

New gametophytes from the Early Devonian Rhynie chert

Hans Kerp, Nigel H. Trewin and Hagen Hass

ABSTRACT: Several new gametophytes are described from the Early Devonian Rhynie chert. The new monotypic genus *Remyophyton*, being the gametophyte of *Rhynia*, is represented by a dense stand of *in situ* preserved gametophytes with antheridia- and archegonia-bearing axes. The gametophytes are remarkably small in comparison to those of other Rhynie chert plants. The generic diagnoses of *Lyonophyton* and *Langiophyton* are emended to include archegonia- and antheridia-bearing axes. All essential stages of the reproductive cycle, i.e. sporophytes, and male and female gametophytes, can now be demonstrated for three of the six land plants from the Rhynie chert, i.e. *Rhynia gwynne-vaughanii*, *Aglaophyton major* and *Horneophyton lignieri*.

KEY WORDS: Devonian, *Lyonophyton*, *Langiophyton*, ontogeny, *Remyophyton*, *Rhynia*.



The Rhynie chert has become famous as the oldest *in situ* fossilised early terrestrial ecosystem (e.g. Remy *et al.* 2000). Because of the excellent preservation of the material, this locality has yielded a wealth of information on early life on land. Six species of early land plants have been described from the chert, most of them in great detail.

Alternation of generations is the phenomenon of the alternation of a multicellular haploid gametophyte and a multicellular diploid sporophyte phase in the life cycle of plants. This life cycle and its universal occurrence in land plants was first recognised by Hofmeister (1851). Ever since Hofmeister's discovery was published in English (Hofmeister 1862), the morphology and development of these two phases have played a fundamental role in systematic botany. Moreover, the evolution of the life cycle has long been considered to be crucial in the transition from an aquatic to a terrestrial life habit in the earliest land plants (e.g. Čelakovský 1874; Bower 1908, 1935; Fritsch 1945). However, current ideas on the evolution of alternation of generations are almost exclusively based on life cycles in extant groups. Because of the very delicate nature of modern pteridophyte gametophytes, the preservation potential of fossil gametophytes is extremely low. Moreover, only anatomically preserved material may show details such as the organization of the antheridia and archegonia, thus proving the gametophytic nature of the fossils. Given the exceptional preservation of plants in the Rhynie chert, it is not surprising that several palaeobotanists began to search for gametophytes. Over the years, several authors claimed to have found gametophytes in the Rhynie chert (e.g. Merker 1958, 1959; Pant 1962; Lemoigne 1967, 1968a, b, 1969a, b, c, 1971, 1975, 1981). However, all the material described by these authors appears to be of sporophytic plants, as is shown in the present paper. Until 1980, the only unequivocal evidence for the presence of fossil gametophytes in the Rhynie chert was restricted to the occurrence of germinating spores of *Aglaophyton major* (Kidston & Lang 1917) Edwards 1986 and *Horneophyton lignieri* (Kidston & Lang 1920) Barghoorn & Darrah 1938, described by Lyon (1957) and Bhutta (1973a, b).

Remy & Remy (1980a, b) described the first anatomically preserved gametophyte with antheridiophores as *Lyonophyton rhyniensis*; this is the gametophyte of *A. major*. Additional information on this taxon was published by Remy & Hass (1991a, 1996). Other antheridiophores were described as *Kidstonophyton discoides* (Remy & Hass 1991b) and considered

to be the gametophyte of *Nothia aphylla* (Kidston & Lang 1920) El Saadawy & Lacey 1979. A third gametophyte with archegoniophores, belonging to *H. lignieri*, was described as *Langiophyton mackiei* (Remy & Hass 1991c). A review of the permineralised Rhynie chert gametophytes, and the gametophytes preserved as compressions and impressions from the Lower Devonian of the Rhenish Slate Mountains (Germany) and Gaspé Bay (Quebec, Canada) was published by Remy *et al.* (1993).

In this contribution, the authors present the formal descriptions of some new types of gametophytes from the Rhynie chert. The diagnosis of *Lyonophyton rhyniensis* is emended to include the newly discovered archegoniophore-bearing axes of *Lyonophyton*. The diagnosis of *L. mackiei* is emended to include antheridiophore-bearing axes. These were mentioned by Remy & Hass (1991c), but never described and figured. Detailed investigations of a series of thin sections of material illustrated as a plant colony growing on a laminated sinter bed (Powell *et al.* 2000, fig. 5) have revealed that this is an *in situ* gametophyte stand of *Rhynia gwynne-vaughanii* Kidston & Lang 1917, consisting of at least 69 antheridiophores and 27 archegoniophores. Following the procedure adopted by Remy and co-workers formally to name gametophytes, this gametophyte is here described as *Remyophyton delicatum*.

The life cycles of three Rhynie chert plants, *A. major*, *R. gwynne-vaughanii* and *H. lignieri*, can now be reconstructed in great detail because both the archegoniophores and antheridiophores are known, and also because several stages of germination are represented. Moreover, *Remyophyton* is the first mature fossil gametophyte of which the complete growth habit is known since it is found as a mature *in situ* stand. The newly discovered gametophytes are compared with the previously described Rhynie chert gametophytes.

1. Geological setting and locality

The Rhynie cherts occur in the northern part of the Rhynie outlier of Lower Old Red Sandstone in Aberdeenshire, Scotland, within a sequence of sedimentary and volcanic rocks, and represent the surface manifestation of one of the earliest known subaerial hot spring systems (Rice *et al.* 1995, 2002). The cherts occur in the upper part of the Dryden Flags Formation in the so-called Rhynie Block (Rice *et al.* 2002) and

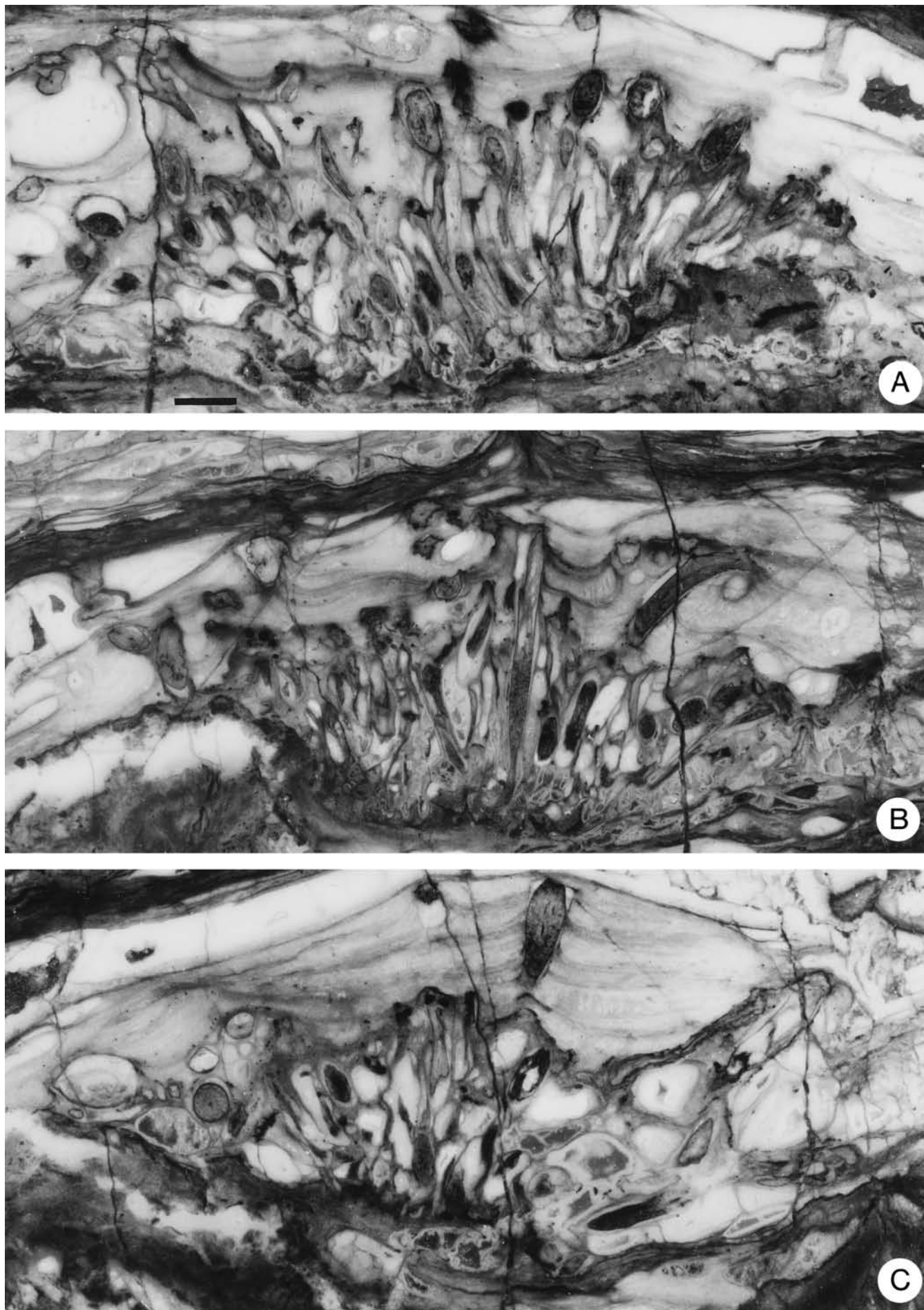


Figure 1 Three serial sections of an *in situ* stand of *Remyophyton delicatum* gametophytes (A–C) growing on a sinter surface and covered by laminated chert: (A) Pb 3682; (B) Pb 3684; and (C) Pb 3386. All figures are at the same magnification (scale bar=2 mm).

