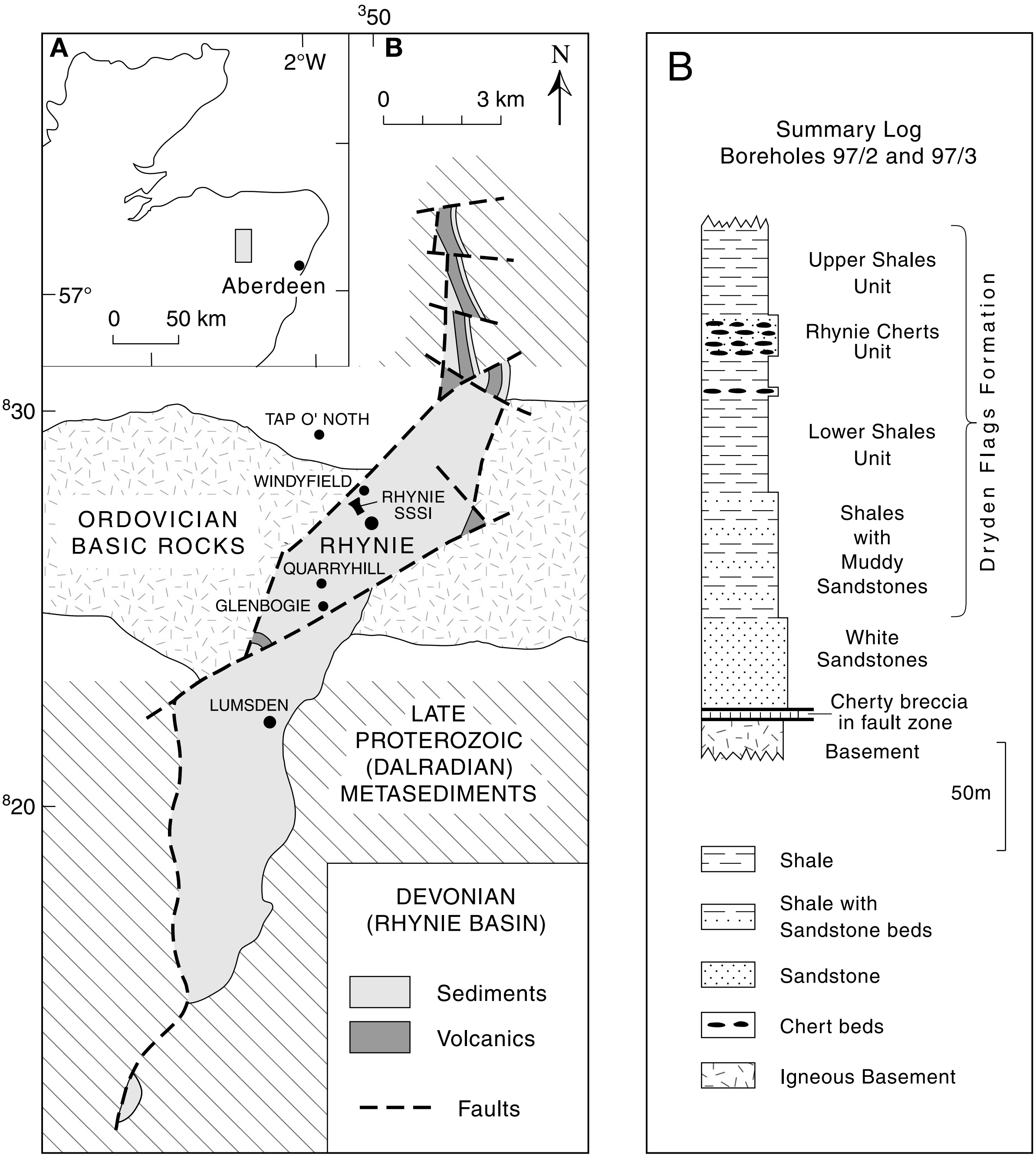

Figure 1 Locality map of the Rhynie area.

2. Early mapping

The Rhynie outlier of ORS is not shown on the earliest published geological map of Scotland, the small sketch by Boué (1820). The outlier is depicted on the issues of Macculloch's geological map of Scotland (e.g. Macculloch 1840), and was investigated by the Reverend Gordon (1801–1893) of Birnie in Moray, who is best known for his geological research in the Elgin area (Andrews 1982). Gordon is recorded by Malcolmson (1859) as having found, in 1839, fossil fish in calcareous nodules at Glenbogie stated to be comparable to those of Lethen, Nairnshire (i.e. Middle ORS, Achanarras fauna). However, Geikie (1879), recording the stratigraphy of the ORS of Rhynie of which he had 'traced the boundaries' with B. N. Peach in 1876, was told by Gordon that 'no record seems to have been kept of them, and that he cannot say what were the species'. The supposed source of the fish is calcareous concretions in the red shales near the base of the sequence. This very doubtful record caused Geikie (1879, pl. 22) to correlate these nodules with the Middle ORS Achanarras equivalent fish beds of Gamrie and Tynet Burn. On the basis of spores, an Early Devonian Pragian age (Rice *et al.* 1995) has been assigned to the Dryden Flags Formation (BGS 1993) at the top of the Rhynie sequence. Given the lack of any firm evidence, despite searches by several people, Gordon's report of Middle ORS fish in the nodules of the Carlinden Shales near the base of the sequence has to be discounted until fossil evidence is produced.

Another early find was that of a cylindrical plant stem described as being 4 feet long and 5 inches wide with a coarsely striated surface. This was found (most probably in the Quarry Hill Sandstone, but the locality is not sufficiently defined) by Reverend Alexander Mackay (1815–1895) in 1854 (Murchison 1859), along with other fossils. One of Mackay's fossils was shown to Hugh Miller, who considered it to represent the tracks of a crustacean [reported in Murchison (1859, p. 432), and also by Miller (1857, p. 435) in the publication of a lecture given in 1855]. This was probably the ichnogenus *Diplichnites*, which has been recorded from the Quarry Hill Sandstone (Carroll 1991). However, Mackay (1861, footnote p. 44) records that, in the autumn of 1858, he 'discovered a large calamite in an Old Red Sandstone quarry of the *Lower Formation* at Rhynie, Aberdeenshire, previously regarded as unfossiliferous. Near it were found curious fern-like markings of great beauty, which Sir Roderick Murchison regards as "*impressions* made on the sand by the pectoral fins of fishes swimming in shallow water." ' Murchison (1859, p. 432) gives credit to Salter for this fishy interpretation. If Mackay's 1858 date for finding the 'calamite' is correct, it cannot have been the find shown to Miller, who died in 1856, so it is possible that Mackay collected from more than one locality. Another sandstone cast of a large plant stem from Quarry Hill, now in the Aberdeen University Geology Museum collections (AUGD 12478), was reported by Newlands (1913). Apart from being an author of geographical texts, Mackay was the first Free Church minister at Rhynie, and 17, The Square, Rhynie was acquired by the church as the manse. In the autumn of 1858, Murchison and Andrew Ramsay (later to succeed Murchison as Director General of the Geological Survey) were guests at the manse for a few days prior to a meeting of the British Association for the Advancement of Science in Aberdeen (Lyon, undated ms).

The succession established by Geikie (1879) was adopted by Wilson & Hinxman (1890) in the Geological Survey memoir to Sheet 76, but they did not repeat Geikie's recorded thicknesses for the sequence. It would seem that Geikie had accepted that his previous correlation based on Gordon's report of fish was incorrect since the strata were placed in the Lower ORS by Wilson & Hinxman (1890), and as Director General of the Survey Geikie would have presumably approved their work. This memoir established that the outlier has a faulted western margin and unconformable eastern margin, and also noted folding within the ORS strata.

However, on the basis of the differences between the fish faunas of the Lower ORS of the Midland Valley and those of the ORS of the Orcadian area, the notion that there was no Lower ORS in the north persisted, and the outlier was generally regarded as being Middle ORS. Westoll (1951) noted that in the Orcadian Basin there was a 'Basement Group' in several areas, lying unconformably beneath dated Middle ORS. He considered that the Rhynie outlier belonged to this group. The 'Basement Group' of Westoll is now firmly established as Lower ORS on the basis of spores. Stratigraphic details have been summarised by Trewin & Thirlwall (2002).

