A CONTRIBUTION TO THE KNOWLEDGE OF THE RELATION BETWEEN PSILOPHYTON AND RHYNIA.

(From the Botanical Laboratory of the Groningen University)

by

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With one plate.

In 1871 the Canadian palaeontologist Dawson (1871, 1888), found in rocks of Devonian age of his native country some plant-remains, which by their habit showed a close resemblance to some marine Algae. These plants were named Psilophyton, Psilophyton princeps being the best known species. This plant possessed slender erect stems, springing from a creeping rhizome, and covered with numerous projecting, often recurved spines, which are often wanting on the thinner branchlets. They were dichotomously forked. The occurrence of sporangia at the top of the ultimate branchlets could be established. Besides this Dawson succeeded in demonstrating the presence of a central bundle, composed of scalariform tracheides. He considered Psilophyton to be a Pteridophyt, chiefly from this characteristic, though in its habit and in the situation of the sporangia it showed a departure from this group.

Afterwards this and allied forms were found in several places, in France, Germany, Bohemia, Norway, etc., in Devonian strata. At that period they seem to have had a widespread distribution. In many cases the deposits in which they occurred showed marine facies. This fact and

their habit being so different from that of the Pteridophyta and more resembling some of the Phaeophyceae, lead to the supposition that the views held by Dawson were erroneous and that Psilophyton belonged to the Sea-weeds. This view has lately been supported by Pohlig (1916, p. 225).

Some years ago, in the middle Devonian of Rhynie, Aberdeenshire, in Scotland, plant-remains were found, petrified by impetration with silicous matter, which showed many structural details. These petrefacts have been studied by Kidston and Lang, (1917—1921) whose investigations threw light on many interesting points. The chief result of their researches was the establishment of the fact, that these are the oldest land-plants known, and in many respects of a very simple structure.

The most typical form of this flora is the genus Rhynia, of which 2 species have been distinguished; their stems are rounded, slender, provided with protuberances and dichotomously forked; the sporangia are placed at the top of the branches. The stems possessed a central vascular bundle consisting of annular tracheides, surrounded by thinwalled tissue and a clearly defined cortex. The epidermis is provided with stomata. These features demonstrate the great resemblance between Rhynia and Psilophyton, on which the authors (1917, p. 776) and E. A. N. Arber (1921) has laid much stress.

The study of this resemblance is of a great importance; if they are identical, it will be possible to clear up some details, not only as regards their morphological features, but also as to their condition of life. This is important for judging whether a number of characteristics, which might be considered as primitive, are really so, or may be considered as adaptations to their mode of growth. For this reason I have investigated some Psilophyton material; I had also at my disposal some thin sections of Rhynia.

The former material is a piece of carbonate of lime, in which besides the Psilophyton-stems there were some shells of Primita spec. and also a scale of a Placoderm, Psilophyton thus being associated with marine fossils. It was from the Devonian strata of Canada, I do not know exactly where [1]). The Psilophyton-stems were of two kinds; some of them were slender, about $2^1/_2$ mM. broad, devoid of spines; others were broader, — 4 mM., with conspicuous spreading sometimes recurved spines. On the top of one the stems the spines were closely arranged. They were treated with Eau de Javelle, which gave a better result than Schultze's maceration liquid; with the latter liquid the pieces of charbonised matter retained their dark colour, became brittle and crumbled to pieces. I found the collodium method a great advantage; the well cleaned fossil was treated with a little of the collodium solution; after a short time the thin membrane could be removed and with it the often very small pieces of charbonised substance adhering to it.

This membrane was then placed in the bleaching solution, and as the collodium holds the particles together they are more easily handled and are less exposed to damage.