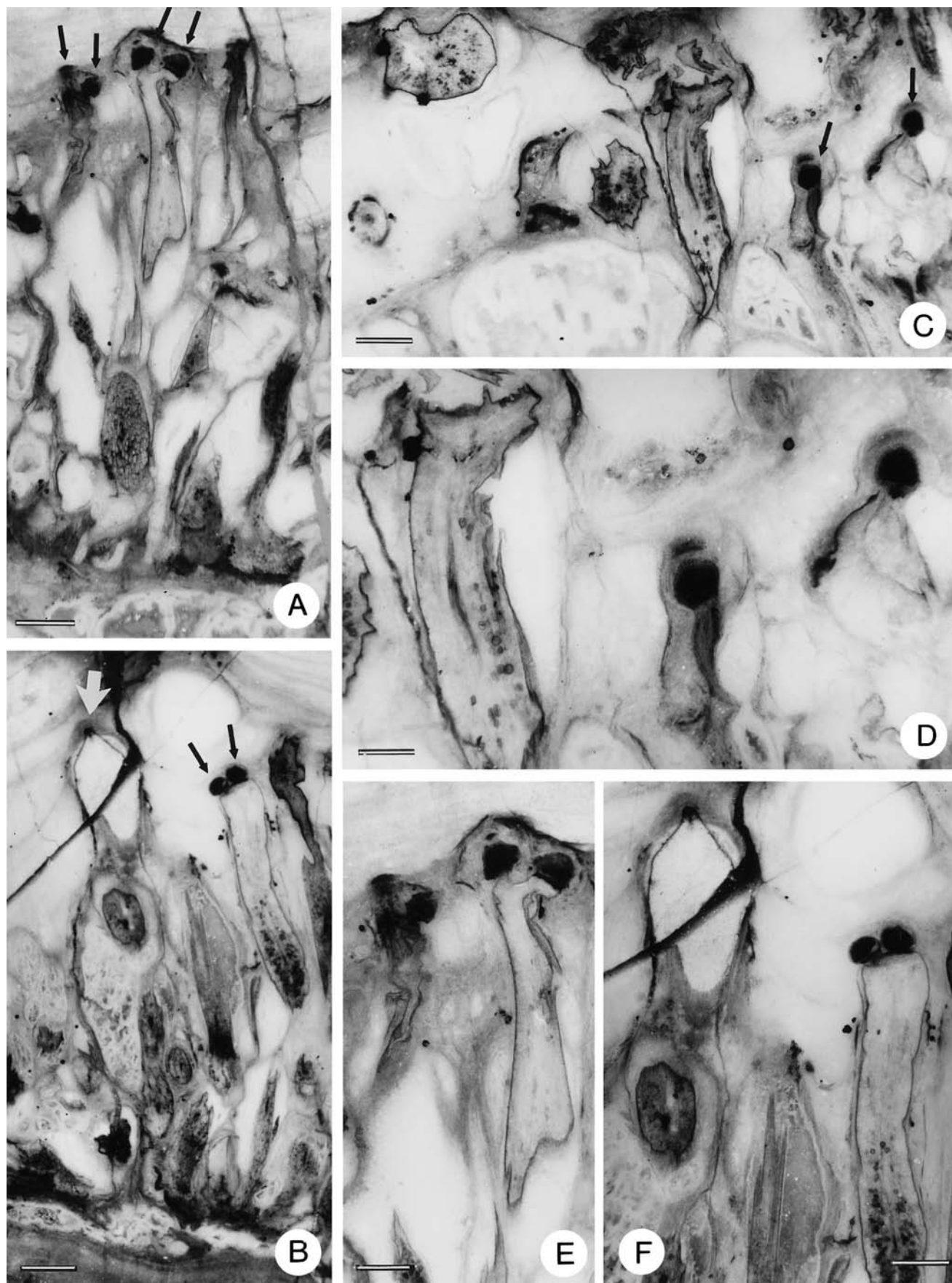


Figure 2 Details of individual *Remyophyton delicatum* axes with antheridia (A–E) and *R. delicatum* axes with archegonia (B, C, F). (A) overview with antheridia-bearing axes, antheridia indicated by arrows, Pb 3686 (scale bar=800 μ m); (B) overview of the holotype with an archegoniate axis (white arrow) and an antheridia-bearing axis (black arrows), Pb 3681 (scale bar=1 mm); (C) overview with an archegoniate axis in cross-section (upper left), an archegoniate axis in longitudinal section (centre) and two axes in longitudinal section bearing antheridia (right, black arrows), Pb 3684 (scale bar=600 μ m); (D) detail of (C) showing an archegoniate axis (left) and two antheridia-bearing axes (right) (scale bar=300 μ m); (E) detail of (A) showing two antheridia-bearing axes (scale bar=400 μ m); and (F) detail of (B) (holotype) showing an archegoniate axis (left) and an antheridia-bearing axis (right) (scale bar=600 μ m).

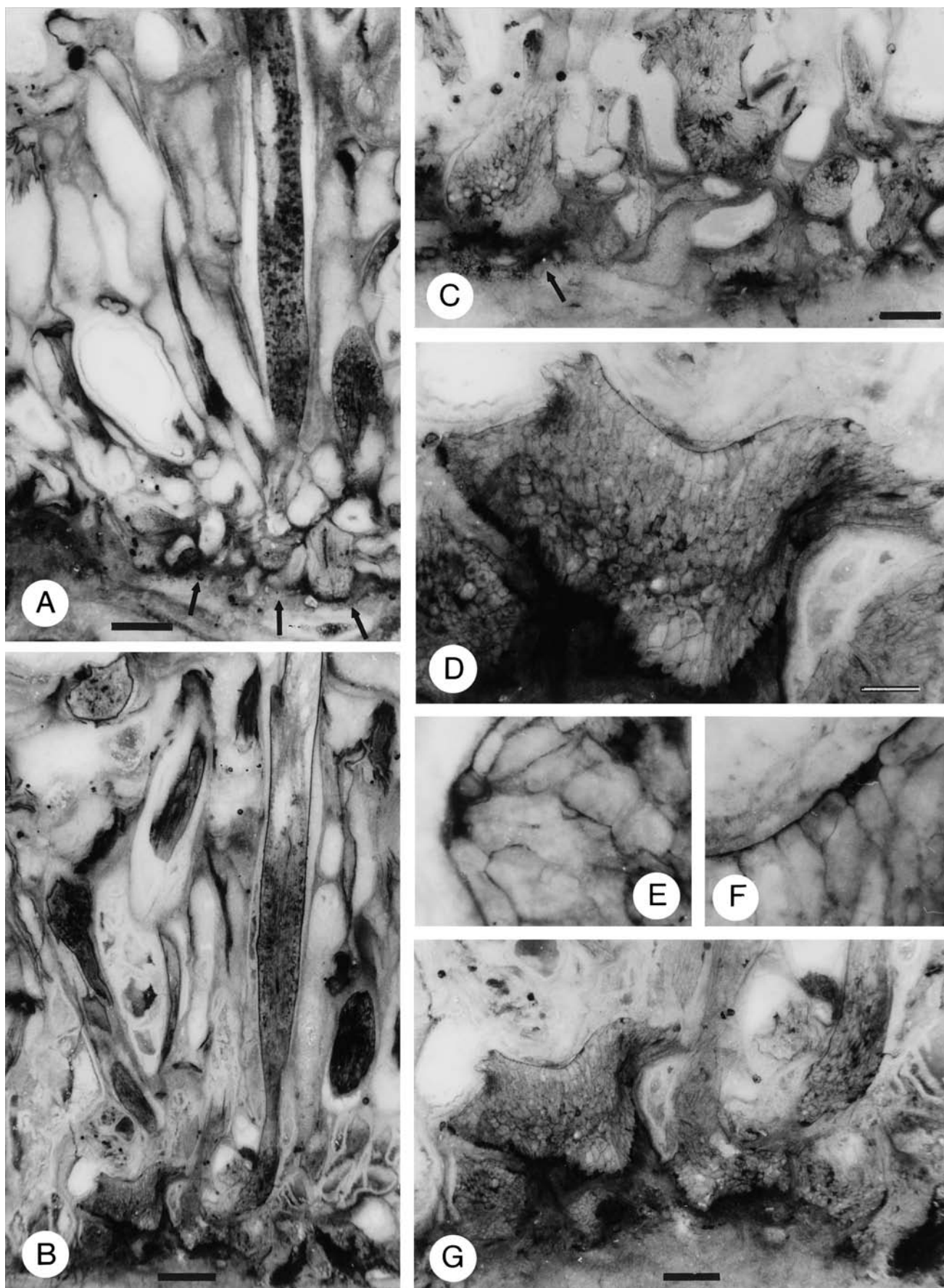


Figure 3 Basal parts of *Remyophyton delicatum* axes (A–G). (A, B) overview with upright standing axes and basal protocorm (arrow), (A) Pb 3685 and (B) Pb 3684 (scale bar=800 μm); (C) basal parts with protocorms (arrow), Pb 3683 (scale bar=400 μm); (D) detail of (B) showing a protocorm (scale bar=200 μm); (E, F) details of the specimens illustrated in (D) showing stomata on the upper surface of the protocorm (scale bars=50 μm); and (G) detail of (B) showing two protocorms (scale bar=400 μm).