3. William Mackie and the Rhynie chert

Dr William Mackie (1856–1932) (Fig. 2) was a native of Aberdeenshire, attending Chapel of Garioch Parish School, Aberdeen Grammar and Aberdeen University, where he graduated in Arts with Honours in Natural Science in 1878 (Campbell 1932). Following a period of teaching science in schools, he returned to Aberdeen in 1886, graduating in medicine in 1888. He then conducted postgraduate study at Aberdeen and Edinburgh on diseases of the eye, following which he set up in medical practice at Elgin where he remained until he retired in 1924 and moved to Glasgow where he died in 1932 (Campbell 1932). Mackie published over 40 articles, and is perhaps best known for his work on sands, sandstones and heavy mineral analysis. He recognised the baryte and fluorite cements in the Elgin New Red Sandstone of the Elgin area, and in the Dalradian, he noted the contemporaneous volcanics within the metamorphic rocks. His last paper, on

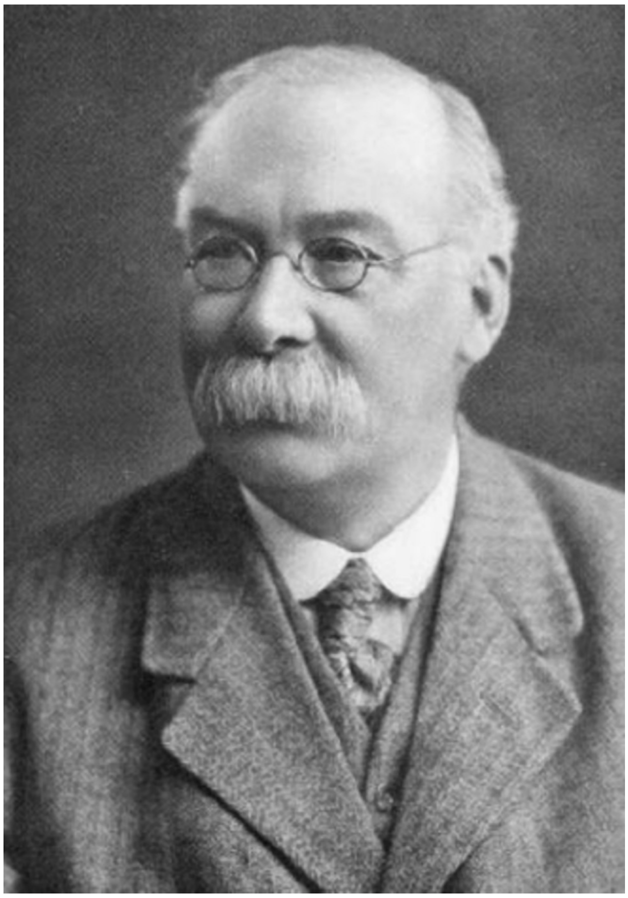

Figure 2 Dr William Mackie.

heavy minerals from the Silurian of southern Scotland was published in 1929.

Mackie was attracted to the geology of the Rhynie area by curiosity regarding igneous rocks noted in the Geological Survey Memoir (Wilson & Hinxman 1890). The rocks he collected in 1910 and sectioned in 1911 were cherty and contained altered clasts of volcanic rocks – not what he expected. Further visits with W. R. Watt in 1911, 1912 and 1913 resulted in the production of a geological map (Mackie 1913) that contains many pertinent observations. Mackie considered that a succession of cherty sandstones and altered igneous rocks older than the ORS intervened between the ORS and the basin boundary fault to the west of Rhynie. These rocks are now considered to be hydrothermally altered ORS deposits (Rice *et al.* 1995).

At the top of his older 'Craigbeg' succession, he provisionally placed the 'black and grey cherts with plant and animal remains' (Mackie 1913, p. 210). Mackie first collected the plant-bearing chert as loose blocks during 1912 (Horne *et al.* 1916). However, he was unsure of the stratigraphic position since the blocks of chert he found in walls and littering the fields lay close to the faulted boundary between his 'Craigbeg' succession and the 'ORS'. Mackie did not find the chert *in situ*, but once he had made thin sections, the spectacular nature of his discovery was clear. Mackie was an acute observer, and records mineralogical and palaeontological features of the chert, noting that 'chalcedonic aggregates' had formed around plant stems and even around a spore. He also correctly noted decay in the plants prior to their 'entombment in chert'. His recognition of animal remains, and his suggestion that they were crustaceans (now *Lepidocaris*) were remarkable.

Mackie figured two sections of Rhynie chert, one with the plant now known as *Rhynia* (Mackie 1913, fig. 5), and the

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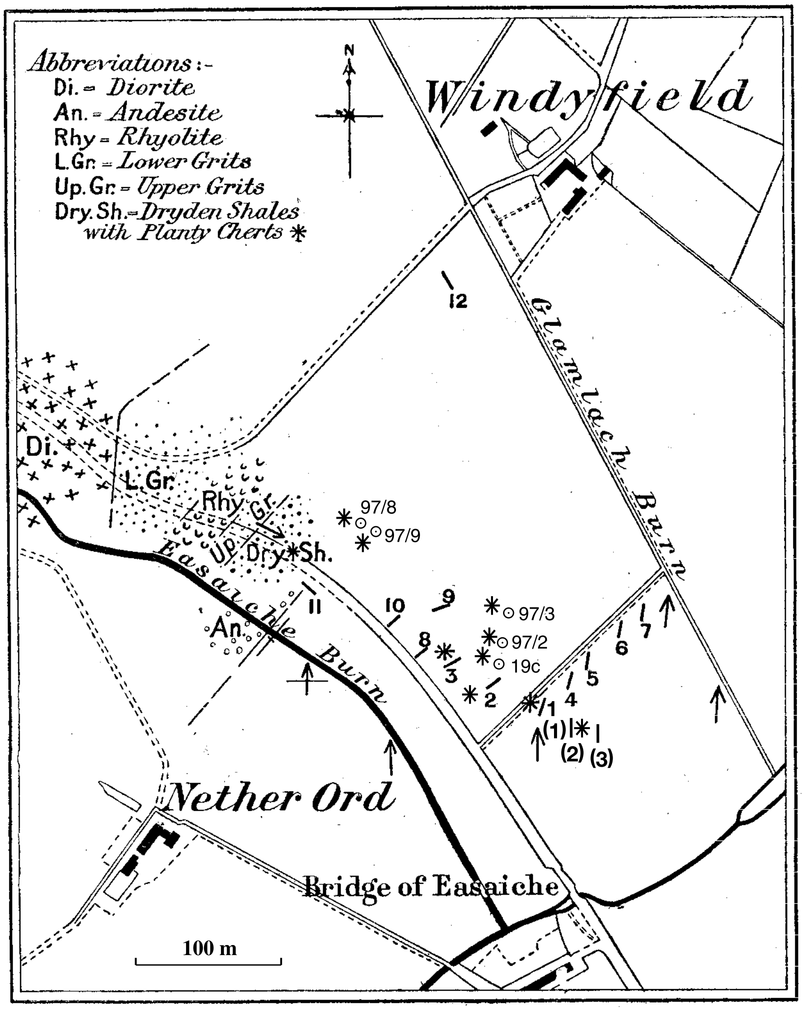

Figure 3 Locations of Tait's trenches 1–12 at Rhynie, as on the map from Horne *et al.* (1916), with the addition of the earlier trenches (numbers 1–3 in brackets) reported in Mackie (1913), and boreholes drilled in 1989 (19c) and 1997 (97/2, 3, 8, 9) which intersected the Rhynie chert.

other with the plant now termed *Asteroxylon* (Mackie 1913, fig. 6), but he did not describe or name the plants, stating that they were being studied by Kidston. It seems that the Rhynie chert story could have started much earlier, about 1880, since Mackie, with hindsight, remembered finding a piece of plant bearing chert 'more than 35 years ago' (Mackie 1913, p. 225). [Although Mackie's paper was read on 21 November 1913, he was able to add a footnote (p. 224) with reference to 'last April (1914)'. Hence there is some doubt regarding actual dates of discoveries.]

Mackie did not content himself with mere description, but went on to interpret the conditions of deposition of the cherty rocks as follows. 'The theory which suggests itself as a competent explanation of the cherty developments, which are such a prominent characteristic of this series of rocks, is that during the decadent phases of local volcanic action, geysers or hot springs were the efficient cause that gave rise to the particular features presented by this suite of rocks' (Mackie 1913, pp. 233–4). He follows this statement with a good description and interpretation of geyserite. Mackie also considered that some of the granitic intrusive activity affected his 'older' cherty rocks. Thus, the major elements of Mackie's observations and interpretations have stood the test of time.

4. Trenching for chert, 1913–1916

Mackie must have informed the Geological Survey of his find since Mr Tait, fossil collector to the Geological Survey, was sent to Rhynie. Tait initially dug three trenches in October 1913 (Horne *et al.* 1916), finding *in situ* chert in two of them (Fig. 3). This exercise clearly showed that the cherts were within the ORS as mapped by Mackie. Thus, towards the end of his paper, after reporting Tait's results, Mackie seemed to have changed his mind on the stratigraphy, but doubts lingered, and he did not go back and modify the earlier part of his paper. The impression is that Tait's evidence came late in the publication process.

The nagging doubts left regarding the age and stratigraphic position of the Rhynie cherts resulted in continued trenching, supervised by Tait, and supported by the British Association and the Royal Society of London (Horne *et al.* 1916). Twelve trenches were opened in this investigation (Fig. 3) with *in situ* chert being found in three. The plant-bearing chert in the trenches was clearly interbedded with sandstones and shales, the Dryden Shales of the ORS.