After 5 days in the liquid they were sufficiently cleared up for microscopical investigation. In some of them it was not possible to find any structure, in others many details were visible. These are well shown in a fragment about 2 mM. broad, of one of the smaller branchlets, which was removed as a whole from the substrate. It was possible with a needle to remove the cuticle from one side of the mineral substance, which occupied the space between the

1) On the label was written: Devonian, Crustacean, Scumenac, Canada. I am much indebted to Prof. Dr. J. H. Bonnema, who kindly placed the material at my disposal.

cuticles, so that it could be studied apart. The cast consisted of an uncoloured substance, which partly could be dissolved in hydrochloric acid, producing bubbles of gas. On one side a longitudinal strap of pigment, probably an indication of a former central vascular bundle, which was more resistent than the surrounding tissue, was seen. The cuticularisation had evidently extended to a portion of the vertical cell-walls abutting on the outer skin, for the network of cells is marked out with perfect clearness on the inner surface of the cuticle. The cells are arranged in longitudinal rows; their average breadth is about 50 μ the length varies from 50 to 100 μ; the transverse walls are mostly placed at right angles to the longitudinal walls, but sometimes oblique. My attention was drawn to a pair of cells which are reniform in shape, each being half as broad as an ordinary cell. This complex shows a great resemblance to a stoma, but near this group there are two similar but less typical groups of cells; a third group is to be seen on the right side which forms a transition over to the ordinary type of cell. Perhaps this can be explained as being rudimentary stomata in which the divisions of the epidermal cells have taken place, but where the differentiation has been arrested. The dark-coloured lines, which separate the lumens of the cells, when examined with a higher magnifying power, appeared not to be homogenous, but as having a longitudinal groove. This is seen as a bright line, about 1 μ broad, running in the dark-coloured band of cuticular substance. In another preparation the arrangment of the cells was less regular; in some of them the cuticle was thickened in its middle part. From this dark spot a longitudinal ridge runs to the adjacent cells. Concerning the chemical composition of the cuticular substance it could be stated, that the pieces of the cuticle deeply stained red with Safranine. With Sudan III after heating, it took also a red colour, very evident, but some-

what obscured by the yellow brown colour of the cuticular substance.

In this respects the cuticles agree with those of existing plants, so that the supposition seems justified that the cuticle of Psilophyton was composed of cuticular substances of the same nature as in existing plants. If it be true, that this fossil belongs to the Devonian, of which I have no doubt, this is as far as I know the oldest occurence of cuticular substance. (Potonié 1920, p. 185).

When the material had been in the bleaching liquid for 24 hours a small piece of it drew my attention by its brighter colour, while the other parts were still darkly coloured. Under the microscope it appeared to consist of an aggregate of spores held together by interwoven mycelium threads. In glycerine by slightly pressing on the cover glass the spores could be separated from each others. Most of them were globular, some of them elongated or elliptical, sometimes adhering to each other, forming a short chain.

The diameter of these spores was about 30—40 μ their wall thin, the content brown, with some long crystals, often aggregated, suggesting a nucleus. Some of the cells were burst so that the dark content had disappeared; the wall now was seen to be without colour. The mycelium threads were colourless also and very thin-walled; they were repeatedly forked without any transverse walls.

If we compare these features with those known in Rhynia, it is evident that similar characteristics are present in the latter also. The occurence of a central vascular strand has already been discussed by previous authors. The dimensions of the cells are nearly of the same order; in Rhynia Gwynne-Vaughani e,g. they are about 50 μ broad (Kidston and Lang 1917, fig. 32) as in Psilophyton; the length varies. In fig. 31 the cells have a dark spot in the middle: sometimes there is a longitudnal ridge as is the case in Psilophyton.

The fungus which occured on Psilophyton is identical with Palaeomyces agglomerans, described by Kidston and Lang (1921, V, p. 862. fig. 39—41); it occurred not only in the tissues of Rhynia major, but also in the matrix and on the outer surface of the plants.

The structure of the outer walls of the epidermis in

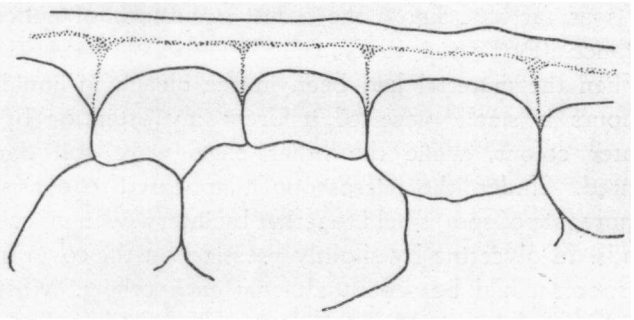

Fig. 4. Rhynia major Kdst. and L. Transverse section of the outer wall of the epidermal cells.

