A CONTRIBUTION TO THE PHYSIOLOGY OF THE GENUS CUSCUTA, VOL. VIII, PP. 53-118

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A Contribution to the Physiology of the Genus Cuscuta[1].

BY

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With Plate VIII.

INTRODUCTION.

IN the course of an investigation into the origin, development, and structure of the haustoria of certain parasitic Phanerogams, the results of which were recently published[2], a number of questions presented themselves which could not be answered from alcohol-material, the only kind then available. Some of the questions concerned the members of the genus *Cuscuta*, and required, for satisfactory study, considerable quantities of these plants alive and in all stages of development. An abundance of such material was most generously put at my disposal by Professor W. Pfeffer, of the University of Leipzig, who very kindly gave me a place in his laboratory and helped me at all stages in my work by suggestions and criticism. The plants used were *Cuscuta Epilinum*, Weihr., cultivated on *Linum usitatissimum*, L.; *C. europaea*, L., on *Urtica dioica*, L., and on various florists' varieties of *Chry-*

[1] Diss. Inaug. at the University of Leipzig, 1894.

[2] Peirce, G. J., On the Structure of the Haustoria of some Phanerogamic Parasites, Annals of Botany, vol. VII, no. XXVII, 1893.

santhemum; and *C. glomerata*, Choisy, on *Impatiens Sultani*, Hook., *I. Balsamina*, L., and *I. parviflora*, DC., &c. Of these the two larger, *C. europaea* and *C. glomerata*, proved most convenient for experimental purposes, owing to their own greater vitality, and also to the fact that their host-plants (except *Urtica*) bear confinement in a rather dry greenhouse very well. *C. glomerata*, an American species, is decidedly better for indoor study than *C. europaea*, attaining under such conditions a larger size than the latter, though differing from it in this respect only slightly out of doors; and the translucent character of its hosts, their large-celled pith and cortex (especially of *I. Balsamina*) make it an almost ideal plant for histological as well as physiological observation.

I began my experiments late in April, and continued them, without interruption, until the middle of August. Some of the material was raised from seed in the comparatively dry, at times cool, at times very hot, greenhouse which forms part of the botanical laboratory of the University of Leipzig. More of it was cultivated in the Botanic Garden: host and parasite were sown or planted together in pots in a frame, and when the hosts had become a few centimetres high, and the *Cuscuta*-seedlings had become well attached to them, the clumps of soil enclosing the roots were removed undisturbed from the pots and set into a warm, not too sunny, well-watered bed. Still more was sown with the seeds of the hosts, quite without precautions in dry and sunny, or in somewhat moist and shady, places. The rest of the material was taken by transfer (as will be described further on) from an unpotted to a potted host, and brought into the small greenhouse above referred to. Owing to the unusual dryness of the season, accompanied in May and June by longer or shorter periods of abnormal coolness, the plants out of doors were not so luxuriant, and did not so long vegetate, as in more favourable seasons, but came sooner and more compactly into bloom. As will be shown further on, these differences from the usual conditions have made clearer some interesting facts which otherwise might have escaped my notice.

From the time of Palm[1] and Von Mohl[2], who studied certain species of *Cuscuta* in the course of their investigations on climbing plants in general, these interesting parasites have been so much studied and written about that, for the sake of a tolerably complete presentation of the new observations which I have to communicate, I must repeat much that is generally known. The student of the plants of this genus is especially indebted to the papers of Ludwig Koch[3], and to the second of these I shall have frequent occasion to refer.

In this paper I shall consider *first* the formation of the haustoria, the conditions necessary for this and for their full development, the general relations of the parasite to its environment; and *second* the penetration of the haustoria into the host.