It is not clear from Horne *et al.* (1916) whether trenches 1–3 of the first phase of Tait's trenching are the same as trenches 1–3 of the 'investigations of the committee'. The measurements given in Mackie (1913) and Horne *et al.* (1916) for the No. 1 trench differ by 19′ (c. 5·7 m); this discrepancy may be a result of extension of the trench after Tait's initial report had been written. However, it seems probable that these are the same 'number 1' trenches since there is no mention of reopening trenches and it is noted that trenches had to be covered up at the end of March 1916. Thus, it is likely that the chert-bearing trenches were open from October 1913 until March 1916, and

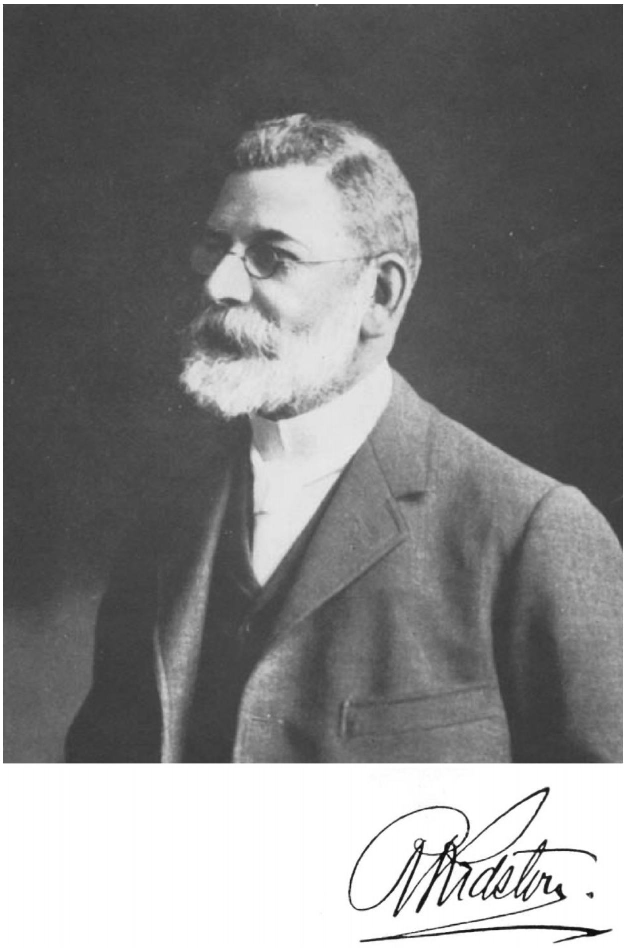

Figure 4 Dr Robert Kidston.

Figure 5 Professor W. H. Lang.

there would have been no merit in digging repeat trenches. However, it is clear from both content and stated locations that trenches 2 and 3 of Tait's original report, quoted in Mackie (1913), are not the same as trenches 2 and 3 of Horne *et al*. (1916, fig. 1). The locations of these trenches are plotted on Figure 3. Meanwhile Kidston (Fig. 4) had been examining Mackie's material and was supplied with samples from all beds exposed in Tait's trench 1 (Kidston & Lang 1917, p. 763). They would also have had access to loose material picked from fields and walls in the area.

5. Palaeontology takes over

Kidston originally planned to collaborate with D. T. Gwynne-Vaughan on the Rhynie plants, but Gwynne-Vaughan died at the age of 44 in 1915 (Scott 1916; Boney 1994). Kidston was then joined by Lang (Fig. 5) in the work on the Rhynie plants, resulting in the classic five-part work (Kidston & Lang 1917, 1920a, b, 1921a, b). Kidston had a long and distinguished career as one of the great 'amateur' palaeobotanists (Lang 1925; Edwards 1984), producing superb monographic work on Carboniferous plants prior to his Rhynie work. Kidston died in 1924. Lang spent 15 years on the staff of the Glasgow University Botany Department before taking the Chair of Cryptogamic Botany in Manchester University in 1909 (Salisbury 1961; Andrews 1980). Lang continued to produce papers on Scottish palaeobotany until 1952, but did not continue work on the Rhynie plants. For more detailed historical information on Kidston, Lang and Gwynne-Vaughan see Liston & Sanders (2004).

The scientific novelty presented by the Rhynie plants was that the internal structure showed excellent details of preservation, beyond comparison with virtually all previously described material. However, the general form of each plant was difficult to reconstruct. This clearly posed problems for Kidston & Lang. The five papers by Kidston & Lang include 52 plates with 425 figures, all but a few of the photographs being taken by Kidston. It is clear that their familiarity with the unusual preservation developed with time, something every 'Rhynie' palaeontologist experiences. In the first paper (Kidston & Lang 1917), read in 1916, they had only recognised two different plants (*Rhynia* and *Asteroxylon*) and described only *Rhynia*. There was then a pause before publication of the second paper in 1920 (although it had been read in 1918). They now recognised the difference between *Rhynia gwynne-vaughanii* and *Rhynia major* (the latter now known as *Aglaophyton*; Edwards 1986), and described *Hornea* (now *Horneophyton*, see Barghoorn & Darrah 1938). In the third part, *Asteroxylon mackiei* was described. Also in this paper are the first illustrations of *Nothia*, which Kidston & Lang thought might be fertile shoots of *Asteroxylon*, but they were careful to note that the two had not been found in direct connection – an important lesson to this day for workers on the chert.

Part 4 (Kidston & Lang 1921a) contains restorations of *Rhynia*, *Aglaophyton* (*R. major*), *Horneophyton* (*Hornea*) and *Asteroxylon*. These reconstructions were hardly bettered for the next 60 years. The last paper in the series (Kidston & Lang 1921b) includes the enigmatic *Nematophyton* (now *Prototaxites*), the charophyte alga *Palaeonitella* and numerous fungi.

The work of Kidston & Lang had an immediate impact, prompting the eminent palaeobotanist Duckinfield Henry

Scott to include a chapter on 'The Psilophytales' in the third edition of his textbook *Studies in Fossil Botany* published in September 1920 (Scott 1920). In the preface to this edition, Scott acknowledged that, with respect to the new chapter on the Psilophytales, 'The discoveries chiefly those of Kidston and Lang, recorded in this chapter, are among the most fundamental yet made in the palaeontological history of plants'. Scott also acknowledged that Kidston & Lang gave him access to the manuscripts and illustrations of parts 2 and 3 (Kidston & Lang 1920a, b); hence, the Rhynie flora came to be incorporated in a textbook only 4 months after the publication of part 3 of Kidston & Lang's (1920b) work. Given the difficulty and time-consuming nature of studies of Rhynie plants, it is maybe not a surprise that there was a long lapse of time before other palaeobotanists ventured to revise the monumental studies of Kidston & Lang. The fundamental significance of the Rhynie plants for taxonomic and evolutionary botany is discussed and referenced by Edwards (2004) and Kerp *et al.* (2004).

The numerous sections of Rhynie chert from Kidston's collection are housed in the Hunterian Museum of Glasgow University, having been transferred from the Botany Department shortly before it suffered a catastrophic fire on 21st October 2001 that destroyed Kidston's literature archive (Liston & Sanders 2004).

In parallel with the early palaeobotanical work, others interpreted and described the arthropods in the 1920s, including those first noted by Mackie (1913). Hirst (1923) described four species of the trigonotarbid *Palaeocharinus*, and also *Palaeocharinoides hornei*. Shear *et al.* (1987) synonymised the genera *Palaeocharinus* and *Palaeocharinoides*, and only *Palaeocharinus rhyniensis* and *P. hornei* are now considered valid species (Dunlop 1994). Five species of mites from the chert were erected by Hirst (1923), later revised by Dubinin (1962). Scourfield (1926, 1940) described the crustacean *Lepidocaris*, and the springtail *Rhyniella* was described by Hirst & Maulik (1926). Crowson (1970) suggested that *Rhyniella* was a modern contaminant in the chert, but Whalley & Jarzembowski (1981) showed convincingly that this is not the case. Hirst & Maulik (1926) also recorded the problematic fragments of '*Crania*' (now *Heterocrania*, the name *Crania* being preoccupied by a brachiopod), interpreted as a euthycarcinoid by Anderson & Trewin (2003). The supposed spider *Palaeocteniza crassipes* Hirst 1923 is now regarded as a juvenile trigonotarbid (Selden *et al.* 1991), and the jaw structure named *Rhyniognatha* by Hirst & Maulik (1926) has been more securely assigned to the Hexapoda (Pterygota) by Engel & Grimaldi (2004).

Several of these discoveries were made by the Reverend William Cran (1856–1933), a native of Rhynie and Congregational Minister at Westhill, Skene, Aberdeenshire, from 1901 to 1930. He was a microscopist with a keen interest in the chert and supplied Kidston & Lang, and the Natural History Museum [then called British Museum (Natural History)] with numerous specimens in which he found material of interest (Lyon 1987). His technique was to examine chips of chert small enough to be at least semi-transparent, a laborious process only suited to the discovery of very small or partial arthropods. Cran's contribution has been recognised in the naming of the mite *Protocarus crani*, the alga *Palaeonitella crani* and the euthycarcinoid *Heterocrania rhyniensis*.