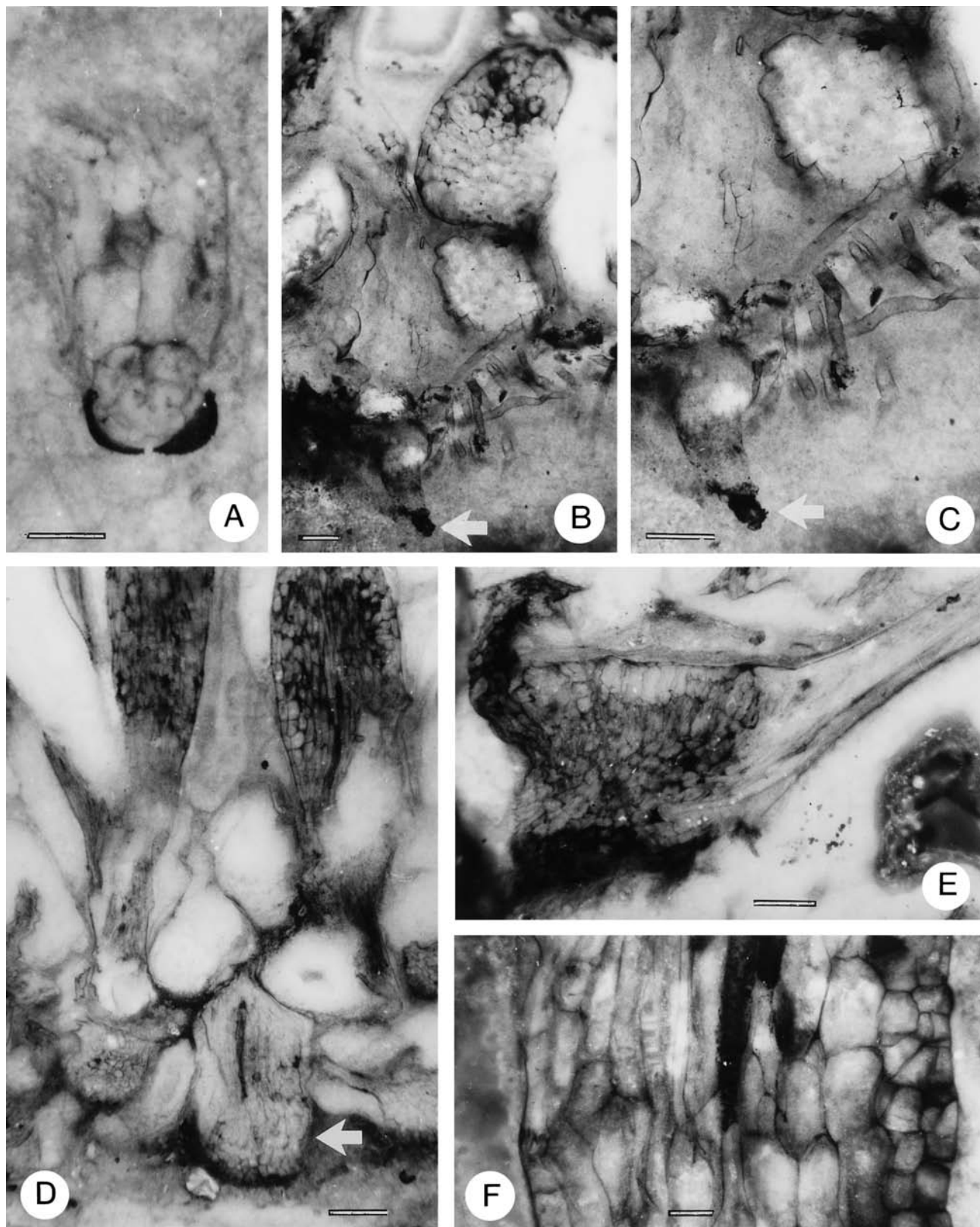
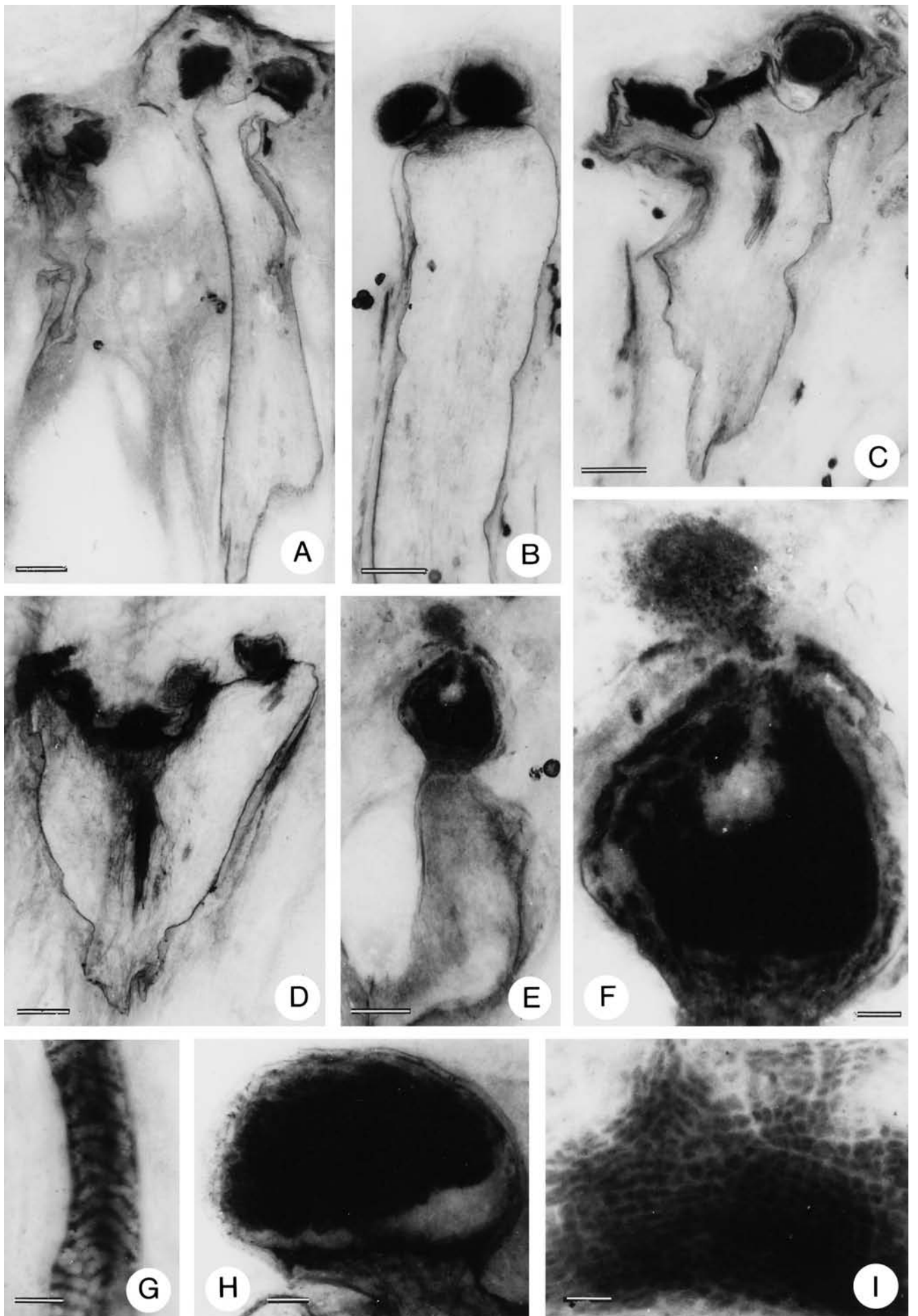


Figure 4 Germinating spore of *Rhynia gwynne-vaughanii* and *Remyophyton delicatum* protocorms (A–F): (A) germinating *Rhynia gwynne-vaughanii* spore with the first cell divisions in the young protocorm, Pb 3687 (scale bar=50 μ m); (B) *Remyophyton delicatum* protocorm with small rhizoids on the lower surface of the protocorm, Pb 3683 (scale bar=100 μ m); (C) detail of (B), the spore is still recognisable (arrow) (scale bar=100 μ m); (D) protocorm with basal parts of tracheid-bearing gametophyte axes (arrow), Pb 3685 (scale bar=300 μ m); (E) dish-like protocorm with rhizoids on the lower surface and stomata on the upper surface, Pb 3681 (scale bar=200 μ m); and (F) longitudinal section through a protocorm with the first tracheids (dark tissue in the centre), Pb 3681 (scale bar=50 μ m).

occur a few hundred metres NW of the village of Rhynie (for maps, see Trewin 2004, p. 286). The chert-bearing Dryden Flags Formation is Pragian in age and has been

radiometrically dated to 396 ± 12 Ma (Rice *et al.* 1995). For further details on the geology of the Rhynie cherts, the reader is referred to Rice & Trewin (1988), Rice *et al.* (1995, 2002),



Trewin (1994, 1996), Trewin & Rice (1992) and other contributions in the present volume.

The specimens with *L. rhyniensis* and *L. mackiei* were collected in the mid-1970s from a temporary trench at the classical locality, which was first described by Mackie (1913). The block with *R. delicatum* was collected as a loose chert block in the same field.

2. Material and methods

The plant specimens are permineralised and preserved in chert. Fixation and silicification of the plant material must have occurred very rapidly because very delicate structures are often very well preserved. The block with *R. delicatum* contains a large number of germinating spores. Two specimens with antheridia shedding their sperm cells, of *L. rhyniensis* and *R. delicatum*, respectively, have been found (Figs 5E, F & 9E). This phenomenon also points to very rapid silicification. Mature antheridia of extant pteridophytes usually burst open and shed their sperm cells on contact with water. This might also have happened to the Rhynie chert antheridia, which were flooded by silica-rich water. Possibly a silica gel formed from the cooling water, preventing the further dispersion of the sperm cells.

The specimens were studied in polished chert sections and thin sections. The latter were made according to the method described by Hass & Rowe (1999). The block of chert illustrated by Powell *et al.* (2000, fig. 5) was cut up into 14 thin sections, and the freshly cut chert surfaces were documented photographically before they were further ground down. Overviews of chert blocks were photographed under oil immersion in polarized light. Thin sections were photographed in transmitted and incident light.

3. Systematics

Remyophyton Kerp, Trewin and Hass gen. nov.
(Figs 1–7)

Etymology. The genus is named after Prof. Dr Winfried Remy (1924–1995), who described the first gametophytes from the Rhynie chert.

Type of the genus. *Remyophyton delicatum* Kerp, Trewin and Hass sp. nov.

Generic diagnosis. Globular to bowl-shaped rhizoid-bearing protocorms entirely consisting of parenchymatic tissue; each protocorm bearing one or two (occasionally three or four?) unbranched aerial axes. Aerial axes with S-type tracheids, except for the basal-most part. Smaller aerial axes, usually bearing antheridia, and larger ones bearing archegonia. Antheridia-bearing axes terminally flattened or slightly bowl-shaped. Antheridia stalked, occurring singly or as a pair on the flattened apices of the axes, or in groups of up to five within the bowl-shaped antheridiophore. Archegonia are positioned laterally and subterminal on the larger aerial axes. Archegonia with massive, protruding necks; the egg chamber is deeply seated within the axial tissues.

Remyophyton delicatum Kerp, Trewin and Hass sp. nov.

Etymology. The epithet refers to the delicate nature of the mature gametophytes.

Specific diagnosis. Globular to bowl-shaped rhizoid-bearing protocorms entirely consisting of parenchymatous tissue; each protocorm bearing one or two (occasionally three or four?) unbranched aerial axes. Aerial axes with S-type tracheids, except for the basal-most part. Smaller, 4–8 (occasionally up to 15) mm long aerial axes bearing antheridia; larger, 10–15 mm (occasionally over 2 cm) long axes bearing archegonia. Antheridia-bearing axes terminally flattened or slightly bowl-shaped. Antheridia, slightly wider than high, stalked, occurring singly or as a pair on the apices of the flattened axes, or in groups of up to five within the bowl-shaped antheridiophore. Archegonia are 190–280 µm long, positioned laterally and subterminally on the larger aerial axes. Archegonia with massive, protruding necks; the egg chamber is deeply seated within the axial tissues.

Holotype. The holotype is stored in the collection of the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität Münster, Münster, Germany, with collection number Pb 3681.

Illustrations of the holotype. Figures 2B, 2F, 4E–F, 5B–C, 5G–H, 6A–B and 6E–F.

Paratypes. Pb 3677 (Fig. 5D), Pb 3678 (Fig. 6D), Pb 3679 (Fig. 6H), Pb 3680 (Fig. 6C, G), Pb 3682 (Figs 1A, 5E, F & 6I), Pb 3683 (Figs 3C & 4B, C), Pb 3684 (Figs 1B, 2C, D, 3, 3D–F & 4D), Pb 3685 (Fig. 3A), Pb 3686 (Figs 1C, 2A, E & 5A, I) and Pb 3687 (Fig. 4A); all thin sections are made from the same block, all specimens are stored in the collection of the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität Münster.

Type locality. The Rhynie chert field, located along the A 941 northwest of the village of Rhynie. Collected as a float block at Grid Reference NJ 495 277, Rhynie, Aberdeenshire, Scotland.

