THE PRESENT STATUS OF *RHYNIA GWYNNE-VAUGHANII* (K. AND L.) Y.L.

YVES LEMOIGNE
Department de Biologie Vegetale, Universite de Lyon, (France)

THE family Rhyniaceae comprises a single genus, *Rhynia*, with one species. It is known only from the famous Devonian beds at Rhynie in Scotland.

HISTORY

The Muir Chert at Rhynie, containing remains of Psilophytes, among them the Rhyniales, was discovered by Dr W. Mackie in 1910.

In the first description of the fossil plants from this chert, Kidston and Lang (1917) recognized only two species, which they called *Rhynia gwynne-vaughanii* and *Asteroxylon mackiei*. However, they were aware of the presence of more plants which they intended to describe later. In this first description Kidston and Lang gave the following diagnoses (p. 780):

"Psilophytales: A Class of Pteridophyta characterized by the sporangia being borne at the ends of certain branches of the stem without any relation to leaves or leaf-like organs."

Rhynia gwynne-vaughanii, Kidston and Lang. n. g. and n. sp.

Psilophyton princeps, Dawson (*pars*)

RHYNIA, Kidston and Lang. n. g.

Diagnosis — Plant gregarious, rootless and leafless, underground rhizomes with rhizoids, generally situated on large, downwardly directed protuberances of the cortex. Aerial stems cylindrical tapering upwards, about 8 inches in height, bearing small hemispherical protuberances. Stems sparingly dichotomous and also bearing lateral adventitious branches. Sporangium large, cylindrical and terminating an aerial stem. Sporangial wall thick, of many layers of cells. Homosporous, spores developed in tetrads about 65 μ in diameter. Stele throughout the plant small, cylindrical, consisting of a solid strand of annular tracheids, surrounded by a zone of thin-walled phloem. Cortex consisting of an inner and outer zone. Epidermis of aerial stems with cuticularized outer wall and stomata.

Locality — Muir of Rhynie, Aberdeenshire.

Horizon — Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

In addition to these diagnoses Kidston and Lang mentioned (1917, p. 765): "Rhizome and aerial stems bore small hemispherical projections which were more or less closely placed without apparent regularity. On some of these bulges tufts of rhizoid-like hairs were borne, while in other cases the projections developed into adventitious branches, usually attached by a narrow base. Some of these branches appear to have been readily detached, and their occurence free in the feat suggests that they served to propagate the plant vegetatively".

Thus, in their first description Kidston and Lang recognized only one species of *Rhynia*. They explained the differences in the structure of the stele as results of differences in position of the sections in different parts of the vegetative body. "That the rhizomes, aerial stems, and sporangia were portions of the same plant might have been inferred from their association in a bed composed of one type of plant only. Their continuity has, however, been directly traced, and is established by anatomical evidence" (Kidston & Lang, 1917, p. 766, 1. 4-7).

Three years later, in 1920, Kidston and Lang published an emendment of the genus *Rhynia*. They wrote: "In part I (1917) a general account was given of the silicified peat bed found at Rhynie, and one vascular plant was described in detail under the name of *Rhynia gwynne-vaughanii*. Further study has shown that they are two species of *Rhynia* which we now distinguish as *Rhynia gwynne-vaughanii* and *Rhynia major*" (Introduction). They further added,

"As mentioned above, two species of *Rhynia* have to be distinguished. Their similarity in organization is so great that they are not always readily separated from one another, and in our former paper they were described together under the name *Rhynia gwynne-vaughanii*. The second species, which we now separate as *Rhynia major*, is larger in all its parts, and differs from *Rhynia gwynne-vaughanii* in the absence of hemispherical projections and adventitious branches from the stems, in the greater size of the stele and xylem strand, and in the much larger size of the sporangia and spores" (p. 603). In this second account Kidston and Lang gave new diagnoses (p. 610-611).

Rhynia — Plant gregarious, rootless and leafless, consisting of subterranean rhizomes attached by unicellular rhizoids, and erect, dichotomously branched, cylindrical aerial stems. Stomata present. Stele consisting of a zone of phloem surrounding a strand of tracheids. Sporangia cylindrical, without columella, terminal on aerial stems. Homosporous. Spores with cuticularized wall, developed in tetrads.

Rhynia gwynne-vaughanii: aerial stems tapering upwards, probably about 20 cm. high, and ranging in thickness from 3 mm. to under 1 mm. Small hemispherical protuberances of superficial tissues of the stem occur, and sometimes, in place of them, adventitious branches, the stele of the branch not being continuous with that of the main stem. Xylem strand of stele slender, only sometimes showing a distinction of smaller central and larger peripheral tracheids. Tracheids with broad annular thickening. Sporangia about 3 mm long and 1·5 mm in diameter. Sporangial wall about 2 mm. thick. Spores about 40 μ in diameter.

Locality — Muir of Rhynie, Aberdeenshire.