Prior to 1930 the dominantly terrestrial nature of the trigonotarbids and mites of Rhynie arthropod fauna had been firmly established, together with the presence of water capable of supporting the aquatic *Lepidocaris*.

Figure 6 Dr A. G. Lyon at the Rhynie chert locality with Tap o' Noth in the background.

6. The dark age: 1929–1957

Following the initial descriptions of the flora and fauna, there was a 'dark age' in which there is little evidence of new discoveries in the Rhynie chert, and few publications discussing the original material. One exception being Scourfield's (1940) contribution on *Rhyniella* and *Lepidocaris*. Accounts of the flora and fauna became incorporated in textbooks (e.g. Seward 1931) and in review articles, but it seems that nobody had the temerity to follow in the footsteps of Kidston & Lang, and there are no records of field studies at the Rhynie chert site. Hence, Tasch (1957), in a palaeoecological re-evaluation of published evidence, relied largely on work published prior to 1930.

7. The re-awakening: Geoffrey Lyon

Alexander Geoffrey Lyon (1918–1999) (Fig. 6) came from a respected Aberdeen family. His university education was clearly disrupted by the war years; he spent a year at Aberdeen University, but eventually graduated in Botany at St Andrews University (1946). He served in the Territorial Army in Egypt and Libya during the Second World War. After completing a Ph.D. on watercress at St John's College, Cambridge, he went to Cardiff University, where he lectured in Botany until he retired in 1973. Following retirement, Lyon purchased 17, The Square, Rhynie, previously the manse occupied by Mackay, and visited in 1858 by Murchison and Ramsay. In the conditions of the gift of the Rhynie site to SNH, Lyon stipulated that the land was to be used only for agriculture and scientific research. Any agricultural income was to be used for the conservation and maintenance of the fields for agriculture, and to contribute to the cost of scientific research on the site. This last condition was handsomely implemented by a contribution of £10,000 from SNH towards drilling investigations in 1997.

Lyon's interest in the chert came to general notice with his publication on the preservation of germinating spores (Lyon 1957), and later the recognition of book lungs in the trigonotarbid arachnid *Palaeocharinus* (Claridge & Lyon 1961), proving it to have been a terrestrial, air-breathing animal. Meanwhile, Croft & George (1959) published details of 'blue-green algae' from the chert. Lyon went on to describe *Nematoplexus* (Lyon 1962); recognised the true fertile structures of *Asteroxylon* (Lyon 1964), and introduced the name *Nothia* for the fertile structures originally described by Kidston & Lang and provisionally assigned to *Asteroxylon*. Thus,

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Table 1 Details of trenching and drilling at Rhynie

Trench/Borehole	Details
Trench 1A	Close to the position of Tait's No. 1 trench. Opened in 1964 for the International Botanical (Edinburgh) Congress excursion. Trench closed after a suite of samples had been collected for the British Museum (Natural History) [BM (NH)] by Dr John Pettit in 1965. A set of samples studied by W. El-Saadawy; results in a Ph.D. thesis (El-Saadawy 1966).
Trench 2A	Opened in 1963 and 1964 for the Botanical Congress excursion. General lithology recorded by A. G. Lyon with the assistance of a member of the British Geological Survey. Copy of the record given to the Survey. Samples used by El-Saadawy (1966). The top (NE end) of the trench had a short lateral extension. Trench closed in 1965. Samples possibly collected for BM (NH). Re-opened in 1965 with a roadward extension; possible source of white chert.
Trench 3A	Opened in 1965, and re-opened in 1967, 1970 and 1971 with extensions. Lyon supplied information on the bed sequence, and a suite of samples, to A. A. Bhutta, but no published record of the results has been traced.
Trench 4A	Opened and closed in 1970. Recorded by D. S. Edwards. Material in the National Museum of Wales (note in letter by D. S. Edwards to Lyon).
Trench 5A	Opened and closed in ?1971. No records traced.
Trench 8A	Opened in ?1969. Position uncertain, recalled by Lyon as 'a poor exposure yielding chert with only scanty plant remains'.
Trench X	Excavated in 1963 'parallel with the boundary fence and more or less opposite the telephone pole'. (The pole has since been removed). Chert 'extensively brecciated and mostly reduced to a coarse gravel'. Severance of a field drain rapidly flooded the trench, which was then closed.
Boreholes 19a and 19b	Test borings in 1988 with an Aberdeen University Geology Department drill to test for chert, no samples retained.
Borehole 19c	Cored borehole drilled in 1988 by Encore rig hired from Moray Firth Exploration by Aberdeen University. Cored 35·4 m at angle of 49° from the horizontal. Results reported in Powell *et al.* (2000b). Core material at Aberdeen University.
Boreholes 97/2, 97/3, 97/8 and 97/9	Cored boreholes intersecting the Rhynie chert sequence. Results reported in Rice *et al.* (2002) and Trewin & Wilson (2004). Core material at Aberdeen University.
Trench 2003	Excavated for the field excursion of the Rhynie conference held at Aberdeen University in September 2003. Section logged and sampled by Trewin, Fayers and Kelman. The material is the subject of current studies of the Rhynie Research Group at Aberdeen University.

Geoffrey Lyon established the fact that the Rhynie chert would still repay further research effort.

In 1964, the International Botanical Congress was held at Edinburgh, and a Congress excursion visited Rhynie where two trenches (1A and 2A) had been opened close to the positions of Tait's trenches 1 and 2 (as in Horne *et al.* 1916). Details of trenching (Table 1 and Fig. 7) are partly compiled from Geoffrey Lyon's notes; there are some question marks remaining, and the records are possibly incomplete. Trenches were left open for long periods, and a lot of material was removed and now seems to be distributed world-wide. The extended period of trenching started in 1963 (Fig. 8), presumably as a trial for the Congress in 1964, and continued until 1971. Several trenches were reopened and extended at various times, and the records of successions are generally poor. The nature of exposure obtained by trenching in the weathered strata near the surface, where the shales are extensively altered, was not conducive to detailed logging, and little sedimentological information can be gained from the surviving records.

Material from trenches 1A and 2A was studied by El-Saadawy (1966), and that from trench 3A by Bhutta (1969). Later, in 1970, David S. Edwards recorded the contents of trench 4 and also used the superb blocks of chert illustrated by Trewin *et al.* (2003) for his thesis work (Edwards 1973). Thus, three Ph.D. theses were produced from this extended period of investigation by trenching. Lyon also found the hairy axes of the zosterophyll *Trichopherophyton* about this time, but the description was not published until much later in collaboration with Dianne Edwards (Lyon & Edwards 1991). This illustrates a feature common to description of the Rhynie biota – the finding of obviously new but fragmentary material, and delay of publication in the hope that more complete material might be found for description.

The trenching phase of investigation of 1963–1971 provided a large amount of material, and considerable quantities exist in museum stores, much of which is still uncut and unstudied. The problem is that skilled labour and supporting finance is needed to cut the chert and make thin sections, and there is no guarantee of success. Geoffrey Lyon, working first out of Cardiff University and latterly from his home at Rhynie, rekindled interest in the chert and its biota, and made the most valuable individual contribution since the work of Kidston & Lang.

8. Winfried Remy, gametophytes and the Münster Palaeobotanical Laboratory

Geoffrey Lyon kept a visitors book at Rhynie, and he entered visits from the Remy family in 1977, 1979 and 1980. It was probably on the first of these visits that Lyon gave Winfried Remy (Fig. 9) the block of chert that would produce the next Rhynie sensation: the gametophytes. Whilst Lyon had described germinating spores, it was Remy who first described the mature gametophyte generation of any of the plants. Remy had already published on the dehiscence mechanism of *Rhynia* sporangia (Remy 1978), but it was a block of chert given to him by Lyon that produced the gametophytes of the plants (Remy & Remy 1980a, b; Remy 1991; Remy & Hass 1991a, b, c). Hagen Hass was involved in Rhynie chert studies with Remy from the start and continues enthusiastically to cut and examine chert in collaboration with Hans Kerp. The continuation of the Münster work and the seemingly endless succession of finds can be firmly ascribed to the quantity of chert

