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Anatomical Observations of the Parasitism of *Cuscuta*

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In honour of the 85th anniversary of Professor Dr. Bohumil Němec.

Parasitism of *Cuscuta* has been observed for a long time. As early as 1827 H. von Mohl had devoted attention to it, and a number of other authors contributed in subsequent years to the knowledge of the way of life of this interesting holoparasite. Thorough anatomical observations were made in 1860 by W. Uloth, and his work was then the basis for research done by other authors. In our country K. Spisar (1910) experimented with *Cuscuta Gronovii* Willd. Knowledge concerning the anatomy of the haustoria of the *Cuscuta* was summarized by A. Sperlich (1925), though not in any exhaustive way. Among the other works on this subject we must draw attention to the thorough study by A. Kindermann (1928). In my own study I should like to point out a few interesting facts of which I have found no mention in the literature available to me, or which differ somewhat from the data given in this literature.

I noticed the phenomena when examining microscope preparations of *Cuscuta epithymum* (L.) Murr., for which clover was the host. I had been preparing these preparations for a number of years for pedagogical purposes. On the basis of these observations I began purposefully to gather material in 1956, in order to test the previously observed phenomena or elucidate those which had not been too clear to me. I gathered this material in the vicinity of Těnovice, near Pilsen. The specimens were fixed in FAA, embedded in paraffin (see J. Pazourek and Z. Pazourková, 1956) and cut with a microtom. The cuts were 15 μ thick. After removing the paraffin they were stained with safranin—aniline blue, with safranin-light green and by the Cajal-Brožek method. I observed the starch both in polarized light and in the preparations stained, after removing paraffin, in Lugol solution and light green.

I enclosed the preparations in solvent polymer "Metaplex" B 34/31 (Kramář, J., 1954).

The first interesting problem I observed was the parasitism of *Cuscuta* on *Cuscuta*. This is a frequent, although not very well known, phenomenon. W. Uloth (1860) mentioned it and K. Spisar (1910) points out that this is a very important fact in the life of *Cuscuta* and explains its purpose. I have found no mention of this problem in the most recent literature on the subject. One may observe three types of anatomical pictures in the microscope preparations. The first is that one *Cuscuta* is at least locally separated from the host, the second twines around it and sends haustoria into it (see Fig. 1). This circumstance could surely be expected, for the phenomenon of one parasite twining around the other and sending haustoria into it is well known. In the same way one branch of the stalk of *Cuscuta* can be a parasite on another or on the main stem. Another type of parasitism of *Cuscuta* on *Cuscuta* is for two stems to run parallel to one another, sending haustoria into each other (see Fig. 2). This instance of parasitism is interesting for several reasons. We know from literature on the subject that *Cuscuta* forms two types of spiral: steep, or rising at a greater angle, and gradual, denser, rising at a smaller angle. The plant is most sensitive on the touch irritation just in these dense spirals. In the present case the haustoria were formed, although the spirals were very steep or the two stems ran almost completely parallel. In addition, the pressure irritating the *Cuscuta* so that it sent haustoria into the other must have been very slight, for even in this case the host *Cuscuta* grew (at least in a certain section) separate from the primary host plant, thus lacking any support whatever. So far I have not succeeded in determining whether one *Cuscuta* is always the parasite and the other always the host, or whether they send the haustoria mutually into each other.

The third case occurs when one *Cuscuta* parasitizes some host and a second *Cuscuta* twines about it and the host, too, sending haustoria into both. The microphotograph (Fig. 5.) shows a rare case of the above-mentioned phenomenon. That is, it presents in one section both the parasite twining around the host (clover), sending haustoria into it, and the second parasite which is just sending haustoria into the first parasite and into the host. We must also note that stem of the first parasite twines around the stem of the host in a very steep spiral, and yet it sends haustoria into it. W. Uloth asserts that in all such cases of parasitism, either of one *Cuscuta* on another or of a secondary branch on the main one, the haustoria never have tracheids. On all my microphotographs it can be clearly seen that in all the above-described cases tracheids are actually formed in the haustoria. Fig. 6 shows the reticulate thickening of the tracheids from the haustoria which one *Cuscuta* sends into another in the case given in Fig. 5. According to A. Kindermann (1928), tracheids differentiate in the haustoria only if there is connection with the water-conducting elements of the host. In all three above mentioned cases I have actually observed the attachment of the tracheids of the parasitic *Cuscuta* to those of the *Cuscuta* serving as host.