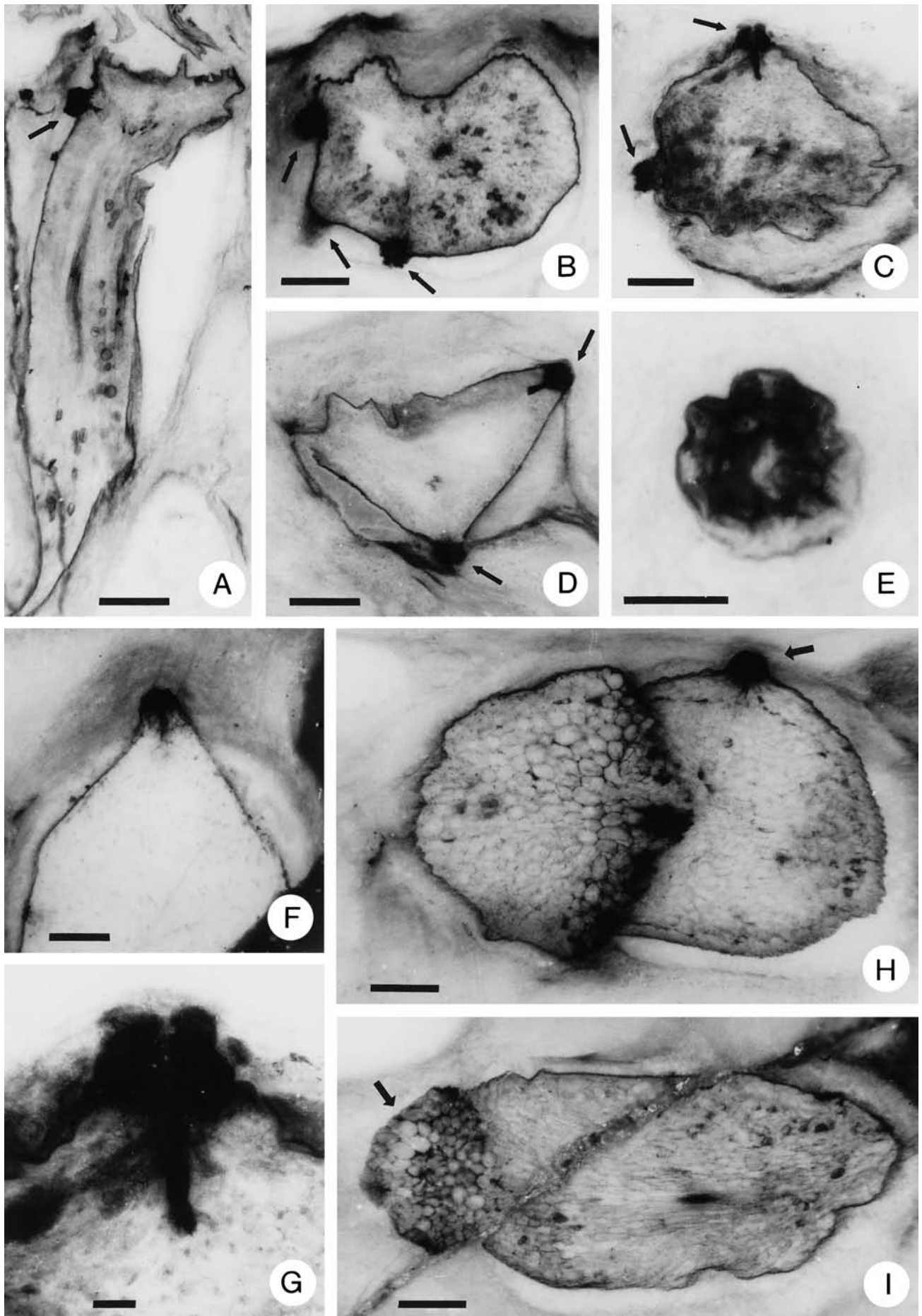
Formation and age. Rhynie Cherts Unit, Dryden Flags Formation, Lower Old Red Sandstone, Pragian.

3.1. Description

Remyophyton delicatum is known from a single monospecific stand of completely preserved mature plants bearing antheridia and archegonia. The whole stand is about 35 mm across and up to 13 mm high, and consists of more than 200 unbranched aerial axes, radiating from a central area of about 15 × 15 mm with more than 100 rhizoid-bearing basal parts (Fig. 1A–C). Aerial axes in the centre of the stand are erect while those at the margins are more or less prostrate. In the central part of the stand, aerial axes are densely packed. Numerous small, 0.4–0.6 mm wide axes are intermingled with a few larger, 0.8–1.3 mm wide ones. The smaller axes are short, being only 4–8 mm long, while the larger ones are generally 10–15 mm long, but some may exceed a length of 20 mm. The margins of the stand consist of more loosely arranged larger axes. Antheridia are predominantly borne on the shorter axes, whereas archegonia are positioned on the larger axes.

The rhizoid-bearing parts of *Remyophyton* (Figs 3A–D, G, 4B–E) are morphologically very variable, from more or less globular or bulbous (Fig. 3C) to irregularly lobed or slightly bowl-shaped (Figs 3D, 4E). The rhizoid-bearing parts are

Figure 5 Antheridia-bearing axes, antheridia and sperm cells of *Remyophyton delicatum* (A–I). (A) detail of Fig. 2A showing two antheridia-bearing axes (scale bar=300 µm); (B) detail of Fig. 2B showing an axis with two antheridia on the flattened apex (scale bar=300 µm); (C) apically widened axis with three antheridia, Pb 3681 (scale bar=300 µm); (D) cup-shaped antheridiophore with five antheridia, Pb 3677 (scale bar=300 µm); (E) axis with a single terminal antheridium releasing its sperm cells, Pb 3682 (scale bar=200 µm); (F) detail of (E) showing the release of sperm cells, the emptied part of the antheridium is marked by a light spot (scale bar=50 µm); (G) tracheids of an antheridia-bearing axis, Pb 3681 (scale bar=20 µm); (H) detail of B showing a single antheridium (scale bar=50 µm); (I) sperm cells, Pb 3686 (scale bar=20 µm).



entirely parenchymatous and completely lack conducting tissue (Figs 3, 4), and are here considered to be protocorms. Smaller, more globular protocorms give rise to a single aerial axis (Fig. 4D, arrow); the boundary between protocorm and the aerial axis is often marked by a more or less circular incision. Bowl-shaped protocorms give rise to at least two aerial axes at their upper side (Fig. 4E). In these protocorms, the centre of the upper surface consists of a patch of prismatic cells (*c.* 90 μm high and 40 μm wide) showing meristematic cell divisions (Fig. 4E). The protocorms are generally up to 1 mm (i.e. between 10 and 15 cells) high and up to 1.5 mm wide. The lower surfaces of the protocorms are densely covered with long, single-celled rhizoids (Fig. 4B, C), which are supported by a two to four cell layer thick hypodermis consisting of radially elongated cells. Stomata may occur on the upper protocorm surfaces (Fig. 3E, F). Careful observations show that many individual protocorms bear only a single aerial axis. However, it is impossible to say whether some of the protocorms are connected or not.

The aerial axes, arising from the protocorms, are 0.2–0.7 mm in diameter and most axes become wider in the apical direction (Figs 2A, B, 3A, B). The lowermost parts of aerial axes lack conducting tissue; mature tissues are absent. The outermost three or four cell layers clearly show meristematic cell divisions.

The first tracheids occur about 1 mm above the base of the aerial axes, which then show the same anatomy and histology as younger *Rhynia* axes, i.e. a one-layered epidermis and hypodermis, a broad cortex, phloem-like tissue and a few tracheids with S-type wall thickenings.

Remyophyton gametophytes are unisexual. Some of the aerial axes have a typical apex and seem to lack gametangia. Most of the smaller axes and a few of the larger ones terminally bear stalked antheridia (Figs 2A–F, 5A–F). Forty-five axes have only a single antheridium, 15 axes have two antheridia, seven axes bear three antheridia and two axes have five antheridia. In small axes, bearing only one or two antheridia, no distinct antheridiophore is formed (Fig. 5A, B, E). The stalked antheridia are positioned directly on the flattened apex of the axis (Fig. 5B). Larger axes are apically slightly peltate or may even have developed bowl-shaped antheridiophores (Fig. 5C, D), bearing three to five antheridia on their upper surfaces. These antheridiophores are 1.2–1.8 mm in diameter.

The antheridia are stalked, and consist of a more or less globular body, being slightly wider than high (210–380 μm high and 240–420 μm wide). The antheridium stalk is 40–90 μm long and 120–280 μm wide, and consists of from two to four layers of rectangular, 20–35 μm high and 10–25 μm wide cells. In many of the stalks, one or more of the layers show black contents, indicating a sealing function (Fig. 5H). The antheridium body shows a single-layered, *c.* 10–30 μm thick wall. In the apical region of the antheridium, the wall may appear double-layered. Inside the body, only large masses of spermatozooids occur; no sterile tissues were found. In immature antheridia, mother sperm cells occur in regular rows and dense packets (Fig. 5I). A single antheridium has opened by an

apical pore and has released a droplet of its sperm content (Figs. 5E, 5F).

The archegonia are positioned laterally and subterminally on the larger axes (Figs. 2B–D, F & 6A, F). In 27 sections of these axes, 35 archegonia have been found. Archegonia seem to be irregularly distributed on all sides of the axes (Fig. 6B–D, arrows), but concentrated in the subterminal regions. The archegonia possess massive, protruding necks, 90–180 μm long and 125–135 μm wide (Fig. 6C, D, F, G). In all well-preserved specimens the neck has a wall, two to three cell layers thick, showing a ring of between 10 and 12 cell files in cross-section (Fig. 6E); most archegonia necks seem to be open. However, in many archegonia, the neck cells show dark contents and have a necrotic appearance (Fig. 6A–H). The distal part of the neck may occasionally be abscised. The neck channel is dark, 15–30 μm wide and ends in an enlarged, 50–70 μm long and 30–35 μm wide, egg chamber. The neck channel and egg chamber are *c.* 190–280 μm long. The egg chamber is deeply seated within the axial tissues.

3.2. Additional observations and discussion

The *in situ* preserved *Remyophyton* stand grew on a sinter surface containing filamentous microorganisms, and overlying a monospecific *Rhynia* stand. Figure 7 shows a reconstruction of the mature *Remyophyton* gametophytes with axes bearing gametangia. The spores must have been washed or blown onto the sinter surface. Just above the sinter surface, numerous germinating spores are dispersed among the rhizoid-bearing parts of *Remyophyton*. Young germlings are axial and parenchymatic, 80–100 μm wide, two to four cells in cross-section, and sometimes still show the adhering spore coat (Fig. 4A–C). There is no filamentous protonemal stage. In older specimens, a distinct apical broadening may be visible, resulting in a more teardrop-like appearance. Occasionally, *Remyophyton* protocorms show a small axial or tear-drop like basal appendage, suggesting that they have developed from young germlings of this type.