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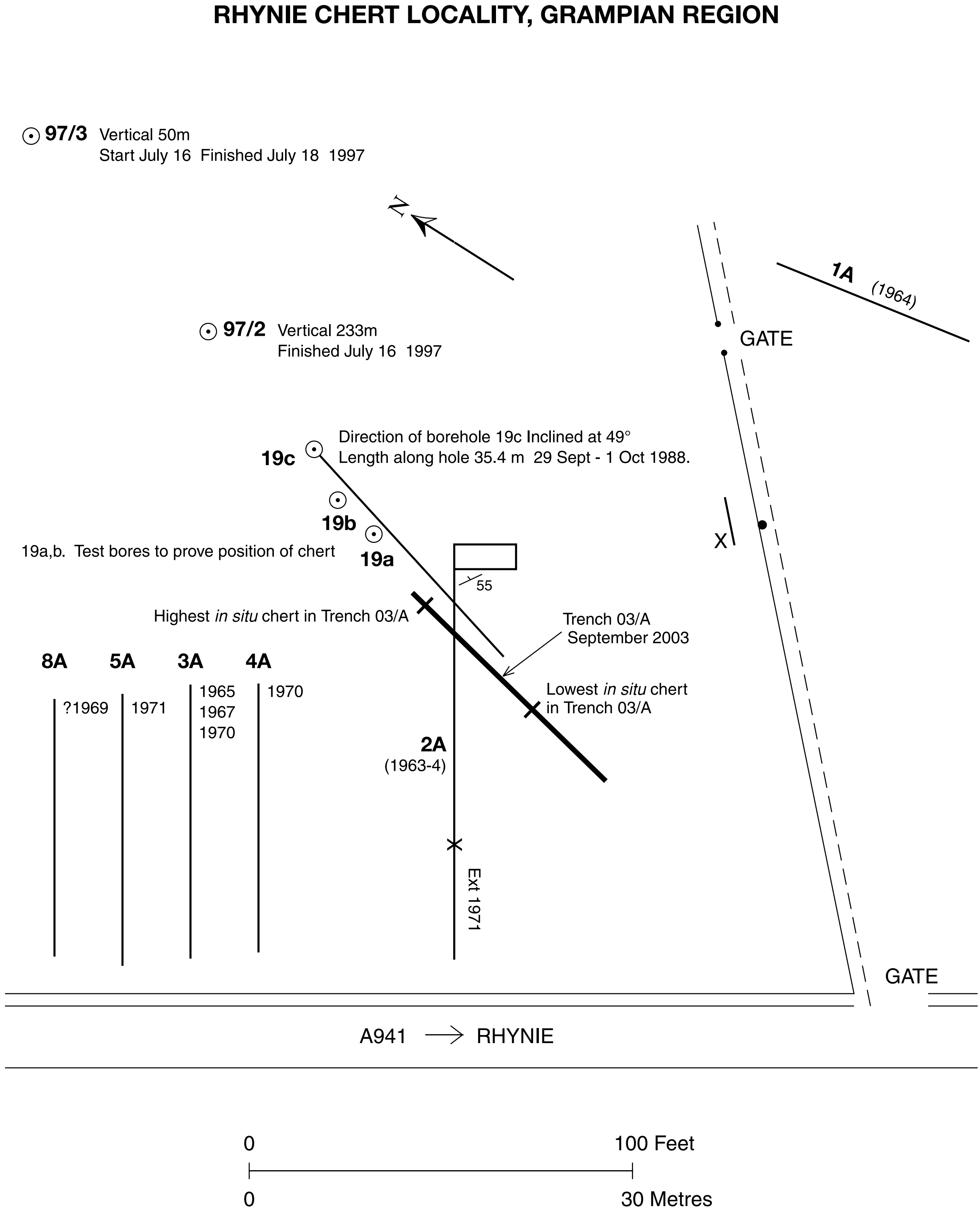

Figure 7 Positions of trenches dug in the period from 1963 to 1971, together with the locations of recent boreholes, and the trench dug in 2003. See Table 1 for details.

examined, combined with years of experience in the study of Rhynie chert sections. A further factor is the use of rock sections rather than surface peels produced by etching of surfaces with hydrofluoric acid. Small, three-dimensional objects are undoubtedly missed when using peels, and good peels can only be produced from a minority of chert blocks. Continuity of research and expertise at Münster has paid excellent dividends.

Studies on fungi led by Tom Taylor in collaboration with the Münster team have advanced knowledge of plant/fungal interaction in the Early Devonian. Particularly significant publications are the description of parasitism by a fungus on *Palaeonitella* (Taylor *et al.* 1992), the recognition of arbuscular mycorrhizal fungi (*Glomites*) in symbiotic relationship with *Aglaophyton* (Taylor *et al.* 1995a), and the oldest known ascomycete fungus within *Asteroxylon* (Taylor *et al.* 1999). The earliest lichen has also been described from the chert (Taylor *et al.* 1995b).

Almost as a by-product of the botanical work at Münster, new animals have been discovered. The latest additions to the

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Figure 8 Trenching at Rhynie 1963. Photo from Lyon archive, Aberdeen University.

Figure 9 Professor Winfried Remy and Renate Remy.

fauna being the harvestman spider described by Dunlop *et al.* (2004), a curious crustacean (Anderson *et al.* 2004), and well-preserved nematode worms which have been discovered in a part-decayed axis of *Aglaophyton*, and await formal description.

Remy was undoubtedly fortunate in the content of the chert samples he was given by Geoffrey Lyon, but it was the persistence of his observation that resulted in the finding and description of the gametophytes. Winfried Remy died on 31 December 1995, having contributed an important chapter to Rhynie research, and valuable contributions continue from Hans Kerp and Hagen Hass at the Münster laboratory as evidenced in this volume.

9. Alternatives to a hot spring model

Mackie (1913) first advocated the hydrothermal action of hot springs and geysers in the waning phase of local volcanicity as the origin of the cherty rocks at Rhynie, citing evidence from his own observations. This line was adopted by Kidston & Lang and thereafter repeated, without the presentation of any additional field or petrographic evidence.

The experiments of Leo & Barghoorn (1976) on preferential silification of wood led to the conclusion that petrifaction is caused by low pH produced by plant degradation, followed by siliceous nucleation around the organic material and precipitation of polymerised silicic acid. Knoll (1985) took the model of Leo & Barghoorn and applied it to silicified plants, including the Rhynie chert.

Parnell (1983) noted similarities in textures within the Rhynie chert to those seen in silcrete from the Middle ORS of Orkney, suggesting that the floating textures seen in the Rhynie chert were a result of replacement of pre-existing sediment. Thus, whilst it was acknowledged that the silica was commonly regarded to be of 'volcanic origin', there was a possibility that weathering processes were involved.

Thus, during the 1980s, tentative suggestions were being advanced questioning the origins of the Rhynie chert as silicified sinters originally deposited from hot springs. The time had arrived for a reappraisal of the geological evidence to be found in the Rhynie area.

10. The Aberdeen-based Rhynie project

Research interest in Rhynie began at Aberdeen University in 1987 when Clive Rice returned from fieldwork in Nevada, USA, bearing a blue-grey chert containing silicified plants which looked similar to the Rhynie chert. The Nevada chert was from the surface expression of a gold-bearing hydrothermal system. Analyses of the Rhynie chert and silicified rocks in the fault zone showed enrichment in arsenic, antimony and gold, and demonstrated that the cherts were the surface features of a precious metal-bearing hydrothermal system, and that the silicification in the area was of hydrothermal origin (Rice & Trewin 1988).

This observation resulted in interest from a mineral exploration company (Moray Firth Exploration) and the drilling of seven cored boreholes within 100 m of the Rhynie chert locality to investigate the hydrothermally altered rocks of the basin-bounding fault zone. These boreholes provided valuable information on stratigraphy and structure, but none intersected the Rhynie chert. Aberdeen University Geology Department then hired the rig and drilled a 35 m hole that produced the first cored sections of the cherts, and importantly, showed the interbedded lithologies (Trewin & Rice 1992; Powell *et al.* 2000a). This borehole (19c) was drilled at 49° to give an intersection normal to bedding, and was located close to Trench 2A (Fig. 7). It became apparent that the stratigraphy and structure were more complex than previously imagined, and that there was potential for a multidisciplinary study on the structure of the basin, palaeoenvironments, mineralisation and age of the deposit. These studies, funded mainly by the National Environment Research Council (NERC), resulted in the geological interpretations of Rice *et al.* (1995) and a Ph.D. by Powell (1994) on the contents of the cherts intersected in borehole 19c, the details of the floral succession and associations being published by Powell *et al.* (2000a). Further surface exploration was carried out using a mechanical digger and a small drilling rig to test to top of bedrock. The results obtained necessitated the reinterpretation of the geological maps of the area (BGS 1993: Rice *et al.* 1995, 2002). This process of refinement of the mapped geology continues to the present day, and constantly provides surprises. The most recent interpretation of the northern part of the outlier is given by Rice & Ashcroft (2004), who assigned a strike-slip control to the faulting in the area.

During surface exploration, a concentration of fossiliferous chert was located at Windyfield some 600 m from the main outcrop of the Rhynie cherts. This chert, now termed the Windyfield chert, yielded the new zosterophyll plant *Ventarura* (Powell *et al.* 2000b) and a number of new arthropods

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Figure 10 Drilling in the Rhynie chert Site of Special Scientific Interest at Rhynie in 1997. View looking east from the top of the upper field with Rhynie in the background. In this view, the area of trenching shown in Fig. 7 is in the far righthand corner of the field with the drilling rig.