I. The Formation of Haustoria.

1. *Germination and early growth.*

If the seeds of one of the three species of *Cuscuta* above mentioned be sown on moist earth, they gradually absorb sufficient water to double their size, and, in eight or ten days, germinate, pushing through the integuments of the seeds roots which are snowy white in colour. Such a root, short, thick, more or less spindle-shaped, devoid of a cap, and with short, though rather numerous hairs (their length varies directly with the amount of moisture), is very feebly geotropic and penetrates the subjacent soil for only one or two millimetres, if at all. Instead of the cells of its central cylinder differentiating into vascular bundles, which are at first radial and separate, later, through secondary thickening, becoming collateral and confluent, the central cylinder consists of no lignified cells at all; the walls remain thin, and, though the

[1] Palm, L. H., Ueber das Winden der Pflanzen, Stuttgart, 1827.

[2] Mohl, H. v., Ueber den Bau und das Winden der Ranken und Schlingpflanzen, Tübingen, 1827.

[3] Koch, L., Untersuchungen über die Entwickelung der Cuscuteen, Hanstein's Botanische Abhandlungen, Bd. II, Heft 3, 1874; Die Klee- und Flachsseide, Heidelberg, 1880.

cells become quite long, they retain throughout their brief existence the appearance of young procambium-cells, being filled with granular protoplasm enclosing large nuclei. This core of thin-walled elongated cells, less like a vascular structure than the central cylinder of the larger Mosses (e. g. *Polytrichum*), is the only indication of the differentiated root-structure which these plants must have possessed before they became parasitic. The cortical cells are approximately cubical, thin-walled, containing abundant protoplasm and large nuclei. Indeed it is a noteworthy, as well as an easily observed, fact that the nuclei of all the living cells of a *Cuscuta* are larger than those of the corresponding cells of its host. The epidermal cells and the root-hairs are slightly cutinized.

The root having penetrated the soil for a short distance, or having grown sufficiently over the surface to give some support, the now rapidly elongating stem, having grown for some distance out of the seed, bends at a point near its union with the root and thus rears its tip, still enclosed within the seed-coats and imbedded in the endosperm from which it draws its nourishment, till it becomes nearly or quite erect. The young stem is yellow or almost white, at any rate not green, and so lacking in chlorophyll that assimilation must be very slight, if at this stage of the plant's history it occurs at all. Frank[1] cites in his text-book an investigation carried on in his laboratory by Temme[2], according to which chlorophyll is present, not merely in quantity sufficient for spectroscopic determination, but also for the evolution of oxygen, as proved by experiments with fuming phosphorus. Such investigations were, however, carried on with older plants, and, though necessarily implying the presence in the seedling of plastids capable of developing into chloroplastids, scarcely yield results which would justify our assuming that the seedling obtains food from any other source than the endosperm in which its tip is imbedded. (As to the amount of chlorophyll

[1] Frank, A. B., Lehrbuch der Botanik, Leipzig, 1892, Bd. I, p. 556.

[2] Temme, F., Berichte der deutschen botanischen Gesellschaft, 1883, p. 485. Also in Landwirthschaftliche Jahrbücher, 1884, Bd. XIII.

in older plants I shall have more to say further on.) The stem being now erect or nearly so, and continuing to grow in length, nutates in wider and wider circles or ellipses in search of some suitable object around which to twine. As first pointed out by Von Mohl [1], the seedling will not twine indiscriminately about any object whose size, form, and position one might suppose to be appropriate, if not directly to nourish, at least to hold it up in its efforts to reach a nutrient support, namely some living plant. Von Mohl tested this by pieces of wire and thin rods of fir-wood kept for three days in contact with the seedling. The plant refused to twine about them, though, when brought into contact with a plant of Nettle, it wound about it within nine hours. Koch [2] and others have confirmed this important observation, but without being able to account for the fact. Koch [3] says—'Der junge Schmarotzer besitzt somit in Bezug auf den von ihm zu befallenden Gegenstand eine gewisse Wahlfähigkeit, deren physiologischer Nutzen nicht zu verkennen ist.'