Horizon — Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

Rhynia major — Plant larger in all its parts than *R. gwynne-vaughanii*, aerial stems tapering upwards, and ranging in thickness from 6 mm. to 1·5 mm. or less. No hemispherical projections or adventitious lateral branches. Stele large, xylem strand of numerous tracheids differentiated as smaller central and larger peripheral tracheids. Sporangia reaching a length of 12 mm. and a diameter of 4 mm. Sporangial wall about 3-4 mm thick. Spores about 65 μ in diameter.

Locality — Muir of Rhynie, Aberdeenshire.

Horizon — Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

After the publication of the "Studies" by Kidston and Lang numerous botanists and paleobotanists have taken a great interest in the Psilophytales, and all of them have wished to know something about the gametophytes of these plants, which for a long time were regarded as the first vascular plants and interpreted as the ancestors of the living vascular plants. I shall quote only a few authors and only in so far as they have contributed to our better understanding of these Devonian plants:

Bower (1935) has suggested that the gametophytes of the earliest colonizers of the land had probably a robust built (particularly the gametophytes of *Rhynia*).

Eames (1936) vaguely speculated that "if gametophyte and sporophyte were much alike in early land plants, some of the sterile fossil branching axes may perhaps be gametophytic".

Fritsch (1945) has with good reasons suggested that "if embryos and gametophytes of Psilophytales are ever discovered it would not be astonishing to find that the latter were of the same general nature as those of Psilotales; the gametophytes may even have been less reduced".

Merker (1959) in his paper entitled "Analyse der Rhynien-Basis und Nachweis des Gametophyten" first criticized the terminology of Kidston and Lang, particularly because they used the term "rhizome" for the creeping axes. If the creeping axis had simply been the horizontal subterranean parts of the same plant as the erect aerial stems one should have expected, in Merker's opinion, that they had been bifurcating with one of the branches curving upwards, in the same way as in *Lycopodium clavatum*, where aerial shoots curve up from the horizontal creeping axes. Among the Rhyniales, however, there is a marked difference between the two parts: the aerial axis usually forms an almost right angle to the horizontal one. Also, according to Merker, the creeping parts (the rhizomes of Kidston and Lang) of *Rhynia* are often

decaying while the erect axis are not. On the basis of observations and his "intuition" (*) Merker said: "Neue Untersuchungen haben nun ergeben, dass die horizontale Basis der "Urlandpflanzen" kein Rhizom sein kann, sondern das vermisste Prothallium darstellt, das dank seiner weitgehen den Beständigkeit dem völlig wurzellosen Sporophyten als Brutpflegeorgan und als Halt in Boden diente" (p. 452).*

Two years later, in 1961, Merker maintains again that the creeping parts ("rhizomes") of *Rhynia major* and *Rhynia gwynne-vaughanii* are gametophytic.

Pant (1962) published an important paper on the problem of the gametophyte of the Psilophytales. He based his conclusions partly on the famous work of Hollaway (1939) on the vascularized gametophytes of *Psilotum*. Pant made it his working hypothesis that it should be possible to discover the gametophytes of the Psilophytales in the material already described. From this starting point and on the basis of his own observations, he arrived at the following conclusions:

"As a result of our studies it now seems that the presumed absence of the gametophytes of the Rhynie Psilophytales is not because of the proverbial 'imperfection of the geological record' but due to erroneous interpretation. The following points are significant:

(a) The close structural similarity between the axes of *R. gwynne-vaughanii* and the vascular gametophytes of *Psilotum*.

(b) The possibility that at least some of the 'stomata', below which the 'hemispherical projections' and 'adventitious branches' of this species are reported to be produced, could be archegonia whose necks had been shed already.

(c) The developmental similarities between the 'hemispherical projections' of *R. gwynne-vaughanii* and the young sporophytes of Psilotales.

(d) The clear demarcation between the tissues of the 'hemispherical projections' and the parent axes.

(e) The structural similarities between the 'hemispherical projections' or 'adventitious branches' of *R. gwynne-vaughanii* and the young sporelings of Psilotales.

(f) The occurence of gametophyte-like non-vascular axes in *R. gwynne-vaughanii*.

(g) The absence of actual organic connection between the indubitable axes of *R. gwynne-vaughanii* and the sporangia assigned to it. It thus appears that at least those axes of *R. gwynne-vaughanii* which bear the 'hemispherical projections' or 'adventitious branches' may well represent the gametophytes of either of Psilophytales described from Rhynie" (Pant, 1962, p. 278).