(Anderson & Trewin 2003). Further work by Fayers (2003) has resulted in new finds of arthropods and demonstrated that the biota is similar to that of the Rhynie chert (Fayers & Trewin 2004). At Windyfield, a block of chert has been found showing the typical botryoidal splash texture of a geyser rim (Trewin 1994), and textures in both the Rhynie and Windyfield cherts are closely comparable to those of modern sinters from Yellowstone National Park, Wyoming, USA, and New Zealand (Trewin 1996; Trewin *et al.* 2003).

Following the success of the first drilling programme, a second phase of drilling was planned with the aims of: (1) determining the full thickness and nature of the chert-bearing sequence (Rhynie chert); (2) coring the sequence at the Rhynie site down to basement as predicted by geophysics; and (3) determining the succession in the Windyfield area and its relationship to the Rhynie site.

With funding mainly from the Carnegie Trust, SNH and Aberdeen University, a drilling programme was executed in 1997 (Fig. 10) with some predicted and some surprising results (Rice *et al.* 2002). Drilling to basement at the Rhynie chert site (borehole 97/2; Fig. 7) proved a succession truncated at 210 m vertical depth by a low-angle fault that contained a cherty breccia, which had acted as a conduit for hot hydrothermal fluids (Rice *et al.* 2002). A thick (+50 m) sequence of silicified tuffs was located near Longcroft Farm (the Longcroft Tuffs), and the Windyfield chert was shown to occur as pods of chert in hydrothermally altered shales.

Although 600 m of hole had been drilled in the 1997 exploration phase, there were still problems with interpretation. This was largely because of the faulted nature of the area and the tendency for boreholes to terminate at fault zones where the drilling bit became stuck in fault gouge. Further information was obtained by digging test pits with an excavator, and Lyall Anderson logged and curated the cores, and continued work on arthropods from the Windyfield chert.

Geoffrey Lyon had taken interest, in his quiet way, in the wider geological investigations as well as in palaeontological finds such as *Ventarura*. However, his health was failing in 1997, and he moved to a nursing home in Aberdeen, where he died in 1999. He left a generous bequest to Aberdeen University to continue work on the geology and palaeontology of the Rhynie area. Thus, the Rhynie Research Project has provided funding for five Ph.D. students (C. L. Powell, S. R. Fayers, S. F. Parry, R. Kelman and J. A. Haddow), and investigations at Aberdeen continue into palaeontology and depositional environments; comparisons with active thermal areas in Yellowstone National Park and New Zealand; the role of bacteria in concentration of heavy metals; and the Caledonian igneous history of the Rhynie area.

11. Interpretations of the Rhynie biota

Following the initial descriptions of the plants and arthropods, mostly prior to 1930, many authors have discussed the biota in the context of palaeoecology, the development of life on land and the palaeoenvironment. This process was started by Kidston & Lang (1921b), who noted the influence of hot springs and compared the deposits to a silicified peat deposited in a sufficiently wet environment to support the aquatic elements of the biota. Tasch (1957) produced a palaeoecological evaluation based entirely on published data. Whilst some of his ideas have to be discarded in the light of new evidence, he undoubtedly stimulated discussion. Contributions by Kevan *et al.* (1975) and Rolfe (1980) provided more detailed evaluations, notably on the arthropod palaeoecology. The description of trigonotarbids preserved inside plant sporangia, as also are mites, inspired interpretations of arthropod–plant ecological relationships.

The Rhynie flora is considered in reviews of terrestrial plant development (e.g. Edwards 1980, 2001), but it is increasingly apparent that terrestrial floras have a long history prior to the Early Devonian. Interpretations of the ecological requirements of the individual Rhynie plants, and the plant associations in the chert, continue to advance as more evidence becomes available from studies of *in situ* material (Powell *et al.* 2000a). The Rhynie biota is also pertinent to general discussions relating to colonisation of the land and early terrestrial ecosystems (Selden & Edwards 1989; Edwards & Selden 1993).

Sedimentological features seen in cores from the Rhynie chert, together with evidence from modern hot-spring areas have constrained interpretations of the environments inhabited by the Rhynie biota (Trewin *et al.* 2003; Trewin & Wilson 2004), showing that the biota at Rhynie was preserved in sinters deposited on a low angle outwash apron from a hot spring system. In the Windyfield chert, the biota is more strongly associated with pools in close proximity to vents (Fayers & Trewin 2004).

12. Rhynie chert for the general public

The lack of any exposure of the Rhynie chert is a disadvantage for scientific interpretation of the site for the benefit of the general public. There is little inspiration to be gained from a green field. Current museum displays, as in the Royal Museum of the National Museums of Scotland in Edinburgh, and at Elgin Museum, provide valuable remote resources. The excellent booklet by Chaloner & Macdonald (1980) was produced to accompany displays in the Royal Museum (then the Royal Scottish Museum) for which models of the sporangia of Rhynie plants were produced. At Rhynie, there is an exhibit in Rhynie School that was opened in May 1995, and accompanied by a brief leaflet outlining the nature of the ancient environment, and the fossil flora and fauna. The exhibit is of an elementary nature, suited to its location. However, most visitors to Rhynie are probably unaware of the exhibit, and the location in a school poses difficulty for access. Models of the Rhynie plants and some arthropods have been made by Stephen Caine for the Rhynie Research Group at Aberdeen University, and have been used in the Royal Society Summer Science Exhibition in London in 2004.

In scientific literature, such as textbooks of geology and biology, and science encyclopaedias, Rhynie normally gains a brief mention. The biota also features in books relating to

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exceptional fossil preservation (Remy *et al.* 1999; Trewin 2001). There has also been press and television coverage generally coinciding with drilling programmes, and a brief mention in *National Geographic* magazine (Westenberg 1999). There are numerous references to Rhynie on the World Wide Web, with major illustrated websites hosted at Münster and Aberdeen universities.

13. Conclusions

There are now more people active in Rhynie-related research than at any other time, and these individuals cover a wide range of disciplines. However, as more is discovered (e.g. by drilling), more questions arise which invite further investigation. It has taken a long time, but between all the currently active researchers, we are now, it is to be hoped, fulfilling the comment of Kidston & Lang (1917, p. 763): 'It is not our sphere to treat of the detailed geology of the Rhynie area; that will be done by other and more competent writers.'

The poorly exposed nature of the rocks of the Rhynie area has been the main hindrance to progress, leading to the persistence of the simple half-graben interpretation from the time of Geikie until the last few years. Application of field geophysics, drilling and excavation has provided new insights into the geological history of the area.

On the palaeontological side, it has become apparent that to find anything 'new' in the chert requires considerable background knowledge of plant and arthropod anatomy, a great deal of application, and a modicum of luck. Whilst some elements of the Rhynie biota are common, many have only been found in single blocks of chert (e.g. *Castracollis* Fayers & Trewin 2003), or are known from very few examples. Nevertheless, effort has been rewarded, and the Rhynie and Windyfield cherts now boast the most diverse Early Devonian terrestrial/freshwater assemblage on earth, and most significantly, they represent an ecosystem preserved *in situ*, rather than an assemblage of transported material.

We can now interpret the environment with greater confidence through comparisons with modern hot spring areas (Trewin *et al.* 2003; Campbell *et al.* 2004; Channing & Edwards 2004; Trewin & Wilson 2004). Far from earlier ideas that the plants and animals we find as fossils were engulfed and killed in boiling water (e.g. Chaloner & Macdonald 1980), we now know that plant preservation took place where the plants were growing, and that silicification took place at temperatures generally less then 35°C. We can also trace the diagenetic changes from sinter to chert (Herdianita *et al.* 2000), and match modern sinter textures with those found in the chert.

It is clear that further progress can be made on our understanding of this early terrestrial/freshwater ecosystem, but that continuity of research groups, collaboration between them and funding are the keys to success. Successful trenching in September 2003 in the area of trench 2A (Fig. 7) has provided new material from several chert beds that is being used in a study of the palaeoecology of this fascinating deposit.

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15. References

Anderson, L. I., Crighton, W. R. B. & Hass H. 2004. A new univalve crustacean from the Early Devonian Rhynie chert hot-spring complex. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 355–69.

Anderson, L. I. & Trewin, N. H. 2003. An Early Devonian arthropod fauna from the Windyfield chert, Aberdeenshire, Scotland. *Palaeontology* **46,** 467–509.

Andrews, H. N. 1980. *The Fossil Hunters, in Search of Ancient Plants*. Ithaca, NY: Cornell University Press.

Andrews, S. M. 1982. *The Discovery of Fossil Fishes in Scotland up to 1845, with Checklists of Agassiz's Figured Specimens*. Edinburgh: Royal Scottish Museum.

Barghoorn, E. S. & Darrah, W. C. 1938. *Horneophyton* a necessary change of name for *Hornea*. *Harvard University Botanical Museum Leaflets* **6**, 142–4.

Bhutta, A. A. 1969. *Studies on the flora of the Rhynie chert*. Unpublished Ph.D. thesis. Cardiff: University College of South Wales.

Boney, A. D. 1994. David Thomas Gwynne-Vaughan, 1871–1915. *The Linnean* **10**, 27–57.

Boué, A. 1820. *Essai géologique sur l'Écosse*. Paris: V. Courcier.