There are a large number of starch grains in the cells of the *Cuscuta*. On closer observation I found that these were complex starch grains with several centres, in extreme cases as many as twelve. These grains can be found in well nourished parasites, not only in the stems and scales, but also in the praehaustorium and in small amounts in some of the cells of the haustorium. However, I found them also in flower stems, in petals and in a markedly simplified form in the pistils and even in the integuments of the ovula. But if the *Cuscuta* parasitizes on another *Cuscuta* without direct relation to the host (Figs. 1 and 2), the amount of starch in the cells is markedly reduced. In some cells we find no starch grains at all, in others only a few. Their form is also simplified so that they have only one centre, or three at the most. Even though quantitative evaluation would be necessary for precise explanation, still one can judge at first glance, according to the starch content, that the parasites are far worse nourished than those in direct contact with the host. In regard to the general development of both plants of *Cuscuta* one may say that they came in contact with the host and that they sent haustoria into it. Since, however, they grew further separated from the host, in the later development and for certain reasons, the nourishment given the previously developed haustoria sufficed for quite normal development, but not for the formation of supplies of starch in the usual amount. Quite definitely, the total amount of starch in both these plants is much smaller than the amount of starch contained in a plant which parasitizes in the usual way. In the tissues of the parasitizing *Cuscuta* we may find perhaps slightly more starch than in the host *Cuscuta*, but the differences are usually not great.

If the *Cuscuta* parasitizes on the stem of clover and another *Cuscuta* parasitizes on it, sending haustoria not only into the first but also into the clover, the amount of starch in both plants is considerable. There is smaller starch content in the stems parasiting on leaves. In the stems which were not attached to the host in a certain part, there was very little starch, but, still, more than in the above-described cases of mutual parasitism of *Cuscuta* on *Cuscuta*, if both stems were locally separated from the host. At the same time it seems that the complexity of the starch grains is in direct relation to their amount.

It is apparent, therefore, that the decreased amount of reserve starch in the *Cuscuta* is caused by the fact that the parasite does not get enough nourishment from the host; mutual parasitism only increases the final effect. At the same time it would be important to determine whether it was not a question of higher osmotic values by transferring the starch into soluble, osmotically active glycides (E. Bergdolt, 1927; M. Lilienstern, 1932).

The parasitic *Cuscuta* harms its host in various ways and to various degrees. For instance, we can see in the case of clover that the affected plants first lag in growth and in development, then turn yellow and finally die. In our observations, however, we never found a case in which the tissue of the stalk died in the vicinity of the haustorium. O. Gertz (1915, 1918), who studied the anatomical relations between host and parasite, also mentions no such occurrence. It is quite different when the *Cuscuta* is a parasite on leaves. The tissue of the leaf to a relatively great degree dries up and dies, in the vicinity of the haustorium. The haustorium itself also dies. The transition from the living and dead part of the leaf is usually relatively sharp (see Fig. 4). If we observe the microscopic picture of the living leaf into which the haustorium is penetrating (Fig. 3), we see that the relation between the parasitic tissue and the tissue of the host is substantially greater, to the benefit of the parasite, than is the case with the stems. The haustorium penetrates the entire thickness of the leaf and its absorbing cells reach the epidermis on the other side of the leaf. At the same time its tracheid system connects with the small vascular bundles of the leaf and thus causes a lack of nourishment in the surrounding parts of the leaves. This, of course, is seen most markedly when the *Cuscuta* sends its haustoria into the margin of the leaf; in the centre the tissues can resist the attack better.

Another interesting phenomenon which I have observed is the position of the nuclei in the epidermal cells of the cushion. These original epidermal cells of the praehaustoria, when placed on the stem and during the further formation of a cushion change to a cylindrical shape. The nuclei of these cells have a relatively permanent position. That is, in most cases we can observe in the preparation that all are placed in approximately the same place in relation to the cell; this is usually near the membrane which touches the host, or at least in that half of the cell which is directed towards the host. This phenomenon can also be seen clearly in the microphotographs of the work of A. K i n d e r m a n n (1928) who stained the preparations with haematoxylin so that the nuclei can be easily perceived. Although I did not study this phenomenon any further, still it is so striking that I believe that it is one example of the activity of the nucleus.

