On *Aecidium graveolens* (Shuttlew.)¹.

BY

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With Plate XIV.

IT was stated by Jacob Eriksson in his work, *Studien über den Hexenbesenrost der Berberitze* (*Puccinia Arrhenatheri*, Kleb.²), that the mycelium of the Rust of the Witches' Brooms of *Berberis vulgaris* (which had been named *Aecidium magellanicum*, Berk., in consequence of my remarks on the subject in Hedwigia, 1876) grows in the interior of the cells of the cambium of the witches' broom. In a paper published in the *Berichte d. Deutsch. Bot. Ges.*, Vol. xv, 1897, pp. 148-152, I questioned these observations, and showed that an intercellular mycelium occurs in the branches of this plant in the pith, in the cortex and in the phloem, which sends out knot-shaped haustoria into the neighbouring cells; but I was unable to observe the intracellular mycelium described by Eriksson.

In a subsequent paper³ this author criticized my results, stating that he had observed only the cambium, while I had given most attention to the pith and the tissues of the cortex, and therefore my observations counted for little as regards

¹ Read before Section K of the British Association, Toronto, 1897.

² Cohn, *Beiträge zur Biologie der Pflanzen*, Vol. viii, Heft I.

³ *Berichte der Deut. Botan. Ges.*, Vol. xv, 1897, pp. 228-231.

the cambium. As I had, however, looked for the mycelium in *all* the tissues of the stem, as is evident from my paper, 'Ueber das Mycelium des *Aecidium magellanicum*, Berk¹,' this criticism is of little weight. Eriksson in fact admits that I had investigated the cambium when he quotes my statement that I did not find the mycelium in it. He further states that while he had worked with living material, I had only examined specimens preserved in alcohol. I do not regard such an objection as a reasonable one; nevertheless this year I have expressly used living material, and have obtained the same results. I have also extended my observations to ascertain how and where the mycelium develops in the branches of the witches' brooms, how it arises in the buds, and how it develops in the leaves which, even in the bud, are covered with the fructification of the Fungus.

For these observations I was able to use material rich in the fungus which was sent to me by Hofgärtner Reuter from the Pfaueninsel near Potsdam, on April 24, 1897, and by Herr J. A. Bäumler, from Pressburg in Hungary, on May 8, 1897. I owe my best thanks to these two gentlemen for this material. The latter was especially valuable to me, inasmuch as it consisted of a large number of young buds growing into elongated branches.

Of course I was not able to decide, in response to Eriksson's wish, whether this mycelium is derived from aecidiospores or from sporidia of germinated teleutospores. Up to the present time we do not know of any observations supporting the idea that such mycelia are different in any respect except in their extension in the host-plant. I have shown in earlier papers that the mycelium developed from the sporidia of the hibernated teleutospores often extends further into the tissue of the host-plant than that derived from the germinating uredospores or aecidiospores, which form in most cases a mycelium restricted to the region of infection (e.g. *Puccinia Oreoselini*, Strauss., and *P. Cyani*, Pass.): but no other

¹ Berichte der Deut. Bot. Ges., Vol. xv, 1897.

difference in the relation of these mycelia to the tissues of the host-plant has ever been observed. Therefore I cannot accept Eriksson's hypothesis that the mycelium of the aecidiospores can bear any relation to the tissues of the branches of the witches' broom, differing from that of the mycelium developed out of the germinating sporidia of the teleutospores.

The investigation of the fresh material, as I have already mentioned, has confirmed my earlier observations. The hyphae are always intercellular, and put out knot-shaped haustoria into the cells between which they grow. They occur in the pith, in the cortical parenchyma, in the phloem, and in the medullary rays (I had forgotten to mention the last in my communication of February, 1897). In the medullary rays the walls of the cells on which the hyphae grow are swollen (Figs. 7-9), and the hyphae send out numerous knot-like haustoria into the parenchymatous cells. I could not be certain that haustoria are also sent out into the wood-cells bordering on the medullary rays. I believe that this does take place, but I am not satisfied that the cells in which it seems to occur are not medullary ray-cells. In the elongated cells of the phloem the branches of the haustoria are sometimes not coiled up into a knot, but lie free in the cell (Fig. 6). The branches are not straight, but are curved or crumpled, and constricted here and there. As I have described earlier (*loc. cit.*), the mycelium is formed in the young branches of the witches' broom in the pith, in the medullary rays, and in the primary cortical parenchyma. In the latter it is often cut off from the surrounding tissue by the formation of cork in the infected tissue, so as to form island-like masses in the cortex¹.

Out of the primary cortical parenchyma in the older twigs the mycelium grows into the phloem and gradually penetrates into it as development proceeds. In the phloem also the infected parts of the tissue are often enclosed as islands by the formation of cork. These ring-like formations of cork

¹ Vide Berichte der Deut. Bot. Ges., Bd. xv, 1827, Taf. iv, Fig. 5.

give a very characteristic appearance to the transverse sections of the older stems of the witches' broom. In these mycelial hyphae, which have a very small lumen, I have never observed the yellow colouring-matter of the Uredineae described by Eriksson (*loc. cit.*) in the mycelial filaments of the cambium, which he states are intracellular. I will at once remark that I have generally observed the yellow colouring-matter of Uredineae only in the mycelial filaments which are exposed to the light, never in those portions of the mycelium which are embedded so deeply in the tissue of the host-plant as not to be exposed to the light.