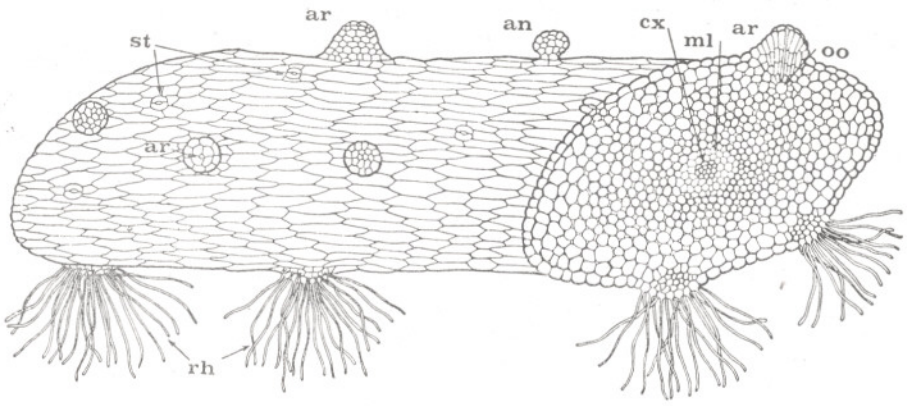
"It is clear from the above account that there is a close structural similarity between the gametophytes of Psilotales (more especially the vascular gametophytes of *Psilotum*) and the axes of *R. gwynne-vaughanii*, and also between the development and structure of 'adventitious branches' in *R. gwynne-vaughanii* and the formation, development and structure of the young sporelings, in Psilotales. Indeed the resemblance between the fossil and the living structures is so close that it is hard to explain it on any other basis than by regarding even the fossil "parent axes" as gametophytic. This nature of the axes of *R. gwynne-vaughanii* explain *ipsofacto* the nature of the curious 'adventitious branches' which then satisfactorily fit in as young sporophytes. On the other hand, if we continue to regard them as 'adventitious branches', they would be without parallel in any other psilophyte or other plants (Pant, 1962, p. 295)".

"... It must, however, be admitted that the present evidence is mainly indirect. Direct proof can be supplied only by demonstrating well preserved sex organs (archegonia and antheridia) on these axes. The possible archegonial nature of at least some of the 'stomata' and the occurence of other archegonium-like structures is perhaps some evidence of the kind but at the present moment no clear antheridia have been observed. Further work is in progress (Pant, 1962, p. 296)".

OBSERVATIONS

Comparative studies on Pteridophytes had also led me to the idea that the gametophytes of the Rhyniales might have been vascularized. Further, the study of Kidston and Lang's publications had directed my interest especially to the diffe-

(*) "Das, was als Rhizom bezeichnet wurde, deutete ich, zunächst nur gefühlsmassig, als Prothallium". (p. 445, l. 26-28).



TEXT-FIGURE 1 — Showing the morphological and anatomical characters of the gametophyte *Rhynia gwynne-vaughanii*. *an*, antheridium, *ar*, archegonium, *cx*, strand of xylem (protostelic), *ml*, phloem, *oo*, oosphere, *rh*, rhizoids, *st*, stomata.

rences which seemed to exist between *Rhynia gwynne-vaughanii* and *Rhynia major*; in particular it did not seem possible to interpret the "adventitious axes" as organs of vegetative propagation. Further, convinced of the importance which the discovery of the gametophyte of the Rhyniales would have for our understanding of the phylogeny of these and other Devonian plants, I started to study, from 1959 onwards, British, Belgian and French Collections of Psilophytes as well as the slides prepared in my own laboratory from samples of Rhynie chert which I collected in 1964 when members of the X International Botanical Congress visited this famous locality under the guidance of Mr. A. G. Lyon and Professor John Walton. The main results of these studies have, till now, formed the contents of the following 6 publications:

1 — One deals with the discovery of archegonia borne by vascularized axes of *Rhynia gwynne-vaughanii* Kidston and Lang (Lemoigne, 1968a): these archegonia were found in a slide in the Lang collection of the Natural History Museum of Manchester. They form small protuberances on the surface of the vascularized gametophytic axis. There are several such protuberances on the same sectioned axis, all of them on the same side of it. Each mature archegonial protuberance shows (Pl. 2, fig. 11 and 12) at its top a rosette of four cells. Between them is the opening of a straight canal leading down to an oosphere in the interior of the gametophyte. In one of the archegonia the nucleus of the oosphere is visible. Measurements were taken in two archegonia: the canal was found to be 310 μ long and the oosphere 70 μ in diameter. To a great extent the archegonium is enclosed in the tissue of the gametophyte, just as it is among the recent Pteridophytes, and in contrast to the pedicellate archegonia of the Bryophytes. The archegonial canal (which, presumably, has arisen as the result of lysis of a series of cells) is surrounded by four rows of cells which are elongated in the same direction as the canal, each row seems to be formed of 5 or 6 cells above each other. The cells of the gametophyte, in contact with the opening or in the vicinity of it, are also arranged in rows and elongated parallel to the canal, so that these cells, together with neck cells form a protuberance. The mature archegonial protuberances are covered by an amorphous substance (which no doubt represents a fossilized mucilage). The oosphere (as seen in Pl. 2, fig. 13 and 14) is surrounded by a layer of cells in regular arrangement. At maturity the cells of the neck of the archegonium and the associated cells were evidently dissolved and formed a mucilage similar to the one found in *Psilotum* and *Lycopodium complanatum*.