I should like to mention further a circumstance which is related to the placement or attachment of the cushion on the host. Different authors explain this problem in different ways. It has been difficult to decide this question up until now. But I noticed in all the observed preparations that there is a certain distance between the cushion and the host. This is evident in all the microphotographs, photographs and sketches of various authors. But the important circumstance is that the profile of the surface of the cushion represents a precise negative of the surface profile of the host's epidermis. There always has been very close connection here, therefore, with the cylindrical cells of the cushion always adapting the shape of their surface to that of the surface of the epidermal cells of the host. This can best be seen in Fig. 3, where it is evident that individual cells of the cushion have the membrane, which is turned to the host, not concave in shape, as might seem to be the case in parasitism on the stem; the entire surface of the cushion touching the host is curved concavely, even when the cells are of differing size, and several cells of the epidermis of the cushion cover one cell of the epidermis of the leaf. The above-described fact testifies to the close attachment of both surfaces, and it seems to speak for the theory that the cushion is held to the host by pressure of the surrounding atmosphere, or by the subpressure created by the separating off of closely adhering areas. Of course it is also possible that the force of the twining stem also takes part in the pressing on of the cushion. This question should be solved by special experiments, for one thing would contradict the theory that the force is exerted by the twining stem: as has already been said, the haustoria form even where the stems do not twine around each other, and here the stem exerts no pressure, or very little. One sees (Figs. 1 and 2) that despite this fact the adhesion was very close even here. The illustration in the study by S p i s a r also shows that the pressure of the twining stem could not be great, otherwise the leaf (willow) around which it twined would have been crushed. But this does not occur, and the same can be said of a number of other specimens such as trefoils, various grasses, eyebright, plantain, etc.

How, finally, the observed gaps do arise, it is hard to say, of course. It is possible that there was mechanical separation in gathering the specimen or twisting in preparing them (especially in fixing or passing through the alcohol series). But there is also a further possibility, that when the haustoria penetrate the plant and are firmly attached to the tissue of the host the cushion loosens with partial prolongation of its own haustorium runners.

S u m m a r y

Different kinds of parasitism of the *Cuscuta* on another *Cuscuta* are described in this paper, from the standpoint of plant anatomy. It was found that in all cases tracheids were formed in the haustoria of the parasitic stem. Attention was also given to the amount and shape of reserve starch-grains. The amount of starch declines in those places where the stem is, at least in a certain section, separated from the host. If it is parasitizing still another stem, the starch content is even further reduced. The complexity of the starch grains also declines as the starch content declines.

Parasitism on leaves was also observed and it was found that haustoria penetrate the entire thickness of the leaf to the epidermis on the other side. If the haustoria are sent into the margin of the leaf, the surrounding tissues die.

On observing the position of the nuclei in the cylindrical, epidermal cells of the cushion,

it was found that there was a tendency to localization toward the host. The surface of the haustoria is a precise negative profile of the surface of the epidermis of the organ affected.

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T e x t t o t h e p l a t e s

Plate VIII. – Fig. 1. – Parasitism of *Cuscuta* on *Cuscuta*. The parasitic stem twines in dense, gradual spirals around the stem of the host *Cuscuta*.