British Geological Survey (BGS). 1993. *Alford, Scotland. Sheet 76W. 1:50 000*. Keyworth: British Geological Survey.

Campbell, K. A., Buddle, T. F. & Browne, P. R. L. 2004. Late Pleistocene silica sinter associated with fluvial, lacustrine, volcaniclastic and landslide deposits at Tahunaatara, Taupo Volcanic Zone, New Zealand. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 485–501.

Campbell, R. 1932. William Mackie, M.A., M.D., LL.D., Physician and Geologist. *Transactions of the Edinburgh Geological Society* **13**, 106–9.

Carroll, S. 1991. *Terrestrial, fluvial and marginal lacustrine ecosystems of the Old Red sandstone of the Orcadian Basin*. Unpublished Ph.D. thesis, University of Aberdeen.

Chaloner, W. G. & Macdonald, P. 1980. *Plants Invade the Land*. Edinburgh: HMSO, The Royal Scottish Museum.

Channing, A. & Edwards, D. 2004. Experimental taphonomy: silicification of plants in Yellowstone hot spring environments. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 503–21.

Claridge, M. F. & Lyon, A. G. 1961. Lung-books in the Devonian Palaeocharinidae (Arachnida). *Nature* **191**, 1190–1.

Cleal, C. J. & Thomas, B. A. 1995. *Palaeozoic Palaeobotany of Great Britain*. Geological Conservation Review Series, **9**. London: Chapman and Hall.

Cordiner, C. 1780. *Antiquities and Scenery of the North of Scotland in a Series of Letters to Thomas Pennant*. London.

Croft, W. N. & George, E. A. 1959. Blue-green algae from the Middle Devonian of Rhynie, Aberdeenshire. *Bulletin of the British Museum (Natural History), Geology* **3** (10), 341–53.

Crowson, R. A. 1970. *Classification and Biology*. London: Heinemann.

Dubinin, V. B. 1962. Class Acaromorpha: mites or gnathosomic chelicerate arthropods. *In* Rodendorf, B. B. (ed.) *Fundamentals of Palaeontology*, 447–73. Moscow: Academy of Science.

Dunlop, J. A. 1994. *Palaeobiology of the trigonotarbid arachnids*. Unpublished Ph.D. thesis, University of Manchester.

Dunlop, J. A., Anderson, L. I., Kerp, H. & Hass, H. 2004. A harvestman (Arachnida: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 341–54.

Edwards, D. 1980. Early land floras. *In* Panchen, A. (ed.) *The Terrestrial Environment and the Origin of Land Vertebrates*, 55–8. London: Academic Press.

Edwards, D. 1984. Robert Kidston, this most professional palaeobotanist. A tribute on the 60th anniversary of his death. *Forth Naturalist and Historian* **8**, 65–93.

Edwards, D. 2001. Early land plants. *In* Briggs, D. E. G. & Crowther, P. C. (eds) *Palaeobiology II*, 63–6. Oxford: Blackwell.

Edwards, D. 2004. Embryophytic sporophytes in the Rhynie and Windyfield cherts. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 397–410.

Edwards, D. & Selden, P. A. 1993. The development of early terrestrial ecosystems. *Botanical Journal of Scotland* **46**, 337–66.

Edwards, D. S. 1973. *Studies on the flora of the Rhynie chert*. Unpublished Ph.D. thesis. Cardiff: University College of South Wales.

Edwards, D. S. 1986. *Aglaophyton major*, a non-vascular land plant from the Devonian Rhynie Chert. *Botanical Journal of the Linnean Society* **93**, 173–206.

El-Saadawy, W. El-S. 1966. *Studies in the flora of the Rhynie chert*. Unpublished Ph.D. thesis. Bangor: University College of North Wales.

Engel, M. S. & Grimaldi, D. A. 2004. New light shed on the oldest insect. *Nature* **427**, 627–30.

Fayers, S. R. 2003. *The biota and palaeoenvironments of the Windyfield chert*. Unpublished Ph.D. thesis, University of Aberdeen.

Fayers, S. R. & Trewin, N. H. 2003. A new crustacean from the Early Devonian Rhynie chert, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **93** (for 2002), 355–82.

Fayers, S. R. & Trewin N. H. 2004 A review of the palaeoenvironments and biota of the Windyfield chert. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 325–39.

Geikie, A. 1879. On the Old Red Sandstone of Western Europe. *Transactions of the Royal Society of Edinburgh* **28**, 345–452.

Herdianita, N. R., Browne, P. R. L., Rodgers, K. A. & Campbell, K. A. 2000. Mineralogical and textural changes accompanying ageing of silica sinter. *Mineralium Deposita* **35**, 48–62.

Hirst, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie chert Bed, Aberdeenshire). *Annals and Magazine of Natural History* (Series 9) **12**, 455–74.

Hirst, S. & Maulik, S. 1926. On some arthropod remains from the Rhynie chert (Old Red Sandstone). *Geological Magazine* **63**, 69–71.

Horne, J., Mackie, W., Flett, J. S., Gordon, W. T., Hickling, G., Kidston, R., Peach, B. N. & Watson, M. S. 1916. The plant-bearing cherts at Rhynie, Aberdeenshire. *In* Report of the Eighty-Sixth Meeting of the British Association for the Advancement of Science, 206–16. London: John Murray.

Kerp, H., Trewin, N. H. & Hass, H. 2004. New gametophytes from the Early Devonian Rhynie chert. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 411–28.

Kevan, P. G., Chaloner, W. G. & Saville, D. B. O. 1975. Interrelationships of early terrestrial arthropods and plants. *Palaeontology* **18**, 391–417.

Kidston, R. & Lang, W. H. 1917. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part I. *Rhynia Gwynne-Vaughani* Kidston & Lang. *Transactions of the Royal Society of Edinburgh* **51** (24), 761–84.

Kidston, R. & Lang, W. H. 1920a. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part II. Additional notes on *Rhynia Gwynne-Vaughani* Kidston and Lang; with descriptions of *Rhynia major*, n.sp., and *Hornea Lignieri*, n.g., n.sp. *Transactions of the Royal Society of Edinburgh* **52** (24), 603–27.

Kidston, R. & Lang, W. H. 1920b. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part III. *Asteroxylon Mackiei*, Kidston and Lang. *Transactions of the Royal Society of Edinburgh* **52** (26), 643–80.

Kidston, R. & Lang, W. H. 1921a. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part IV. Restorations of the vascular cryptogams, and discussion of their on the general morphology of the pteridophyta and the origin of the organisation of land-plants. *Transactions of the Royal Society of Edinburgh* **52** (32), 831–54.

Kidston, R. & Lang, W. H. 1921b. On Old Red Sandstone plants showing structure, from the Rhynie Chert bed, Aberdeenshire. Part V. The Thallophyta occurring in the peat-bed; the succession of the plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. *Transactions of the Royal Society of Edinburgh* **52** (33), 855–902.

Knoll, A. H. 1985. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Philosophical Transactions of the Royal Society of London* **311**, 111–22.

Lang, W. H. 1925. Robert Kidston 1852–1924. Obituary notices of Fellows Deceased. *Proceedings of the Royal Society B* **98**, xiv–xxii.

Leo, R. F. & Barghoorn, E. S. 1976. Silicification of wood. *Harvard University Botanical Museum Leaflets* **25**, 1–47.

Liston, J. J. & Sanders, H. L. 2004. The 'other' Glasgow boys: the rise and fall of a school of palaeobotany. *In* Wilding, R., Burek, C. & Bowden, A. (eds) *On the History of Palaeobotany*. London: The Geological Society.

Lyon, A. G. 1957. Germinating spores in the Rhynie chert. *Nature* **180**, 1219.

Lyon, A. G. 1962. On the fragmentary remains of an organism referable to the nematophytales, from the Rhynie chert, '*Nematoplexus rhyniensis*' gen. et. sp. nov. *Transactions of the Royal Society of Edinburgh* **65** (4), 79–87.

Lyon, A. G. 1964. Probable fertile region of *Asteroxylon mackiei* K. and L. *Nature* **203**, 1082–3.

Lyon, A. G. undated ms. *The Rhynie Free Church and its Manse; a Brief History*. Aberdeen: Lyon Archive, Aberdeen University.

Lyon, A. G. 1987. The Rhynie Chert. *The Deeside Field* **19**, 140–4.

Lyon, A. G. & Edwards, D. 1991. The first zosterophyll from the Lower Devonian Rhynie chert, Aberdeenshire. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **82**, 323–32.

Macculloch, J. 1840. *A Geological Map of Scotland*. London: G. F. Crutchley.

Mackay, A. 1861. *Manual of Modern Geography; Mathematical, Physical and Political*. Edinburgh: W. Blackwood & Sons.

Mackie, W. 1913. The rock series of Craigbeg and Ord Hill, Rhynie, Aberdeenshire. *Transactions of the Edinburgh Geological Society* **10**, 205–36.