Bierhorst has recently (1971) in his book entitled "*Morphology of Vascular Plants*" written:

"The stem of *Rhynia gwynne-vaughanii* shows bumps along its surface, some of which appear as undeveloped lateral branches. They entergrade with smaller

and smaller ones down to small surface eruptions involving relatively few cells. The smaller ones seem to have a central channel leading to a large cell or intercellular space below the surface. Lemoigne (1968a) called such structures archegonia and, therefore, assumed that some of the plants were gametophytes. His diagrammatic reconstruction of one such structure appears in Fig. 6-1 G. The so called archegonia were much more likely hydathodes or secretory structures of some kind. Several other authors have in the past suggested that some of the rhynialean axes may have been gametophytes; some even said that they 'probably were' gametophytes".

It is surprising that Bierhorst has preferred to reproduce my diagrammatical drawing instead of my microphotograph of the archegonium, and I find it difficult to accept that the drawing has been changed so that the oosphere is replaced by a cavity. No doubt this change weakens my interpretation of the entire structure as an archegonium.

I am also surprised that Bierhorst, with his eminent knowledge of plant morphology in other fields, can regard these structures as "hydathodes or secretory structures of some kind". In my Laboratory two of my assistants have carried out research on hydathodes and various kinds of glands, and I can affirm that the structures described and interpreted in my papers as archegonia of *Rhynia gwynne-vaughanii* are really archegonia and certainly no kind of "hydathodes or secretory structures".

2 — In a paper entitled "Contribution ä la connaissance du gamétophyte *Rhynia gwynne-vaughanii* K. et L.: Probléme des protubérances et processus de ramification" (1969a) I have shown that:

a) Some of the protuberances borne by gametophytic axes of *Rhynia gwynne-vaughanii* have been formed in connection with archegonia; most, if not all, of the protuberances that Kidston and Lang said they had observed under stomata are in fact connected with archegonia (cf. Pl. 1, fig. 1; Pl 2, fig. 11 and 13).

b) Other protuberances, all of them on one side of an axis, bore rhizoids. This type of protuberance have also been observed on axes of *Rhynia major* K. and L. (cf. Pl. 1, fig. 4, 6, 7 and 9).

c) "Vascular protuberances" are ramifications. The branchings of *R. gwynne-vaughanii* were of a different kind. The "vascularized protuberances" observed by Kidston and Lang were interpreted by them as organs of vegetative propagation; these organs were often thicker than the axes bearing them and strongly attached to them, although their vascular systems appear not connected. In my opinion they were either young sporophytes or simple branches.

d) The gametophytic axes of *R. gwynne-vaughanii* mostly branched by very unequal bifurcation, but sometimes by trifurcation giving rise to axes of different thickness. The gametophyte of *R. gwynne-vaughanii* seemed to branch sparingly; I have never observed erect ramifications (but have no proof that they did not occur).

3 — A fourth paper with the title: "Organe assimilable à une anthéridie et stomates épidermiques, portés par des axes rampants du type *Rhynia gwynne-vaughanii* Kidston et Lang" (1969b) was based on the following observations:

a) On a transversal section (Pl. 2. fig. 15 and 16), rather thick and slightly oblique, of an axis with the structure of *R. gwynne-vaughanii* K. and L. (slide No. 2427, Hunterian Museum Univ. Glasgow) there is a kind of globular swelling of the epidermis, 200 μ in diameter. It is not an embryonic sporophyte (which would have been found in level with an archegonial protuberance), nor is it a secretory gland or any of the kinds of protuberances known from the axes of Rhyniales: those bearing rhizoids, or containing archegonia, nor can it be explained as a young branch or the result of an attack by a parasite. From all such structures it differs in shape and size. In fact, it has a great resemblance to the antheridia of *Psilotum*, *Botrychium* and *Ophioglossum*. Although we know nothing of the internal structure of this body it seems very likely that it represents an antheridium.

b) In several sections of *R. gwynne-vaughanii* (if the slides were thick and slightly oblique) I have seen stomata (the two cells surrounding the ostiolum measured 90 μ×70 μ together). These stomata are identical with the stomata in the epidermis of the sporophyte *R. major* K. and L. and also comparable to those of Anthoceros (Bryophyta). Already Kidston and Lang reported the presence of stomata in *R. gwynne-vaughanii* but only in those axes

which they regarded as aerial stems, while they explicitly said they had never found them in "rhizomes". Slide No. 2427 (Kidston Coll. Glasgow) is particularly interesting because, in one and the same section of an axis, I found both a stomata and protuberances bearing rhizoids (Pl. 1, fig. 4 and 7).

In my opinion the gametophyte *R. gwynne-vaughanii* K. and L. was neither submerged in water nor subterranean, but probably spreading out on the soil surface (as witnessed by the presence of stomata and by the presence of rhizoids borne on protuberances always situated on one side).

