The Earliest Known Land Flora.¹

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THE vegetable kingdom is made up of plants of most varied size, character, and habitat. Comparing those various types, the view becomes ever more insistent that dependence on water is the master-factor determining their existence. As we range their diverse forms according to probable sequences of descent, those which we regard as the most primitive according to their structure and mode of reproduction are those which are habitually the most dependent upon constant water supply. It is the same with the animal kingdom. These broad results were summed up by Weismann some forty years ago in the statement that the birth-place of all animal and plant life lay in the sea. If this be true, it follows that all life on exposed land-surfaces has been secondary, and derivative.

Geologists tell us that from the remote past land-surfaces have stood exposed above the level of the ocean. The continents and islands may have differed from time to time in their outline and area from those of the present day. But we may believe that from a very early period land-surfaces have had a continuous existence, so that life upon land may itself have been continuous from the time when living organisms first emerged from their natal waters. Such beliefs throw back to the very remote past the possible origin of life upon dry land. But still the probability remains that aquatic life antedated that event. These considerations lead inevitably to the questions: When was dry land first invaded from the water? What were the first land-living plants and animals like? And how did they rank as compared with modern life?

Leaving zoologists to solve these questions for their own branch, we botanists are to-day in a better position than ever before to answer them with regard to plants. Though still far from being able to visualise the beginning of the story, recent discoveries have made it possible to see clearly and in detail the nature of the earliest known land flora, which is that of a period older than the Upper Devonian. During recent years fossil plants of early Devonian age have been found in Sweden and in Scotland in greater profusion than ever before, while the Scottish specimens are so well preserved that they are now almost as well known in structural detail as plants of the present day. Already in this room repeated lectures have been given on the Palæozoic flora. Many plants of the Carboniferous Period have been described here in microscopic detail, and they are mostly referable to affinity with such living types as ferns, club-mosses and horsetails. Some, such as the Sphenophylls and Pteridosperms, represent classes which have since died out. But, speaking generally, the flora of the coal is composed of plants comparable with

the lower vascular plants now living. They possessed stems, leaves, roots, and sporangia. Some even produced seeds like modern Gymnosperms.

Passing back from the Carboniferous period to the Upper Devonian, the flora, though more restricted, may still be described in terms applicable to the living vegetation. The plants include among others the gigantic fern-like *Archaeopteris hibernica*, from Kiltorkan, co. Kilkenny; the large Lycopod *Bothrodendron*, from the same source; and the large-leaved *Pseudobornia*, from Bear Island. Flat leaf-expansions are here seen, and the plants named have been referred in their general characters respectively to affinity with the ferns, club-mosses, and horsetails. But between the Upper Devonian and the strata that lie below geologists tell us that a vast period of time intervened. The evidence of the plant-remains supports this. The earlier Devonian fossils so far known are meagre in number of forms. In their characters they differ more markedly from the plants of the present day than any of their successors. They were rootless, and there appears to be a complete absence of large, flattened leaf-expansions. It is upon them that the new discoveries have shed so interesting a light. Conversely, that light is reflected back by comparison upon the more recent forms. In fact, a new chapter has been opened in plant-morphology, and a new class of vascular plants, the Psilophytales, has been established to receive these representatives of the oldest known land flora. The study of them is leading to new interpretations of the form shown by plants of later periods, and ultimately of the present day.

Until 1913 the plants of the early Devonian rocks were very imperfectly known. Their recognised characters were chiefly negative. There was no evidence of broad leaf-surfaces, nor was it clear whether or not they bore leaves as distinct from stems. The existence of true roots was also doubtful. The best known plants were constructed of approximately cylindrical stalks bearing lateral spines. These stalks arose from a branched and creeping base. Some of them showed crozier-like curves when young, and sporangium-like bodies were sometimes found upon them. The most distinctive of these plants were grouped by Dawson in his genus *Psilophyton*, and he published a reconstruction of the species *P. princeps*. It was, however, the subject of adverse criticism by his contemporaries, and the validity of the genus was questioned.