Malcolmson, J. G. 1859. On the relations of the different parts of the Old Red Sandstone in which organic remains have recently been discovered in the counties of Moray, Nairn, Banff and Inverness. *Quarterly Journal of the Geological Society, London* **15**, 336–52.

Miller, H. 1857. *The Testimony of the Rocks*. Edinburgh: Constable & Co.

Murchison, R. I. 1859. On the sandstones of Morayshire (Elgin etc.) containing reptilian remains; and their relations to the Old Red Sandstone of that country. *Quarterly Journal of the Geological Society, London* **15**, 419–39.

Newlands, G. 1913. Note on a fossil plant from the Old Red Sandstone, Rhynie, Aberdeenshire. *Transactions of the Edinburgh Geological Society* **10**, 237.

Parnell, J. 1983. Ancient duricrusts and related rocks in perspective: a contribution from the Old Red Sandstone. *In* Wilson, R. C. L. (ed.) *Residual Deposits: Surface Related Weathering Processes and Materials*, 197–209. Special Publication **11**. London: Geological Society London.

Powell, C. L. 1994. The palaeoenvironments of the Rhynie cherts. Unpublished Ph.D. thesis, University of Aberdeen.

Powell, C. L., Trewin, N. H. & Edwards, D. 2000a. Palaeoecology and plant succession in a borehole through the Rhynie cherts, Lower Old Red Sandstone, Scotland. *In* Friend, P. F. & Williams, B. P. J. (eds) *New Perspectives on the Old Red Sandstone*, 439–57. Special Publication **180**. London: Geological Society London.

Powell, C. L., Edwards, D. & Trewin, N. H. 2000b. A new vascular plant from the Lower Devonian Windyfield chert, Rhynie, NE Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **90** (4) (for 1999), 331–49.

Read, H. H. 1923. *The Geology of the Country Around Banff, Huntly and Turriff (Sheets 86 and 96)*. Memoir of the Geological Survey, Scotland.

Remy, W. 1978. Der Dehiszenzmechanismus der Sporangien von *Rhynia*. *Argumenta Palaeobotanica* **5**, 23–30.

Remy, W. 1991. Forebears of the terrestrial plants. *German Research* **3/82**, 12–13.

Remy, W., Selden, P. A. & Trewin, N. H. 1999. Gli strati di Rhynie. *In* Pinna, G. (ed.) *Storia Naturale D'Europa*, 28–35. Milan: Associazione Paleontologica Europea. Jaca Book.

Remy, W. & Hass, H. 1991a. Ergänzende Beobachtungen an *Lyonophyton rhyniensis*. *Argumenta Palaeobotanica* **8**, 1–27.

Remy, W. & Hass, H. 1991b. *Kidstonophyton discoides* nov. gen. nov. spec., ein Gametophyt aus dem Chert von Rhynie (Unterdevon, Schottland). *Argumenta Palaeobotanica* **8**, 29–45.

Remy, W. & Hass, H. 1991c. *Langiophyton mackiei* nov. gen., nov. spec., ein Gametophyt mit Archegoniophoren aus dem Chert von Rhynie (Unterdevon Schottland). *Argumenta Palaeobotanica* **8**, 69–117.

Remy, W. & Remy, R. 1980a. Devonian gametophytes with anatomically preserved gametangia. *Science* **208**, 295–6.

Remy, W. & Remy, R. 1980b. *Lyonophyton rhyniensis* n. gen. et nov. spec., ein Gametophyt aus dem Chert von Rhynie (Unterdevon, Schottland). *Argumenta Palaeobotanica* **6**, 37–72.

Rice, C. M., Ashcroft, W. A., Batten, D. J., Boyce, A. J., Caulfield, J. B. D., Fallick, A. E., Hole, M. J., Jones, E., Pearson, M. J., Rogers, G., Saxton, J. M., Stuart, F. M., Trewin, N. H. & Turner, G. 1995. A Devonian auriferous hot spring system, Rhynie, Scotland. *Journal of the Geological Society, London* **152**, 229–50.

Rice, C. M., Trewin, N. H. & Anderson, L. I. 2002. Geological setting of the Early Devonian Rhynie cherts, Aberdeenshire, Scotland: an early terrestrial hot spring system. *Journal of the Geological Society, London* **159**, 203–14.

Rice, C. M. & Ashcroft, W. A. 2004. The geology of the northern half of the Rhynie Basin, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003), 299–308.

Rice, C. M. & Trewin, N. H. 1988. A Lower Devonian gold-bearing hot-spring system, Rhynie, Scotland. *Transactions of the Institute of Mineralogy and Metallurgy* **97**, B141–4.

Rolfe, W. D. I. 1980. Early invertebrate terrestrial faunas. *In* Panchen, A. L. (ed.) *The Terrestrial Environment and the Origin of Land Vertebrates*, 117–57. London: Academic Press.
Salisbury, E. J. 1961. William Henry Lang 1874–1960. *Biographical Memoirs of Fellows of the Royal Society* **7**, 147–60.
Scott, D. H. 1916. David Thomas Gwynne-Vaughan. *Annals of Botany* **30**, i–xxiv.
Scott, D. H. 1920. *Studies in Fossil Botany*, 3rd edn. London: A & C Black.
Scourfield, D. J. 1926. On a new type of crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire) – *Lepidocaris rhyniensis* gen. et sp. nov. *Philosophical Transactions of the Royal Society of London* **214**, 153–87.
Scourfield, D. J. 1940. Two new and nearly complete specimens of young stages of the Devonian fossil crustacean *Lepidocaris rhyniensis*. *Proceedings of the Linnean Society* **152**, 290–8.
Selden, P. A., Shear, W. A. & Bonamo P. M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Aranae. *Palaeontology* **34**, 241–281.
Selden, P. A. & Edwards, D. 1989. Colonisation of the land. *In* Allen, K. C. & Briggs, D. E. G. (eds) *Evolution and the Fossil Record*, 122–52. London: Belhaven Press.
Seward, A. C. 1931. *Plant Life Through the Ages*. Cambridge: Cambridge University Press.
Shear, W. A., Selden, P. A., Rolfe, W. D. I., Bonamo, P. M. & Grierson, J. D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *Novitates* **2901**, 1–74.
Tasch, P. 1957. Flora and fauna of the Rhynie chert; a paleoecological reevaluation of published evidence. *University of Wichita Bulletin* **36**, 1–24.
Taylor, T. N., Hass, H. & Remy, W. 1992. Devonian fungi: interactions with the green alga *Palaeonitella*. *Mycologia* **84**, 901–10.
Taylor, T. N., Remy, W., Hass, H. & Kerp, H. 1995a. Fossil arbuscular mycorrhizae from the Early Devonian. *Mycologia* **87**, 560–73.
Taylor, T. N., Hass, H., Remy, W. & Kerp, H. 1995b. The oldest fossil lichen. *Nature* **378**, 244.
Taylor, T. N., Hass, H. & Kerp, H. 1999. The oldest fossil ascomycetes. *Nature* **399**, 648.
Trewin, N. H. 1994. Depositional environment and preservation of biota in the Lower Devonian hot-springs of Rhynie, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84** (for 1993), 433–42.
Trewin, N. H. 1996. The Rhynie cherts: an early Devonian ecosystem preserved by hydrothermal activity. *In* Bock, G. R. and Goode, J. A. (eds) *Evolution of Hydrothermal Ecosystems on Earth (and Mars?)*, 131–49. Chichester: John Wiley & Sons.
Trewin, N. H. 2001. The Rhynie chert. *In* Briggs, D. E. G. & Crowther, P. C. (eds) *Palaeobiology II*, 342–6. Oxford: Blackwell.
Trewin, N. H., Fayers, S. R. & Kelman, R. 2003. Subaqueous silicification of the contents of small ponds in an Early Devonian hot spring complex, Rhynie, Scotland. *Canadian Journal of Earth Sciences* **40**, 1697–1712.
Trewin, N. H. & Rice, C. M. 1992. Stratigraphy and sedimentology of the Devonian Rhynie chert locality. *Scottish Journal of Geology* **28**, 37–47.
Trewin, N. H. & Thirlwall, M. F. 2002. Old Red Sandstone. *In* Trewin, N. H. (ed.) *The Geology of Scotland*, 4th edn, 213–49. London: The Geological Society.
Trewin, N. H. & Wilson, E. 2004. Correlation of the Early Devonian Rhynie chert beds between three boreholes at Rhynie, Aberdeenshire. *Scottish Journal of Geology* **40**, 73–81.
Westenberg, K. 1999. From fins to feet. *National Geographic* **195** (5), 114–27.
Westoll, T. S. 1951. The vertebrate-bearing strata of Scotland. *In* Swinton, W. E. (ed.) *The Correlation of Continental Vertebrate-bearing Rocks. Proceedings of the International Geological Congress, London 1948*, **11**, 5–21.
Whalley, P. & Jarzembowski, E. A. 1981. A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature* **291**, 317.
Wilson, G. J. S. & Hinxman, L. W. 1890. *Explanation of Sheet 76, Central Aberdeenshire*. *Memoir of the Geological Survey, Scotland.*

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