The aerial axes of *Remyophyton* show the same anatomy and histology as younger *Rhynia* axes in having a single-layered epidermis and hypodermis, a broad cortex, phloematic tissue, and a few tracheids with S-type wall thickenings. However, it should be noted that hemispherical projections, which are so typical of *Rhynia* axes, are completely absent in both the smaller and the larger aerial axes of *Remyophyton*.

Three larger axes show a somewhat enigmatic histology in cross-sections. In these three axes, a tissue consisting of larger cells with thicker walls than the normal tissue of the gametophytic axes has developed at one side of the axes. This new tissue forms a bulge-like outgrowth of the axis (Fig. 6H, I) that may even exceed the original diameter of the parental axis, as is shown in Fig. 6H, which shows the development of this much coarser tissue on an archegonia-bearing axis. Irregular cell divisions and cells with thickened walls occur at the boundary between the normal and the ‘coarser’ tissue. These bulges have a normally developed epidermis and cuticles, indicating that it is unlikely that they represent wound tissue.

Figure 6 Archegoniate axes and archegonia of *Remyophyton delicatum* (A–I): (A) detail of Fig. 2B showing a longitudinal section through an archegoniate axis with an archegonium in lateral position (arrow) (scale bar=300 μm); (B) detail of Fig. 2B showing a cross-section through an archegoniate axis with three archegonia (arrows) (scale bar=300 μm); (C) cross-section through an archegoniate axis with two archegonia (arrows), Pb 3680 (scale bar=300 μm); (D) cross-section through an archegoniate axis with archegonia (arrows), Pb 3678 (scale bar=300 μm); (E) the entrance of the neck canal of an archegonium showing *c.* 10 cells, Pb 3681 (scale bar=50 μm); (F) detail of Fig. 2B showing a longitudinal section of an axis with an archegonium (scale bar=200 μm); (G) detail of (C) showing an archegonium (scale bar=50 μm); (H) an axis with an archegonium (arrow) and a different type of tissue with much larger cells (left) resembling that of young *Rhynia gwynne-vaughanii* sporophyte axes, Pb 3679 (scale bar=300 μm); (I) an axis showing the typical anatomy of the gametophyte axes and a different type of tissue with larger cells (arrow left), Pb 3682 (scale bar=300 μm).

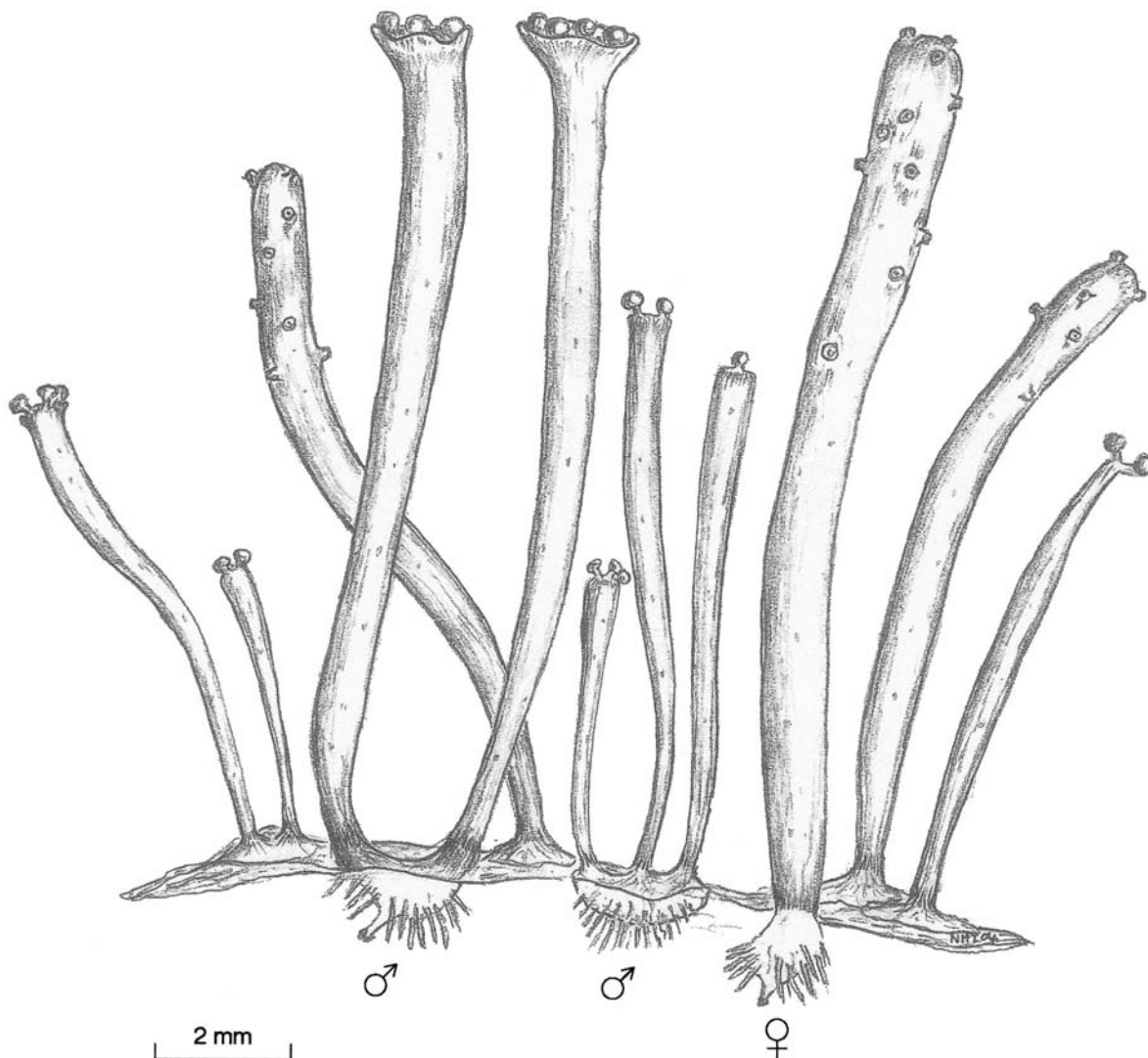


Figure 7 A reconstruction of mature male and female *Remyophyton* gametophytes. The antheridia are generally borne on shorter axes and the archegonia on longer ones. The substrate has been omitted to reveal the protocorms and rhizoids.

They resemble the basal parts of lateral branching in *Rhynia* axes, which might suggest that these irregularly developed tissues are related to fertilised archegonia or even developing sporophytes.

Lyonophyton Remy & Remy 1980 nov. emend.

Original generic diagnosis. Remy & Remy (1980b, *Argumenta Palaeobotanica* 6, 42); previously emended by Remy & Hass (1991a, *Argumenta Palaeobotanica* 8, 12).

Emended diagnosis. Gametophyte with aerial axes consisting of mature tissues, including conducting tissues. Gametangia-bearing axes unisexual, with a one-layered epidermis, a massive parenchymatic cortex, phloematic tissue and a massive conducting strand of numerous tracheid-like cells with wall thickenings consisting of bubble-like bodies forming clusters and chains.

Antheridiophore-bearing axes unbranched with terminal, peltate, disc- to cup-shaped antheridiophores. Antheridiophores entire-margined to lobed; conducting tissue extending into the individual lobes. Antheridia borne on the upper surface of the antheridiophore and on the inner sides of the lobes, and more densely concentrated on the interior sides of the lobes. Antheridia spherical to pear-shaped, stalked.

Archegonia-bearing axes dichotomously branched. Individual archegonia standing alone; laterally inserted below the axes apices, subapically and on the flattened apices. Archegonia stout, with a deeply embedded egg chamber.

Remark. The generic diagnosis, which originally referred to antheridium-bearing axes only, is emended to include archegoniate axes.

Lyonophyton rhyniensis Remy & Remy 1980 nov. emend.

Original generic and specific diagnosis. Remy & Remy (1980b); previously emended by Remy & Hass (1991a).

Emended diagnosis. Gametophyte with aerial axes consisting of mature tissues, including conducting tissues. Gametangia-bearing axes unisexual, with a one-layered epidermis, a massive parenchymatic cortex, phloematic tissue and a massive conducting strand of numerous tracheid-like cells with wall thickenings consisting of bubble-like bodies forming clusters and chains.

Unbranched axes, 1–2 mm in diameter, bearing peltate, disc- to cup-shaped, 2.8–9.0 mm wide antheridiophores. Small antheridiophores entire-margined, larger ones lobed; individual lobes fleshy, up to 1.5 mm long and 0.5–2.0 mm wide, with conducting tissue. Antheridia are borne on the upper