4 — The study of endophytic fungi in *R. gwynne-vaughanii* and *R. major* (1971) has lead me to the following conclusions:

The axes of gametophytes (*R. gwynne-vaughanii*) and sporophytes (*R. major*) harboured several endophytic fungi which differed from each other in morphological and biological characters. One of these fungi, which was *common* to the gametophytic and sporophytic phases of *Rhynia*, produced respectively mycothallus and mycorrhiza, an additional proof of the specific identity of the *Rhynia gwynne-vaughanii* (Kidston and Lang) Y. Lemoigne. It is possible that long endocortical hyphae, cheifly intercellular, belong to the same symbiotic fungus. Among the other fungi observed, were one generally located in the necrosis zones (and producing clusters of sporocysts); another invading superficial cells (and closely related to the genus *Rhizoctonia*); and several other ones which produced sporocysts and spores varying in size and structure; all were probably parasites with a gradient in their virulence.

There were also saprophytic fungi invading dead and decaying tissues. Such saprophytes appear commonly also in these sections of the sporophytic axis of *Asteroxylon mackiei* K. and L. that I have had the opportunity to study microscopically.

CONCLUSIONS

Rhynia major K. and L., and, *Rhynia gwynne-vaughanii* K. and L. have been considered as two distinct species of sporophytes. However, they represent one species, *R. gwynne-vaughanii* being the, gametophyte and *R. major* the sporophyte, both of them vascularized. According to the rules of priority I propose to keep *Rhynia gwynne-vaughanii* as the name of only species of *Rhynia* known to us.

New diagnoses of the genus Rhynia and its only species are proposed:

Class: PSILOTOPSIDA (plants with a vascularized gametophyte and a sporophyte which is simple)

+ order of the Psilotales
— family of the *Psilotaceae*,
● genus *Psilotum*.
— family of the *Tmesipteridaceae*,
● genus *Tmesipteris*,
— family of the *Rhyniaceae*
● genus *Rhynia*

Rhynia gwynne-vaughanii (Kidston and Lang) Y. Lemoigne *Diagnosis*: Sporophyte and gametophyte distinct, vascularized, having an epidermis with cuticularized outer wall cells and stomata. All the axis without leaves or spines. The gametophyte is a system of branched, vascularized axis spreading on the ground, with rhizoids generally situated on hemispherical protuberances localized on the lower side. The axis bear archegonial protuberances and antheridia. Each mature archegonial protuberance shows at its top a rosette of four cells, between them the opening of a canal leading down to an oosphere in the interior of the gametophyte; the oosphere is surrounded by a layer of cells in regular arrangement. At maturity the cells of the protuberance (cells of the neck of the archegonium and associated cells) dissolved and formed a mucilage. The antheridia globular and they appear as a kind of globular swelling of the epidermis of about 200 μ in diameter. All the axis are protostelic. The gametophyte probably with chlorophylle.

The sporophyte is a system of naked branched protostelic or siphonostelic axis creeping on the ground and bearing:

— on the lower side rhizoids generally localized on protuberances,

— on the upper side erect (simple or branched?) naked protostelic axis.

The sporangia, large, homosporous, borne lonely at the top of erect axes: the sporangial wall thick, of many layers of cells. The spores developed in tetrads about 65 μ in diameter.

Locality — Muir of Rhynie, Aberdeenshire (Scotland),

Horizon — Devonian.

Remarks

1) All characters known from *Rhynia gwynne-vaughanii* are those of a Pteridophyte and not of a Bryophyte.

2) My observations confirm the correctness of Dr D. D. Pant's ideas.

3) The following points are still obscure: we do not know for certain if the erect axes of the sporophyte were simple or branched, and if all erect axes (or, in case, if all their ultimate ramifications) ended in sporangia.

4) There is a close affinity between *Rhynia* and *Psilotum*. I do not think, however, that there is any phylogenetic relationship with the Anthocerotales.

5) In a recent paper, entitled "The Taxonomic position of the Psilotales in the light of our knowledge of devonian plant life" (Palaeobotanist, 20 (1) 33-88, 1973), p. 35, F. P. JONKER writes: "... *Rhynia* consequently shows an almost isomorphic alternation of generations, quite unknown up till now in order Pteridophytes. I am astonished that this leads Lemoigne (1968) to the conclusion that his discoveries have made it clear that both *Psilotum* and *Tmesipteris* belong together with *Rhynia* in the same order Psilotales, of the Psilophyta. He argues this by pointing to the vasculiferous gametophytes. In my opinion considerable differences exist in the gametophytes of *Psilotum* and *Tmesipteris* on the one side and Rhynia on the other side if we accept that *Rhynia gwynne-vaughanii* is the gametophyte of *R. major*. *Psilotum* and *Tmesipteris* have subterraneous, though sometimes slightly vascularized prothallia and the gametophyte of *Rhynia* is in that case a dichotomously organized erect plant, provided with a haplostele, a cortex, an epidermis with stomata, and a subterraneous rhizome". For F. P. JONKER the order Psilotales (genera *Psilotum* and *Tmesipteris*) shows more affinity to the phylum *Lycopodiophyta* in his opinion the order Psilotales is to be derived from the *Protolepidodendraceae*)