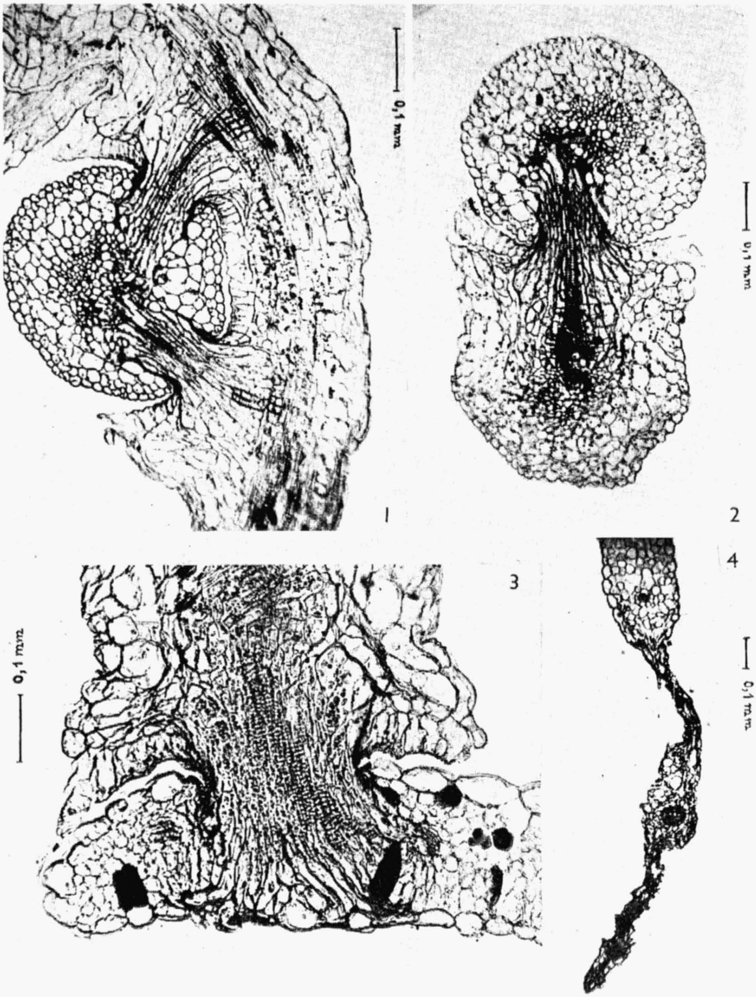
Fig. 2. – Parasitism of *Cuscuta* on *Cuscuta*. The parasitic stem runs approximately parallel to the stem of the host *Cuscuta*.

Plate IX. – Fig. 3. – Haustorium penetrating the margin of leaf of *Lotus corniculatus* L. The absorbing cells penetrate into the epidermis on the opposite side of the leaf.

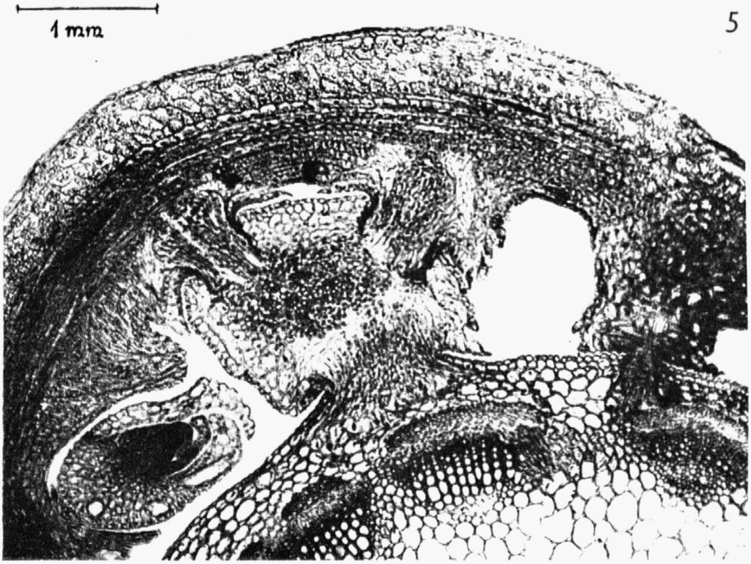
Fig. 4. – Leaf margin of *Plantago lanceolata* L. attacked by *Cuscuta*. The tissue near the haustorium is dying.

Fig. 5. – Parasitism of *Cuscuta* on *Cuscuta*. The affected stem runs approximately parallel to the stem of the plant host (clover), and sends haustoria into it; the stem of the parasitic *Cuscuta* twines in dense spirals around the first *Cuscuta* and around the host as well, sending haustoria into both.

Fig. 6. – Haustorium formed in parasitism of *Cuscuta* on *Cuscuta*. Reticulate thickened tracheids are quite usual in such cases.



J. P a z o u r e k : **Anatomical Observations of the Parasitism of *Cuscuta*.**



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