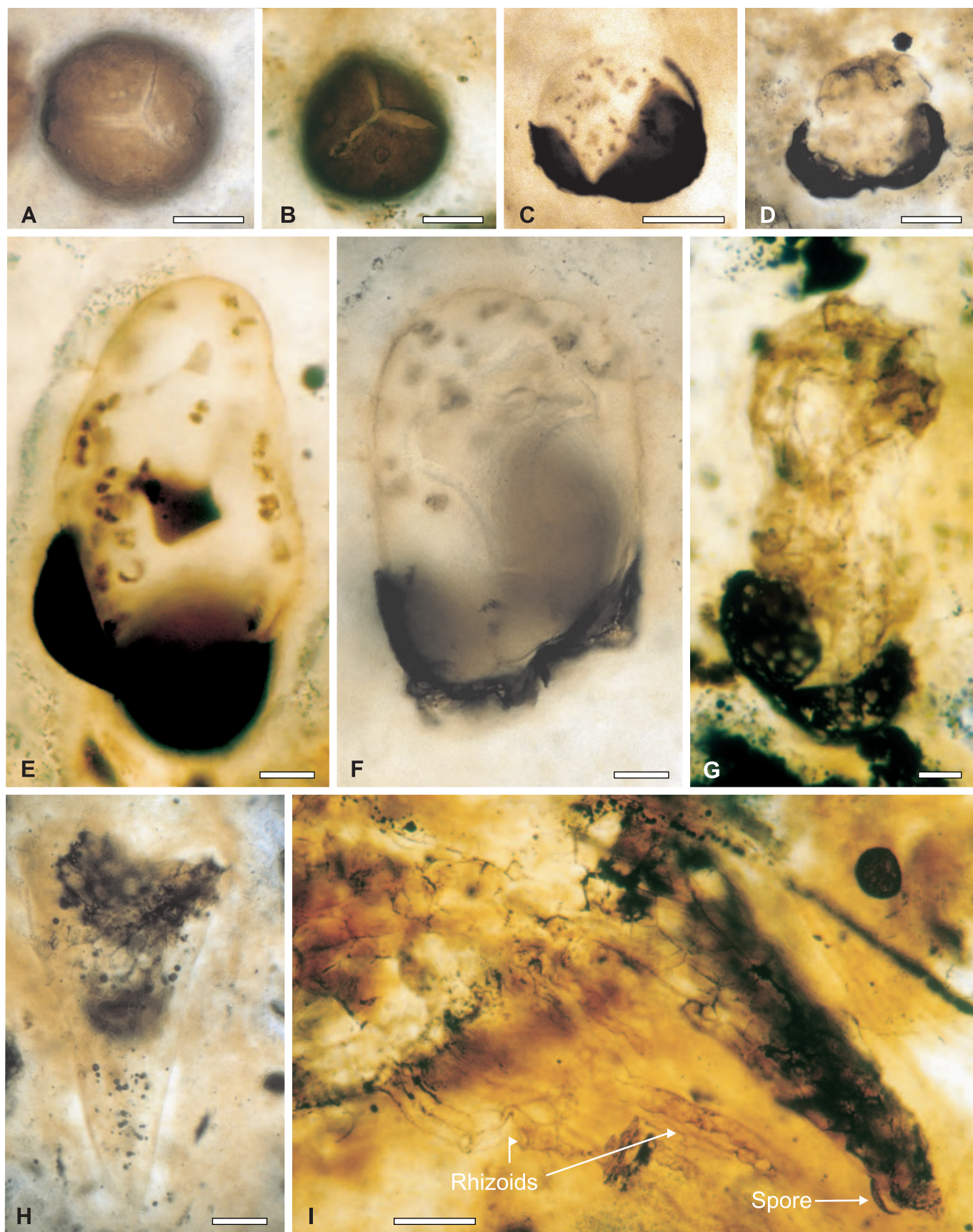
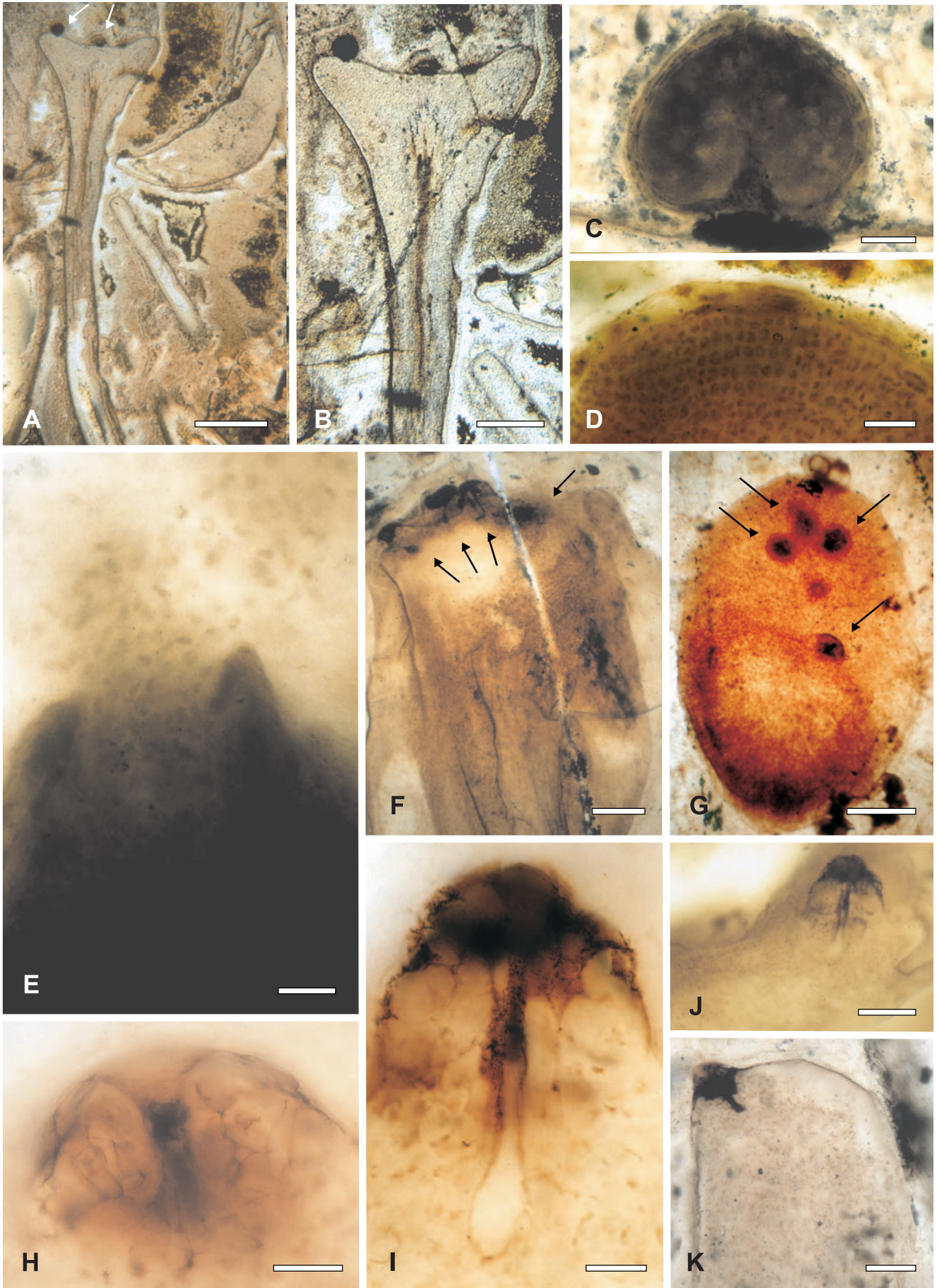


Figure 8 Spores, germinating spores and young gametophytes of *Aglaophyton major* (= *Lyonophyton rhyniensis*) (A–I): (A) trilete spore of *A. major*, Pb 1951 (scale bar=30 μ m); (B) swollen *A. major* spore with opening of the trilete mark, Pb 1202 (scale bar=30 μ m); (C) germinating spore opened along the trilete mark, Pb 1365 (scale bar=50 μ m); (D) germinating spore opened along the trilete mark with a young gametophyte showing the first cell divisions, Pb 1205 (scale bar=50 μ m); (E) germinating spore opened along the trilete mark, Pb 1251 (scale bar=20 μ m); (F) germinating spore with young gametophyte, spore already being deteriorated, Pb 1254 (scale bar=20 μ m); (G) germinating spore opened along the trilete mark with a young gametophyte growing out and showing differentiation into cells, Pb 1693 (scale bar=20 μ m); (H) a young gametophyte with widened apex forming a protocorm, Pb 1669 (scale bar=100 μ m); (I) a young gametophyte with terminal part of the initial axis grown out into a dish-like protocorm with rhizoids on the lower surface, the original spore is still visible, Pb 1698 (scale bar=100 μ m).



surface of the antheridiophore and on the inner sides of the lobes; standing loosely in the central part of the antheridiophore and more densely on the lobes. Antheridia more or less spherical, occasionally kidney- to pear-shaped, 250–600 µm in diameter, attached with a short (*c.* 100 µm long) stalk and having one or two layers of small dark cells at the junction of the stalk and the antheridiophore. Antheridium wall one or two cell layers thick; inner cells smaller and more isodiametrical than the outer ones. Antheridia with an apical operculum and a central column of sterile tissue, extending to about one-fourth to one-half length of the antheridium. Small strands of sterile tissue departing from the central column extending to the antheridium walls. Sperm occurring in rows and packets. Individual sperm cells coiled, *c.* 2 µm in diameter and 20–30 µm long.

Archegonia-bearing axes dichotomously branched. Individual archegonia standing alone, laterally inserted below the axes apices, subapically and on the flattened apices. Archegonia stout, 80–160 µm high, nearly hemispherical, slightly wider than long. The wall of the archegonium neck consists of two to three layers of cells; in cross-section showing more than 10 cells. Neck channel narrow ending in a *c.* 50 µm long and 30–40 µm wide, deeply embedded egg chamber.

3.3. Additional descriptions and discussion

A few dozen well-preserved axes showing the typical *Aglaophyton/Lyonophyton* histology occur in a block of white chert collected in the 1970s at the Rhynie field from a trench that was first opened in 1964. Twelve of these axes bear archegonia. The block was cut into a series of 40 thin-sections. The flora within the white chert is preserved *in situ*, all plants standing more or less in vertical position. The archegonia-bearing axes are accompanied by a few poorly preserved antheridiophores of *Lyonophyton*, a larger number of fertile *Horneophyton* specimens, mats of *Palaeonitella*, and numerous germinating spores. The *Palaeonitella* mats may suggest aquatic conditions before silicification took place.

The axes with the typical *Aglaophyton/Lyonophyton* histology dichotomise regularly showing the typical *Aglaophyton* mode of branching (cf. Edwards 1986, fig. 23). Three categories of resulting branches prevail: (1) a few axes are 2.5–3 mm in diameter; (2) a large number of axes are 1–1.5 mm in diameter; and (3) a few axes are *c.* 0.5 mm in diameter. The first two types show the well-known histology of *Aglaophyton/Lyonophyton*, i.e. a single-layered epidermis with numerous stomata, a hypodermis one to three cell layers thick, a massive parenchymatic cortex, phloematic tissue, and a massive conducting tissue of numerous tracheid-like cells with wall thickenings consisting of bubble-like bodies, forming clusters and chains. A zone with arbuscles (vesicular arbuscular mycorrhizae) is often visible below the hypodermis. Axes and axis sections are *c.* 0.5 mm in diameter and usually only show juvenile to meristematic tissues.

Nine axes, 1–1.5 mm in diameter, bear a total of 23 archegonia, and three archegonia are borne on axes only 0.5 mm in diameter. Single archegonia are laterally inserted within mature tissues below the apices of the axes in the subapical

regions and on the flattened apices of the axes. They are concentrated in the subapical regions and on the apices (Fig. 9F–G, K). One apex shows a group of five densely positioned archegonia (Fig. 9G). The apical tissues in which the mostly well-developed and mature archegonia are embedded are still meristematic. However, a few archegonia do not seem to have opened.

The archegonia are stout, nearly hemispherical and slightly wider than long (120–170 µm wide and 80–160 µm long). The wall of the archegonium neck consists of two to three layers; in a few specimens, the tip of the neck appears to consist of a single layer. Top views of the wall of the neck show an irregular ring of more than ten cell files (Fig. 9H). The neck channel is *c.* 15 µm in diameter, and ends in a *c.* 50 µm long and 30–40 µm wide egg chamber (Fig. 9I, J). The neck channel and egg chamber are 180–190 µm long.

The diagnosis is emended to include the archegonia-bearing axes described above. For detailed descriptions of the antheridia-bearing axes, refer to Remy & Remy (1980b), Remy & Hass (1991a, 1996) and Remy *et al.* (1993).

Langiophyton Remy & Hass 1991 nov. emend.

Original generic diagnosis. Remy & Hass (1991c).

Emended generic diagnosis. Gametophyte with aerial axes consisting of mature tissues, including conducting tissues. Gametangia-bearing axes unisexual; epidermis with stomata and glands.