I am astonished that the morphology of the gametophyte of *Rhynia gwynne-vaughanii* is not the same for F. P. JONKER as for me (In my opinion the gametophyte was not a "dichotomously organized *erect* plant ... with a subterraneous rhizome"). On the other hand I have considered not only one but a *group* of *comparisons* between *Psilotum-Tmesipteris* and *Rhynia*. I think that *Psilotaceae*, *Tmesipteridaceae* and *Rhyniaceae* are in the same phylum *Psilophyta*.

REFERENCES

BOWER, F. O. (1935). Primitive Land Plants. *London*.

BIERHORST, D. W. (1971). Morphology of Vascular Plants. *New York & London*.

EAMES, A. J. (1936). Morphology of the Vascular Plants. Lower Groups (Psilophytales to Filicales). *New York*.

FRITSCH, F. E. (1945). Studies in the comparative morphology of the *algae*. IV. Algae and the archegoniate plants. *Ann. Bot.* (N.S.) **9**: 1-29.

HOLLOWAY, J. E. (1939). The gametophyte, embryo and young rhizome of *Psilotum triquetrum* Seward. *Ann. Bot.* (N.S.) **3**: 313-336.

KIDSTON, R. & LANG, W. H. (1917). On Old Red Sandstone Plants showing Structure from the Rhynie Chert Bed Aberdeenshire. Part I. *Rhynia Gwynne-Vaughanii* Kidston and Lang. *Trans. R. Soc. Edinburg.* L, 1, **24**: 761-784.

Idem (1920). On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire, Part II. Additional Notes on *Rhynia Gwynne-Vaughanii* Kidston and Lang; with Descriptions of Rhynia major, n. sp., and *Hornea Lignieri*, n.g., n. sp. *Ibid.* L. II: 603-627.

LEMOIGNE, Y. (1968a). Observation d'archégones portés par des axes du type *Rhynia gwynne-vaughannii* Kidston et Lang. Existence de Gamétophytes vascularisés au Dévonien. *C.R. Acad. Sci. Paris.* **266**: 1655-1657.

Idem (1968b). Les genres Rhynia Kidston et Lang du Dévonien et Psilotum Seward actuel appartiennent-ils au même phylum ? *Bull. Soc. Bot. Fr.* **115**: 425-440.

Idem (1969a). Contribution à la connaissance du Gamétophyte *Rhynia gwynne-vaughanii* Kidston et Lang: Probléme des protubérances et processus de ramification. *Bull. Soc. Linn. Lyon.* **4**.

Idem (1969b). Organe assimilable à une anthéridie et stomates épidermiques portés par des axes rampants du type *Rhynia gwynne-vaughanii* Kidston et Lang. *C. R. Acad. Sci. Paris.* **269D**: 1393-1395.

Idem (1970). Nouvelles diagnoses du genre Rhynia et de l'espèce *Rhynia gwynne-vaughanii, Bull. Soc. Bot. Fr.* **117**: 397-320.

LEMOIGNE,Y & BOULLARD B., (1971). Les Champi ons endophytes du " *Rhynia gwynne-vaughanii* " K. et L.: Etude morphologique et déductions sur leur biologie. *Botaniste.* LIV: 49-89.

MERKER, H. VON (1958). Zum fehlenden Gliede der Rhynien Flora. *Bot. Notiser.* **111**: 608-618.

Idem (1959). Analyse der Rhynien. Basis und Nachweis des Gametophyten. *Ibid.* **112**: 441-452.

PANT, D. D. (1962). The gametophyte of the Psilophytales. *Proc. Summer School Bot. Darjeeling*: 276-301.

EXPLANATION OF PLATES

PLATE 1

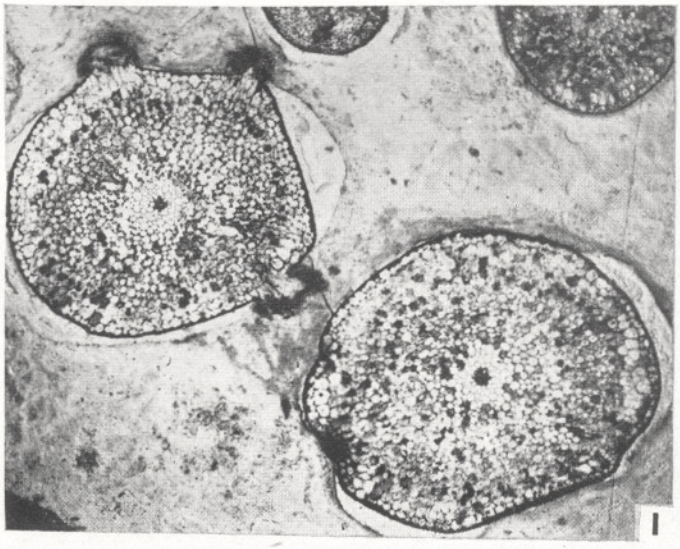
Rhynia gwynne-vaughanii (Kidston and Lang) Y. Lemoigne