It was upon a field so open as this that light has now been shed. From fresh-water deposits of early Devonian age round Lake Rörågen, on the frontier between Norway and Sweden, Dr. Halle collected many specimens of fossil plants. But they were mostly impressions, and showed only imperfect preservation of their microscopic

¹ Discourse delivered at the Royal Institution on Friday, April 30.

structure. He distinguished several genera of plants with branched cylindrical stems bearing small thorn-like appendages, and some of them distal sporangia. Many of his specimens were referred to *Psilophyton princeps*, and bore out in the main the reconstruction of Dawson. Halle was able to confirm the existence of a central vascular strand in *Psilophyton*, consisting of tracheides, a fact which ranks it with certainty among vascular plants of the land. But the most distinctive novelty which Halle discovered in the Röragen beds was a fossil which he called *Sporogonites*. It consisted of a simple stalk bearing a terminal capsule. From its form, and the character of its contents, he held it to be a sporogonium comparable with that of the Bryophytes; but a generalised type, not referable to any exist-

the new observations of early Devonian plants in Scotland was recorded. Dr. Mackie, of Elgin, found at Rhynie, in Aberdeenshire, certain isolated blocks of chert containing plant remains. A little later the source of these blocks was traced to a bed of chert, older than the Upper Devonian, found *in situ* by the Scottish Geological Survey. Its origin appears to have been this. An exposed land-surface existed there in Middle or Lower Devonian time, subject to intervals of inundation. It became periodically covered by vegetation. By decay of its stems and underground parts a bed of peat would be formed. The peat was then flooded, and loose sand deposited over it. Again the vegetation was repeated, and so successive bands were formed to some 8 ft. in thickness.

Then followed water with silica in solution, supplied from some fumarole or geyser. The peat-bed was thus sealed up, and the plants preserved with astonishing perfection.

From this bed of chert four distinct vascular plants have been recognised, and described in the minutest detail by Dr. Kidston and Prof. Lang. They are all essentially similar in type, though sufficiently different to be placed in three genera, named respectively *Rhynia* (two species), *Hornea*, and *Asteroxylon*. *Rhynia* and *Hornea* are leafless and rootless, while *Asteroxylon* is also rootless, but it bears leaves of a simple type. The plants thus clearly indicate

Photo]

[Dr. Kidston.

FIG. 1.—Vertical section through the protocorm of *Rhynia Lignieri* with rhizoids, embedded in peat ($\times 14$).

ing group of them. An alternative suggestion was that *Sporogonites* may represent only the upper part of a more highly developed sporophyte, perhaps on the line of descent of the Pteridophytes. Thus the presence of *Sporogonites* does not actually prove the existence of Bryophytes as we now know them in the early Devonian rocks. But nevertheless it has a peculiar interest. Hitherto there has been no certain record of the existence of any moss-like type in the Palæozoic period. The demonstration of so moss-like a sporangium as *Sporogonites* is certainly the most thrilling of the facts brought forward by Dr. Halle.

In 1913, three years before Dr. Halle's publication of these discoveries at Röragen, the first of

a primitive state prevalent at that period. They conform in general features to the type of *Psilophyton* as described by Dawson, and as recognised in greater detail by Halle. But here in the Rhynie chert the structural details are so well preserved that these earliest of all known vascular plants can be examined and described almost as well as any modern living plants. Some have even been found standing erect as in life. Through untold ages, like the legendary Knights of the Round Table, they have thus awaited the revivifying touch of modern science.

Of the four plants so far described from the Rhynie chert, *Hornea Lignieri* is relatively simple. From a distended and lobed protocormous base rose the stems, which bifurcated. These bore

distal sporangia, which represent their transformed tips. Sometimes the sporangia were themselves forked. The protocorm was bedded in the peat, and parenchymatous, with many rhizoids (Fig. 1). The cylindrical stems stood upright from it, and were about 2 mm. in diameter. They were traversed by a simple stele with a solid core of tracheides, surrounded by phloem. The stele forked at the dichotomies of the stem, but stopped short at the base of the sterile columella, which ran upwards into the flat-topped, and apparently indehiscent, sporangium. The latter appears as a transformation of the end of the stalk, which is simply an ordinary branch of the plant. The spores are tetrahedral, as they are in all of these plants of the chert. The general aspect of *Hornea* is such as to provoke comparison with the Bryophytes, notwithstanding certain strongly divergent characters. This may have some real sig-

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[Dr. Kidston.