Archegoniophores terminal on erect axes, peltate, cup-shaped; conducting tissue in the basal part of the archegoniophores funnel-shaped and then separating into many single strands. Numerous archegonia in the interior part and on the inner margins of the cup-shaped structure. Archegonia with a large neck and a deeply sunken egg chamber. Neck channel surrounded by eight or more cells.

Antheridiophores terminal, bowl-shaped, entire-margined with a deep central depression, bearing 50 or more antheridia on the interior surface. Antheridia densely spaced, elongated and thin-walled.

Remark. The generic diagnosis, which originally referred to archegoniate axes only is emended to include antheridia-bearing axes.

Langiophyton mackiei Remy & Hass 1991 nov. emend.

Original diagnosis. Remy & Hass (1991c).

Emended diagnosis. Gametophyte with aerial axes consisting of matured tissues, including conducting tissues. Gametangia-bearing axes unisexual; epidermis with stomata and glands. Guard cells of the stomata on axes and lower surfaces of archegoniophores only in contact with epidermal cells. Glands on gametangiophores small and fissure-like, not sunken; glands on the lower side of gametangiophores larger and deeply sunken with funnel-shaped openings.

Archegoniophores terminal on erect axes, peltate, cup-shaped, 4–9 mm wide and 3–5 mm high; conducting tissue in the basal part of the archegoniophores funnel-shaped and then

Figure 9 *Lyonophyton rhyniensis* gametophytes with antheridia-bearing axes (A, B), antheridia (C, E), sperm cells (D, E) and archegoniate axes (F–H) and archegonia (I–K): (A) longitudinal section through an antheridia-bearing axis with a cup-shaped antheridiophore (left) and an isolated antheridiophore (right), the antheridia are the black dots inside the cup-shaped antheridiophores, Pb 0021 (scale bar=2 mm); (B) detail of Fig. 8A showing the antheridiophore with antheridia (scale bar=1 mm); (C) longitudinal section through an antheridium showing the sterile tissue in the centre, Pb 0004 (scale bar=100 µm); (D) sperm cells inside an antheridium, Pb 0021 (scale bar=30 µm); (E) detail of an antheridium releasing sperm cells, Pb 0011 (scale bar=20 µm); (F) longitudinal section of an axis with five archegonia on top, Pb 3385 (scale bar=200 µm); (G) top view of the apex of an archegoniate axis with four archegonia, Pb 3380 (scale bar=300 µm); (H) detail of Fig. 8G, an archegonium with the opening of the neck canal (scale bar=30 µm); (I) an archegonium in longitudinal section showing the neck, neck canal and egg chamber, Pb 3386 (scale bar=30 µm); (J, K) sections through terminal regions of archegoniate axes (J) Pb 3386 and (K) Pb 3387 (scale bars=100 µm).

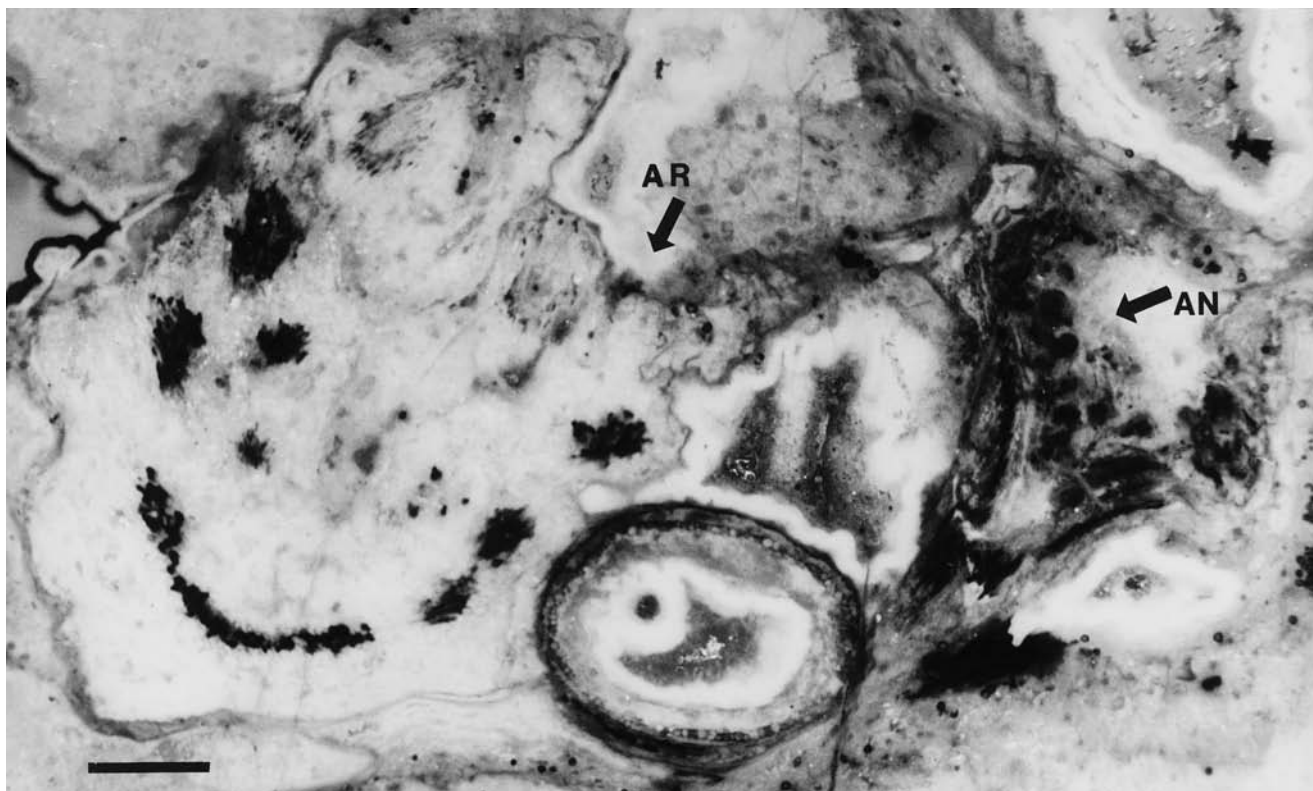


Figure 10 Oblique section through an archegoniophore (AR) and antheridiophore (AN) of *Langiophyton mackiei* with an *Aglaophyton major* axis in cross-section shown in between, Pb 0472 (scale bar=1 cm).

separating into up to 30 single strands. Numerous (up to 30) projections arise from the upper surface of the archegoniophores; some of the central ones are finger-shaped, while others consist of a basal stalk and distal cup-shaped region. Each projection usually bears a single terminal archegonium, but they may also bear archegonia along their sides.

Archegonia with a massive free neck, 80–150 μm (four to six cells) high and 80–170 μm wide with one layer of cells. The neck appears cone-like or columnar in longitudinal section; in cross-section, the neck consists of 10 to 12 cells. Neck channel 10–20 μm wide and *c.* 200 μm long, ending basally in the deeply sunken egg chamber. Egg chamber up to 45 μm wide and 50 μm high.

Antheridiophores terminal, bowl-shaped, entire-margined with a deep central depression, bearing about 50 antheridia on the interior surface. Antheridiophores are 2.5–6 mm wide and up to 3.5 mm high. Antheridia are densely spaced, elongated and thin-walled, 100–200 μm wide and 100–300 μm long.

3.4. Additional descriptions and discussion

Remy & Hass (1991c, pp. 72 & 95) referred to nine antheridiophores of *Langiophyton*. However, these have never been described or documented, and no additional material has been found since.

The antheridiophores occur together with archegoniophores of *Langiophyton* (Fig. 10). The axes bearing antheridiophores and archegoniophores show the same characteristic features (Remy & Hass 1991c, p. 95). The nine axes with antheridiophores are poorly preserved. However, they show sufficient anatomical and morphological features to distinguish them from antheridiophores of other taxa from the Rhynie chert.

Each axis terminally bears a single bowl-shaped antheridiophore, being 2.5–6 mm in diameter and up to 3.5 mm high (Figs 10, 11A–G). The antheridiophore-bearing axes are 1–1.5 mm in diameter, but it should be noted that these axes

are shrunken. The antheridiophores are not lobed, but are entire-margined and have a deep central depression (Fig. 11F, G). The antheridia are densely spaced within the bowl-shaped antheridiophore (Figs 10C–G, 11A). Each thin section shows 15 to 30 antheridia, suggesting the presence of several dozens per antheridiophore. The outlines of the antheridia are irregular, but they are mostly elongated, being 100–200 μm wide and 100–300 μm long. The antheridium wall is thin, only *c.* 10 μm wide. The sperm are very poorly preserved, and appear as masses of granular and decayed material.

The antheridiophores and the antheridiophore-bearing axes show two types of conducting tissue. The central tissue consists of dark and elongated cells with uniformly thickened walls. The surrounding conducting tissue is transparent and consists of pitted cells with characteristic rows of double bars or double knots along the walls. The dark conducting tissue forms a large and hollow strand in the axes, and within the antheridiophores, it widens into a very large ring of tissue. In oblique and transverse sections through the margins of the antheridiophores, this tissue appears as a large and more or less continuous, dark central band (Fig. 11A, arrow).

The diagnosis is emended to include the antheridiophore-bearing axes described above. For detailed descriptions of the archegonia-bearing axes, refer to Remy & Hass (1991c) and Remy *et al.* (1993).