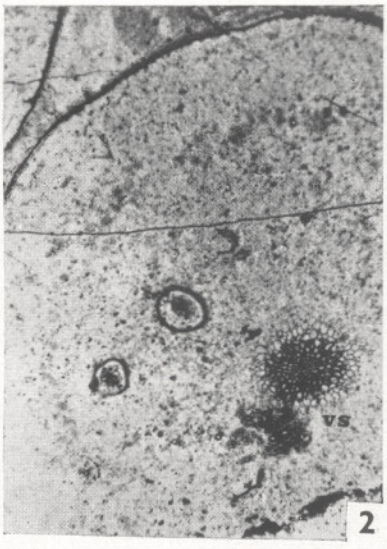
1. Two transversal sections of the axis of the gametophytes. We can see, on the left, a section with 3 archegonial protuberances. × 20.
2. A part of the transversal section of an axis of the sporophyte. × 25.
   vs — vascular strand.
3. Part *vs* of the fig. 2, vascular strand (protostele) with xylem, in the center, and phloem, of an axis of the sporophyte. × 50.
4. Transversal section of an axis of the gametophyte with 2 protuberances bearing rhizoids. × 25.
5. Stomata of the epiderm of the gametophyte. × 100.
6. Transversal section of an axis of the sporophyte: 2 protuberances with rhizoids can be seen on the right of the lower part of the figure (P). × 12.
7. A part of the transversal section of an axis of the gametophyte. × 40.
   st: stomata.
   p: protuberance bearing rhizoids.
8. A stomata of the sporophyte. × 200.
9. Part of the fig. 6: the two protuberances with rhizoids. × 30.
10. Epidermis with stomata of the sporophyte. × 40.

PLATE 2

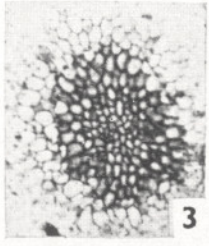
Rhynia gwynne-vaughanii (Kidston and Lang) Y. Lemoigne

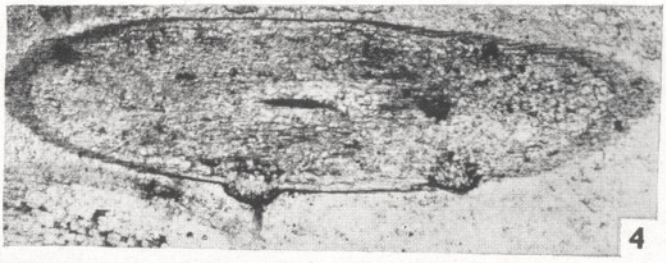
11. Transversal section of an axis of the gametophyte showing a beautiful archegonial protuberance (A). × 40.
12. Part (A) of the fig. 11. Archegonial protuberance showing at its top a rosette of four cells, between them is the opening of a canal leading down to an oosphere (oo) in the interior of the gametophyte. × 300.
13. Transversal section of an axis of the gametophyte; two archegonial protuberances (A) can be seen. × 30.
14. Part of the fig. 13: an archegonial protuberance with an oosphere (oo) surrounded by a layer of cells in regular arrangement. × 75.
15. Part of the fig. 16: a globular antheridium. × 60.
16. Transversal section of an axis of the gametophyte showing one antheridium (a). × 30.
17. Diametral section of an axis of the gametophyte: we see very well the vascular elements of the phloem. × 40.
18. Longitudinal view of the elements of the phloem of *Psilotum nudum*. × 300.