As I have already stated elsewhere¹, the spermogonia appear on the whole surface of the first leaves, which are developed in April and the beginning of May, and the aecidia appear between the spermogonia; on the later leaves of the infected buds are found single larger or smaller groups of aecidia only, while the latest formed leaves are altogether free from the Fungus. At the end of April or the beginning of May a large number of these buds had already put out branches with long internodes. The leaves of these branches are free from the Fungus, as I have said. If longitudinal sections of these long branches be examined at the end of April or beginning of May, the hyphae in the pith will be seen growing in a longitudinal direction into the region of the merismatic tissue (Fig. 1). These mycelial strands are intercellular, and occur in the actually dividing cells of the parenchyma of the pith. The cells around these mycelial strands are sometimes more elongated than the others, and remain for some time in this condition, while the neighbouring cells are undergoing transverse division (Figs. 2, 4). This intercellular mycelium often sends into these neighbouring parenchymatous cells haustoria of the same kind as those already described (Figs. 2, 4). From these longitudinal mycelial threads horizontal threads grow out laterally (Fig. 2). These are the threads which grow into the medullary rays,

¹ Verhandl. des Botan. Vereins der Provinz Brandenburg, Sitzungsberichte, 1875, pp. 87-89 (which was also published in Hedwigia, 1876, No. I).

and especially into the spaces between the vascular bundles where the leaves come off. These mycelial strands grow next spring into the buds which are formed at this place, and form spermogonia and aecidia over the whole surface of their leaves.

I will here shortly recapitulate these observations. The mycelium always grows between the cells, and gives off haustoria into them. In the first spring the hibernating mycelium grows into the developing buds, and forms spermogonia and aecidia on the whole surface of the first leaves. In the case of those short shoots which grow out into branches with long internodes, the mycelium grows directly into the pith and continues to grow with the merismatic tissue. This also takes place in the spring. From these medullary mycelial strands branches grow outwards, but these do not penetrate into the leaves. They pass through the medullary rays into the primary cortical parenchyma, and especially through the openings in the vascular cylinder, where the young leaves are given off to the axillary buds, from whence, in the following spring, the mycelium enters into the first developing leaves. As the branches of the witches' broom increase in thickness, the mycelium spreads from the primary cortical parenchyma into the phloem. Both in the primary cortical parenchyma and in the phloem the rows of cells affected by the mycelium are enclosed more or less completely by a cylindrical cork-formation, and are thus separated from the less affected tissue.

What, then, is the tubular mycelium in the cambium-cells described and figured by Eriksson (*loc. cit.*, Fig. 5, Pl. II), containing, contrary to what is observed in the mycelial strands of Uredineae growing in tissues not exposed to light, the yellow colouring-matter of the Uredineae? Leaving aside for the present the yellow colouring-matter, his figure resembles more than anything else the young cells of the cambium with horizontal transverse walls, the contents of which are contracted by plasmolysis. It is often the case in elongated cells that the plasmolyzed contents are for the

most part retracted only from the longitudinal walls, while remaining more or less in contact with the short horizontal or oblique walls (Fig. 10). These contracted cell-contents then resemble a tube placed longitudinally in the empty cells, and if the plasmolyzed contents are not retracted from the common transverse wall of neighbouring cells, they present the appearance of a continuous tube passing through the cell-cavities. Eriksson's figure appears to me to strongly suggest such plasmolytically contracted cell-contents, although it must be borne in mind that I have not examined Eriksson's preparations.

It is well known that the wood of the young Barberry is yellow, and that this is caused by the yellow cell-sap which is found even in the young wood-cells, thus indicating that the colouring-matter exists in a state of solution, and not in the form of yellow granules. The yellow colouring-matter of the granules observed by Eriksson in the tubes, which appear to me to be nothing more than plasmolyzed cell-contents, may be connected in some fashion with the colouring-matter of the young wood-cells. In making preparations, if the cells are cut across, the yellow sap flows out into the water, and then they appear colourless. The granules of the young wood-cells do not appear yellow. I cannot decide whether the yellow tint of the granules figured by Eriksson may not be due to the colouring-matter of the wood-cells seen through the cambium-cells (especially as Eriksson mentions in a foot-note to his paper in the *Ber. d. Deutsch. Bot. Ges.*, Vol. xv, 1897, p. 229, that *all* the granules appeared yellow, and not as the lithographer has by mistake indicated, a few of them only), or whether they represent the first appearance of the yellow colouring-matter of the wood-cells. In no case have I been able to observe in the mycelium of any of the Uredineae not exposed to the light any trace of yellow colouring-matter. Even in the mycelium of the cortical parenchyma and the phloem no colouring-matter is found.