4. General discussion

Several (palaeo)botanists have claimed to have found gametophytes in the Rhynie chert. Merker (1958, 1959) interpreted horizontal axes of *R. gwynne-vaughanii* as gametophytes and upright ones as sporophytes. However, the above author was unable to demonstrate gametangia and hence to prove the gametophytic nature of the horizontal axes. Pant (1962) regarded the entire *R. gwynne-vaughanii* plant as gametophytic. He suggested that the hemispherical projections were the sites

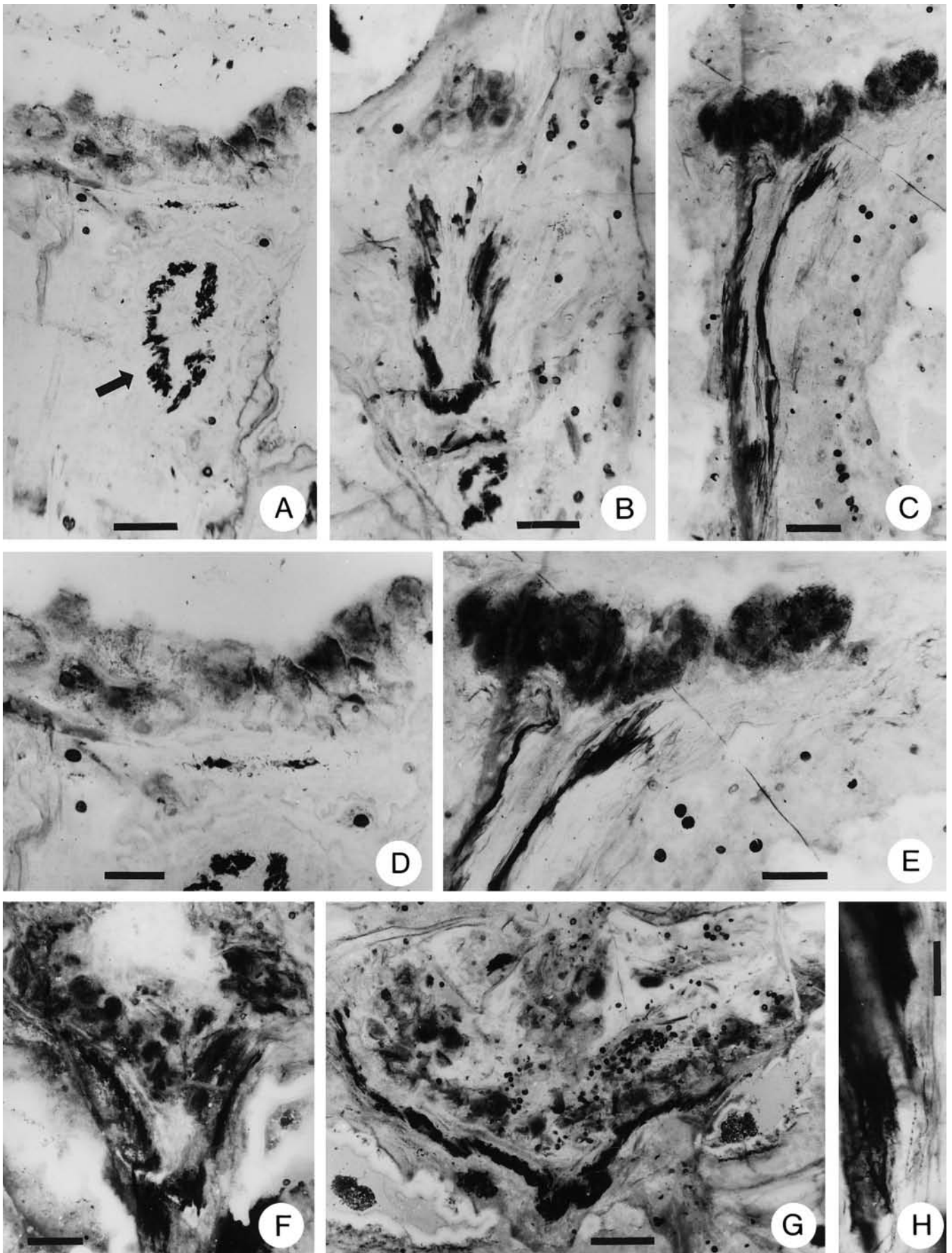


Figure 11 Antheridiophores of *Langiophyton mackiei* (A–H): (A, B) two serial sections through an antheridiophore with massive dark conducting tissue in the stalk and antheridiophore (10A arrow), the antheridia are very densely packed, (A) Pb 0616 and (B) Pb 0619 (scale bar=500 μ m); (C) longitudinal section through an antheridiophore with only antheridia, conducting tissue and cuticle preserved, Pb 0640 (scale bar=500 μ m); (D) detail of (A) showing densely packed, flask-like antheridia (scale bar=400 μ m); (E) detail of (C) showing densely packed antheridia and conducting tissues, Pb 0640 (scale bar=400 μ m); (F) detail of Fig. 10, oblique section through a bowl-shaped antheridiophore with numerous antheridia on interior surface, Pb 0472 (scale bar=500 μ m); (G) longitudinal and marginal section through a bowl-shaped antheridiophore with antheridia on the interior surface, Pb 0301 (scale bar=1 mm); (H) detail of (E) longitudinal section through an antheridiophore showing both types of conducting tissue (dark=xylem-like elements; bright=phloem-like elements with paired, pearl-like wall thickenings (scale bar=50 μ m).

of the archegonia and that the adventitious branches were young sporophytes. Lemoigne (1967, 1968a, b, 1969a, b, c, 1971, 1975, 1981) interpreted *R. gwynne-vaughanii* as the vascularised gametophyte of *A. (al. R.) major* and he combined both species under the first name. Lemoigne (1968a, b) described certain structures as archegonia. Based on his illustrations, these are thought to represent cross-sections of stomatal complexes which are just developing into hemispherical projections (Remy & Hass 1991c). The structure he illustrated as an antheridium (1969c) is totally enigmatic. A major point in Pant's and Lemoigne's reasoning was the lack of evidence that *R. gwynne-vaughanii* actually bore sporangia, as had originally been supposed by Kidston & Lang (1917). Bhutta (1969) described a sporangium attached to a short axis showing the typical anatomy of *R. gwynne-vaughanii*. Edwards (1980) found several sporangia attached to *R. gwynne-vaughanii* axes, and he could convincingly demonstrate the sporophytic nature of this species. Edwards (1986) made a detailed study of the conducting tissues of *R. gwynne-vaughanii* and *R. major*, and concluded that their conducting tissues were rather different. Therefore, he established the genus *Aglaophyton* to accommodate the species formerly known as *R. major*. In a fairly recent paper, Frey *et al.* (1997) claimed to have found a gametophyte–sporophyte junction in *H. lignieri*, thus returning to the old ideas of Merker (1958, 1959). However, their suggestion, based on a single figure of a poorly preserved specimen illustrated in the literature (Taylor & Taylor 1993), is by no means convincing.

Until 1980, the only unequivocal evidence for gametophytes were the germinating spores described and illustrated by Lyon (1957) and Bhutta (1973a, b). Remy & Remy (1980a, b) described the first anatomically preserved gametophytes under the name *L. rhyniensis*. *Lyonophyton rhyniensis* is based on excellently preserved material showing details such as sperm and sperm mother cells inside the antheridia. Another gametophyte with antheridia was described as *Kidstonophyton discoides* (Remy & Hass 1991b) and an archegoniate gametophyte was described as *Langiophyton mackiei* (Remy & Hass 1991c); in both taxa, the gametangia are preserved in great detail. *Lyonophyton rhyniensis* and *K. discoides* are the antheridia-bearing gametophytes of *A. major* and *N. aphylla*, whereas *L. mackiei* is the archegoniate gametophyte of *H. lignieri*. With the discovery of these three forms, the existence of free-growing vascularised gametophytes in the Rhynie chert flora was firmly established. Although the life cycles of several Rhynie chert plants could be reconstructed in considerable detail, none of these life cycles was known completely because either the male or female gametophytes were unknown. With the here-described archegoniate axes of *L. rhyniensis* and the antheridia-bearing axes of *L. mackiei*, all essential stages of the life cycles of *Lyonophyton/Aglaophyton* and *Langiophyton/Horneophyton* have been demonstrated. For *Lyonophyton/Aglaophyton*, a whole series of developmental stages of the gametophytes can be documented, ranging from germinating spores via young gametophytes to mature ones (Figs 8 & 9; Remy & Hass 1996). *Remyophyton*, the gametophyte of *Rhynia*, of which antheridia- and archegonia-bearing axes are documented here (Figs 1–7), is the third example of an early land plant of which all essential stages of the life cycle are known. This means that the essential stages of the life cycle of three of the five best-known Rhynie chert land plants have now been documented (Table 1). Of one plant, *Nothia aphylla*, only the antheridia-bearing axes have been described; the archegoniate axes are still unknown. Although *Asteroxylon mackiei* Kidston & Lang 1920, the largest of all Rhynie chert plants, is fairly common in certain chert beds, this species is still rather poorly known in comparison to the earlier mentioned species.

Table 1 An overview of the sporophytes and gametophytes from the Rhynie chert, and their relationships

Sporophyte	Gametophyte
<i>Rhynia gwynne-vaughanii</i>	<i>Remyophyton delicatum</i> ♀ ♂
<i>Aglaophyton major</i>	<i>Lyonophyton rhyniensis</i> ♀ ♂
<i>Horneophyton lignieri</i>	<i>Langiophyton mackiei</i> ♀ ♂
<i>Nothia aphylla</i>	<i>Kidstonophyton discoides</i> ? ♂
<i>Asteroxylon mackiei</i>	?
<i>Trichopherophyton teuchansii</i>	?

Trichopherophyton teuchansii Lyon & Edwards 1991 is a rare species of which more information on the sporophytes is needed, and the gametophytes have not been found.

Although the life cycle of three of the Rhynie chert plants is now known in much greater detail than that of any other fossil land plant, one feature still remains unknown: the gametophyte–sporophyte junction. The gametophyte–sporophyte junction in early land plants has been the matter of much debate. So far, no unequivocal evidence for a gametophyte–sporophyte junction has been given. The development of tissues resembling those of young (sporophytic) *Rhynia* axes on archegonia-bearing *Remyophyton* axes (Fig. 6H, I) might represent such a gametophyte–sporophyte junction. However, definite proof cannot be given.

The material here described as *R. delicatum* confirms Edwards' (1980) opinion that the assumptions of previous authors who interpreted (parts of) *R. gwynne-vaughanii* as gametophytes are incorrect. *Remyophyton* is the first example of an *in situ* preserved stand of mature gametophytes. This material nicely shows how dense the gametangia-bearing axes were standing, and also the size differentiation between archegonia- and antheridia-bearing axes within the same stand. This new gametophyte material also documents a greater diversity of Early Devonian gametophytes than previously known, both with regard to their organisation and size.

In comparison to other Rhynie chert gametophytes, mature plants of *Remyophyton* are very tiny, only a few millimetres high. They seem to bridge the size gap between the tiny Silurian *Cooksonia*-like plants, and Early Devonian Rhyniophytes and Zosterophyllophytes.

In *Remyophyton*, a special gametangiophore may be absent, and the antheridia and archegonia may be directly borne on the aerial axes. *Remyophyton* is not only the smallest of all known Early Devonian gametophytes, but it also shows the simplest organisation. However, the female axes have great similarities to those of *Lyonophyton*. The largest male axes occasionally form terminal peltate to bowl-shaped antheridiophores with widely spaced globular antheridia. The antheridial stalks have a distinct dark sealing layer. Antheridiophores and antheridia of *Remyophyton* show more similarities to those of *Lyonophyton* than to those of other gametophyte taxa. On the other hand, male gametophytes of *Langiophyton* and *Kidstonophyton* share numerous morphological and anatomical features, such as elongated antheridia, which are densely packed on the upper surfaces of unlobed antheridiophores and a very massive conducting tissue consisting of two cell types.

Thus, morphologically and anatomically, the Rhynie chert gametophytes seem to represent two basically different types of organization: the *Remyophyton/Lyonophyton*-type and the *Langiophyton/Kidstonophyton*-type.

All gametophytes from the Rhynie chert which have been described so far share a further common feature. They all have aerial axes which cannot be distinguished histologically from those of their sporophytes, suggesting that this may be a level of organization typical for Early Devonian land plants.

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