1



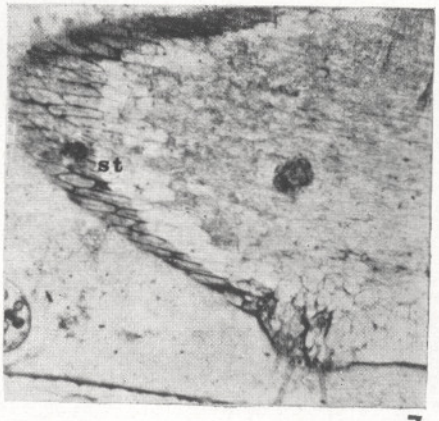
2


3


4

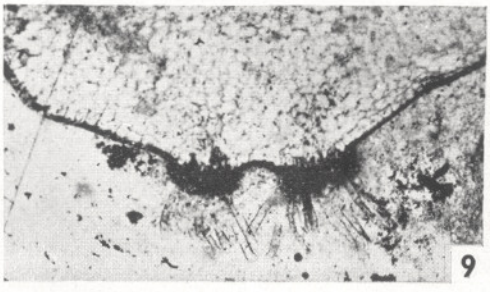

5

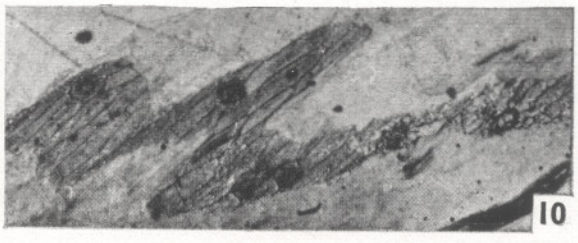
6



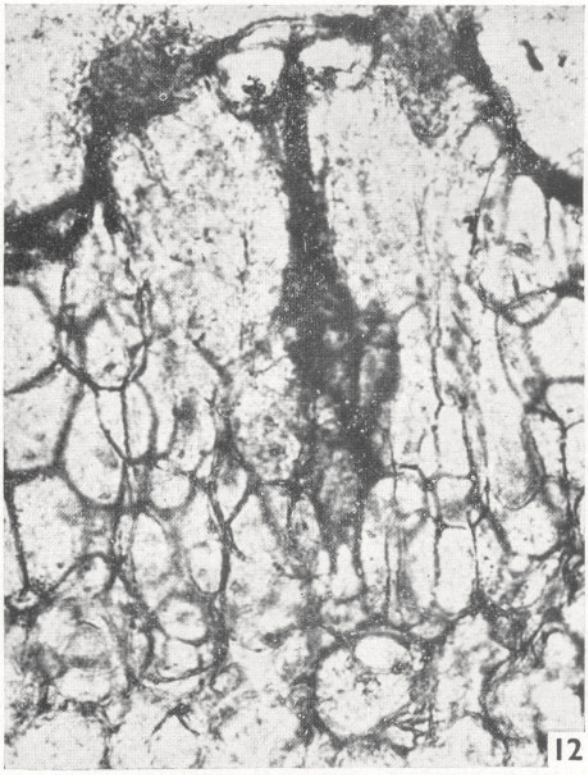
7

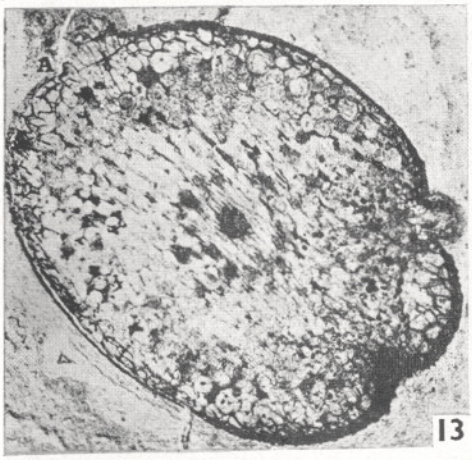

8


9

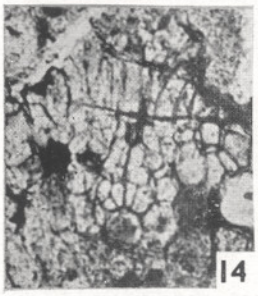

10

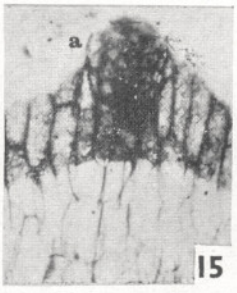
11


12

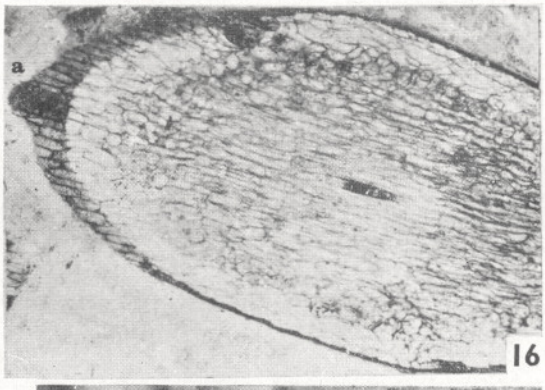


13


14

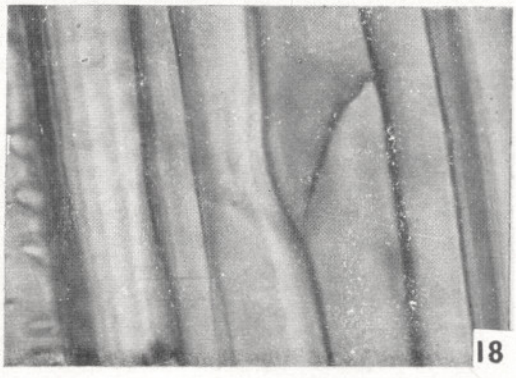


15



16


17


18