Rhynia was very seldom preserved; in some thin sections [1]) however I could see some details. On the outer side of the epidermis there is a cuticle of only a few μ thick. Its substance is clearly defined from the rest of the preparation by its brighter yellow colour. In many cases only this cuticle is shown; in other places however there is a similar layer, having the same colour and structure on the inner side of the wall, doubtless of the same nature. Between this layer there is some pigment, which is continuous in the radial walls between the epidermal cells. These facts lead to the supposition that in a number of cells cutine layers are disposed on the inner side of the primary cell-wall only to the surface of the leaf; in transverse section

[1]) E.g. in section B 34 of the Palaeobotanical collection of the Botanical Laboratory, Groningen.

they are separated from each other by the radial walls of the epidermal cells and from the outer cuticle by the primary cellwall. The pigment which occurs in the thin sections is a remainder of the latter.

When an epidermis is altered during fossilisation, the cuticular substance because of its different chemical composition was more resistent to decay, and after treatment with Eau de Javelle the radial walls of the epidermal cells wholly disappeared, thus leaving a furrow in the cuticular substance which is seen as a line in the dark-coloured bands, which mark the boundary between the epidermal cells, In this way the somewhat peculiar structure of the cuticle in Psilophyton might be explained in accordance to the structure of the cuticle of Rhynia.

Thus the resemblance between Psilophyton and Rhynia is not only in their general habit and in the position of the sporangia, but also the structure of the cuticle shows similar features and on both plants the same fungus lived. The presence of a well developped cuticle and cuticular layers combined with the habit and the presence of rudimentary stomata suggest a xerophytic habit. The supposition that these plants were sea-plants seems no longer tenable.

Litterature.

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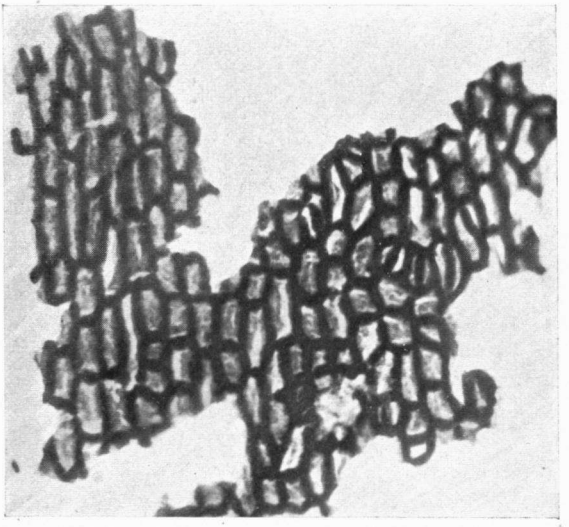

Fig. 1. Psilophyton spec. Surface view of a part of the cuticle. The abortive stomata are shown on the right.
50 ×

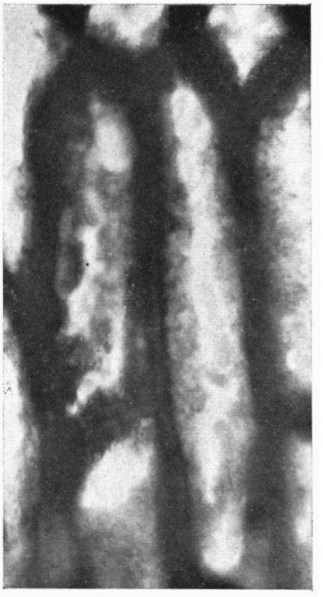

Fig. 2. Psilophyton spec. Some cells of the left of the cuticle of fig. 1, showing the groove between the cells.
250 ×

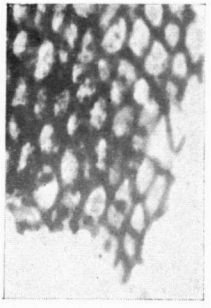

Fig. 3. Psilophyton spec. Surface view of another part of the cuticle, showing the darker central spot and the longitudinal ridge.
50 ×