It seems to me that these results are of special interest, because Eriksson has lately maintained the theory of the

‘mycoplasmastadium’ of Uredineae¹. In the case under discussion we can observe in succession the mycelium itself entering the buds, wintering there, and the following spring penetrating into the young leaves of the sprouting shoots, and there developing organs of fructification. The annual development of this parasitical Fungus does not exhibit the ‘mycoplasmastadium’ of Eriksson. There is no ground here for such a theory.

In conclusion I will give a short account of the identification of the European species producing the witches’ broom on Barberry. In 1875 and 1876, when I had distinguished the aecidium producing the witches’ broom of *Berberis vulgaris* from the aecidium of *Puccinia graminis*, I at first thought I had discovered a new species; but I found afterwards, to my great surprise, that Berkeley had described in Hooker’s *Flora Antarctica*, II, pp. 450–451, a similar aecidium on *Berberis ilicifolia*, Forst., from the Straits of Magellan, and then I identified it as *Aecidium magellanicum*, Berk. On the ground of the similarity of appearance of the parasite, I believed that the aecidium of the witches’ broom in Europe was identified with this aecidium of Berkeley, and accordingly I named the fungus causing the witches’ broom of *Berberis vulgaris*, *Aecidium magellanicum*, Berk. All the later authors have followed me. Subsequently this identification appeared to me doubtful, as the cultures of Peyritsch and Eriksson had demonstrated that *Puccinia Arrhenatheri* (Kleb.), Eriks., (= *P. magellanica*, Peyr.) on *Arrhenatherum elatius* belongs to the aecidium of the witches’ broom of *Berberis vulgaris*, whilst no *Arrhenatherum* or *Avena* occurs in Patagonia. In the *Berichte der Deutsch. Bot. Ges.*, Vol. xv, 1897, pp. 270–276, I have shown that in Patagonia and Chile another aecidium occurs on *Berberis buxifolia*, Lam., which causes witches’ broom, and which is well distinguished from the European species by the remarkable nestlike formation of

¹ See ‘Vie latente et plasmatique de certaines Urédinées,’ *Comptes Rendus*, 1897, Mars, and ‘Der heutige Stand der Getreiderostfrage,’ *Berichte der Deut. Bot. Ges.*, Bd. xv, 1897, pp. 192–194.

its growth on single nodes, by the withering of the branches, by the swelling of the nodes which bear the witches' brooms, and by the absence of spermogonia. I have called this species *Aecidium Jacobsthalii Henrici*, P. Magn. It differs also from the *Aecidium magellanicum*, described by Berkeley on *Berberis ilicifolia*, Forst., which may be a third species attacking *Berberis*. The European Fungus forming the large witches' broom on the Barberry, with a great many elongated erect branches, can therefore no longer be called *Aecidium magellanicum*. It may be designated either as *Aecidium graveolens*, Shuttlew., which name was found by Cooke in the Paris Herbarium, or as the aecidium of *Puccinia Arrhenatheri* (Kleb.), Eriks.

I am deeply indebted to Mr. Harold Wager for having translated my German manuscript into English.

EXPLANATION OF FIGURES IN PLATE XIV.

Illustrating Prof. Magnus' paper on *Aecidium graveolens*.

The figures which accompany this paper were drawn from nature in my presence by Dr. Paul Roeseler.

Fig. 1. Longitudinal section of apex of spring shoot (in May, 1897) developed from a bud of witches' broom. At M. M. the mycelium is seen growing in the pith up to the merismatic region of the apex. $\times 68$.

Figs. 2 and 3. Portions of Fig. 1 more enlarged. Fig. 2 from part marked *A*, and Fig. 3 from that marked *B*. Showing longitudinal tracts of intercellular mycelium with some haustoria: at *A*. a horizontal tract is given off. $\times 420$.

Fig. 4. Similar longitudinal section of pith at apex of spring shoot, with intercellular mycelium and haustoria. The parenchymatous cells near the mycelium are more elongated than the others, and less divided by horizontal walls. $\times 420$.

Fig. 5. Transverse section of young pith, with transverse sections of intercellular mycelium-threads. The walls in which the mycelium-threads occur are swollen. $\times 420$.

Fig. 6. Longitudinal section of the phloem of an infected branch of witches' broom. In the elongated cells the haustoria are not knot-like.

Fig. 7. Medullary ray in transverse section of an infected stem, with mycelium and haustoria. $\times 420$.

Figs 8 and 9. Medullary rays in tangential section of an infected stem, with mycelium and haustoria. The walls in which the mycelium-threads occur are much swollen. $\times 420$.

Fig. 10. Tangential section of the very young wood in the neighbourhood of the cambium. The cell-contents are plasmolytically contracted, and withdrawn from the longitudinal walls, but not from the oblique transverse walls. $\times 420$.

Fig. 1.

Fig. 3.

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Fig. 7.

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Fig. 8.

Fig. 9.

Fig. 1.

Fig. 3.

Fig. 4.

Fig. 6.

← B →

← A →

Fig. 2.

Fig. 5.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 7.

Magnus, P. 1898. "On Aecidium graveolens (Shuttlew.)." *Annals of botany* 12, 155–163. <https://doi.org/10.1093/oxfordjournals.aob.a088688>.

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