FIG. 2.—Aerial stem of *Rhynia major* seen in transverse section ($\times 20$).

nificance in view of its small size, and relatively simple structure.

Rhynia major is larger and better preserved, but still it also is structurally simple. It had a less distended rhizome, from which the robust cylindrical stems arose. These consisted, as in *Hornea*, of a central stele with solid xylem-core and investing phloem, surrounded by a massive cortex, of which the inner region appears to have been photosynthetic. Outside was a well-marked epidermis with stomata. These and the vascular tissue prove the aerial habit of the plant (Fig. 2). The stems ended in solitary massive sporangia, as much as 12 mm. in length, without a columella, and filled with tetrahedral spores (Fig. 3).

Neither of the species described bore any appendages on its stems. But *Rhynia Gwynne-Vaughani*, though smaller than *R. major*, shows a feature of morphological advance towards some-

thing in the nature of appendages. The upright stems bifurcate as before, bearing distal sporangia similar to, but smaller than, those of *R. major*. But near to their base there are "hemispherical projections," apparently of superficial origin. Some of these gave origin to tufts of hair, but others produced adventitious branches, which, having narrow bases, were easily detached, and served as means of vegetative propagation. Though these organs are not easily ranked with those of living plants, they are something in advance of what is seen in *Hornea* and *R. major*. The sporangia are relatively small, and there is no clear evidence of their dehiscence.

The largest, as it is also the most complex, of these plants is *Asteroxylon Mackiei*. Its base

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[Dr. Kidston.

FIG. 3.—Sporangium of *Rhynia major* filled with spores ($\times 54$).

consisted of branched rhizomes, which burrowed after the manner of Stigmarian rootlets, and each was traversed by a vascular strand with undifferentiated xylem; but curiously enough rhizoids are absent. These rhizomes passed over into upright aerial stems, which attained a diameter of as much as a centimetre, and had a complex structure. They forked, and bore externally small and simple leaves. The stele had a stellate xylem very like some Lycopods. From its rays issued strands passing to the bases of the leaves, but not entering them. As in Lycopodium, more than one vertical series of leaf-traces may issue from each

ray of the stellate xylem, a fact that confirms the Lycopod comparison (Fig. 4). Longitudinal

cortex of stem and rhizome often contain fungal hyphæ. It is possible that in the rhizome these

Photo]

[Dr. Kidston.

FIG. 4.—Large stem of *Asteroxylon* cut transversely just below a dichotomy, and showing leaves attached externally ($\times$ about 10).

sections show the relations of epidermis, cortex, phloem and xylem, and the way in which the inner

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[Dr. Kidston.

FIG. 5.—Stoma of *Asteroxylon Mackiei* in surface view ($\times 210$).

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may have been concerned in mycosliric nutrition. Higher powers demonstrate the tracheides as irregularly, or spirally, barred, but not scalariform. An endodermis has been seen delimiting the cylindrical stele, and mesarch protoxylem is found in the xylem-rays. The leaves are parenchymatous, the vascular strands stopping short at their bases. The epidermis has been found to bear very perfect stomata (Fig. 5). The essential points of structure of the plant are thus fully known.

In certain blocks sporangia have been found attached to profusely dichotomising stalks of simpler structure than the main stems of *Asteroxylon*, and not definitely attached to them. They are associated, however, with stems of *Asteroxylon*, while those of *Hornea* and *Rhynia*, from which they are structurally distinct, are absent from the blocks. The association makes it probable that these peculiarly forked branches and sporangia really belong to *Asteroxylon*. The sporangia are relatively small and pear-shaped, and they had a distal dehiscence. The whole plant of *Asteroxylon* was thus more advanced in various respects than any of the other three plants of the chert.

(To be continued.)