Through the integuments of the seed the embryo receives from the moist soil, or damp substratum of any sort on which the seed may rest, sufficient water to cause it to germinate, other conditions of temperature, &c., being favourable. The spindle-shaped and but feebly-developed root continues to secure moisture through its hairs from the substratum, and thus provides the necessary amount of water for the solution and transportation of the food-substances stored in the endosperm. The root is, however, a short-lived structure, beginning to die generally within seven days after its appearance, and hence it can supply only a small quantity of water in all. Under favourable conditions, primarily a damp substratum and a moist atmosphere, the root doubtless supplies enough water completely to convert the reserve food-materials in the endosperm into transportable and available solutions; but if, owing to the surrounding air being dry, the transpiration of

[1] Mohl, H. v., loc. cit.

[2] Koch, L., Hanstein's Botanische Abhandlungen, Bd. II, Heft 3, p. 110, 1874.

[3] Koch, L., Die Klee- und Flachsseide, Heidelberg, 1880, p. 17.

the seedling be greatly increased, and the neither thick-walled nor strongly-cutinized epidermal cells of the stem be unable to counterbalance the loss by their own absorption, the growth of the seedling will be greatly lessened in speed and amount, and thereby its chances of finding a suitable support will be diminished. Any dry object with which it comes into contact also draws water from it. Hence it is evident that, in this respect at least, it is disadvantageous to the plant to wind about dry and innutritious supports. The length to which the seedling can grow is proportional to the amount of water which it can absorb and retain, that is, to its turgescence. Seeds sown on sunny dry beds in the garden germinate slowly, the roots of the seedlings die soon, the stems attain a length of only a few centimetres, usually not more than five, unless a host be quickly found. If, on the contrary, the bed be a moist and shady one, or still better, if the seeds be sown on damp earth in a pot covered by a bell-glass, the seedlings can attain surprising lengths. Not only is the total amount of growth greater, but the length of the living part of the seedling is also greater. From the dying root most of the nutritive materials are removed to younger parts. Thus fed, the tip of the stem can continue to grow, and thus the area explored by it in its circumnutation is increased. Not only does the dying root yield its substance for the nutrition of the tip of the stem, but the stem dies also from below upwards, and from it too the nutritive substances are transferred to the youngest parts. Owing to the ability of the growing part to extract food from the oldest and least useful parts, the seedling is capable of a slow locomotion. The advantage of this is quite obvious, for in this way the seedling can approach a suitable plant which was at first beyond reach, and finally can lay hold on it.

If the root be not already dead before the seedling has found a host about which it can twine, it quickly dies when the youngest part of the stem begins to wind. The direction of winding in every case which has come under my observation was in the direction of circumnutation, namely the reverse of the hands of a watch. The stem of the seedling, like the stem of the older plant, as I shall show later, is sensitive to contact-irritation for only a short distance from the tip and only in the growing part, and the irritability is greatest near the middle of the growing region, diminishing rapidly in both directions. If, therefore, the stem be brought by its nutation into contact with a host so that a non-irritable or only slightly irritable part be applied to the host, either no twining will take place, or only a loose steep spiral will be formed, until the irritable part touches. Then the *Cuscuta* rapidly forms one or more close spirals, the direction of the curved part of the stem being as nearly horizontal as possible. As I shall show later, the object of these close spirals is two-fold : they bring many more points of the stem into intimate contact with the host ; and they hold the stem, which would otherwise be pushed away from it by its own growth and by the growth of the haustoria, closely applied to the host. When such close spirals are made, haustorial formation is induced by the intimate contact. The origin, structure, and development of the haustoria were described and figured in detail in my previous paper[1]. Suffice it to say here that the haustoria originate, like typical roots, deep in the cortex, break through the overlying cortical and epidermal tissues, penetrate into the host and, attaching themselves to the vascular bundles, draw from them through tracheids and sieve-tubes the various solutions which they contain. Exactly how the haustoria make their way into the host was one of the questions which I set myself to answer, and of this I shall speak at length in the second part of this paper.

One or more turns in a short close spiral having been made about the host, the root, unless already dead, and the stem below the first point of contact, die quickly, yielding their substance as nourishment to the youngest parts of the seedling. The root and stem remain for only a short time as an empty, dry, shrivelled filament which the wind quickly snaps and blows away. The nourishment obtained from them

[1] Loc. cit.