STUDIES IN IRREGULAR NUTRITION

No. 1.

The parasitism of Cuscuta reflexa (Roxb.)

University of Glasgow

Botany Department

10th Jany, 1925.

I herewith present as a thesis for the degree of Ph.D. these "Studies in Irregular Nutrition"

I declare that these are the results of my unaided research.

Fig. 1.
C. reflexa on flower stalk of.
Pelargonium zonale. (X 4).

× hypertrophy of host. stem
due to parasite.

Fig. 2.
C. reflexa on stem of Pelargonium zonale. (X 1.)

This piece of work was undertaken as the result of certain observations made during class work on irregular nutrition. This particular species of Cuscuta was being successfully grown at the time in Glasgow Botanic Gardens, and my sincerest thanks are due to Mr. Banks, the Curator of the Gardens, who has very kindly allowed me to have abundant material at all times during the past three years, and has also provided me with various host plants upon which to grow the parasite. He has also allowed me to make observations on the plants growing in the Gardens, and to take photographs whenever I wished.

During the course of our Summer term's work on the physiology of nutrition, I had occasion to refer to Pierce's work on the parasitism of various species of Cuscuta (Annals of Botany, 1893-1894). This work appears to be the recognised work on the subject, since it is quoted in all the text books.

The most noticeable discrepancy in the behaviour of Cuscuta reflexa when compared with the species described by Pierce, is that it produces obvious anatomical changes in its host in many cases. Pierce states:- "the effects on the host are mainly physiological, it rarely happening that anatomical changes take place in consequence of the presence of haustoria". Now when Cuscuta reflexa is grown on the ordinary greenhouse geranium (Pelargonium zonale) swellings of the host tissues, visible to the naked eye, develop in the regions surrounding the haustoria. (Figs. 1 & 2). Secondly I could not demonstrate to/

Fig. 3.
Cuscuta reflexa on Ficus europæa.

to the students of the class an unmistakable example of the union of the phloem elements of the parasite with the corresponding elements of the host, and as this species is considerably larger than any described by Pierce, one would expect that such connections should be more easily observed.

In this paper, which is intended to be the first of a series on irregular nutrition, I shall;

(1) describe the formation and penetration of the haustorium,
(2) explain the establishment of intimate connection with the host,
(3) describe the changes brought about in the host tissues by the parasitism and
(4) make some suggestions as to the manner in which the parasite obtains its food supply from the host plant.

In its twining around its host the parasite forms two different kinds of spirals, viz:- Long loose spirals and short close spirals (fig. 3). The former serve in reaching other host plants and in carrying the parasite to the periphery of its host, where it can display its flowers to best advantage. These long loose spirals do not grip the host stems tightly, nor are they possessed of haustoria. The short close spirals grip the host firmly and possess haustoria.

When a haustorium is about to be formed, the epidermal cells of the parasite stem immediately overlying the haustorial initials become modified.

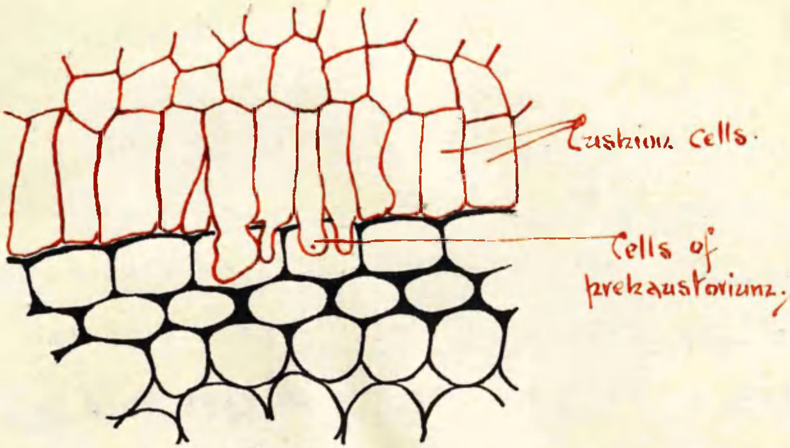


Fig. 4.

Fig. 5.

Fig. 6.

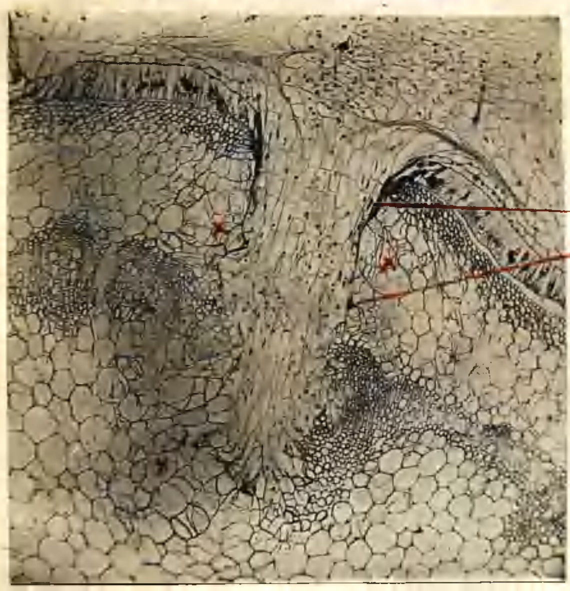
A more or less circular patch of these cells is rejuvenated. The cells of this patch grow out towards the host epidermis,as papillate hair-like outgrowths,(cf.Bower,"Botany of the Living Plant,page 192) their walls become thin, their nuclei increase greatly in size, and their protoplasm becomes dense and granular. This area of altered epidermal cells consists of two distinct regions. The cells of the outer region grow only until they reach the epidermal cells of the host, to these they apply themselves closely, so closely in fact that the outer walls of both epidermises seem to fuse. This outer region of altered epidermal cells of the parasite stem is known as the "cushion". (Pierce "Annals".1893,page 295). The group of cells in the centre of this altered area behave differently. When they reach the epidermal cells of the host,they dissolve their way through them by the help of an enzyme which they secrete. This portion of the parasite's epidermal cells constitutes the "prehaustorium".(fig. 4) (Pierce "Annals".1893,page 295).

In order to demonstrate the behaviour of these altered epidermal cells, the parasite was induced to form a close spiral round a stick of pith, which was kept moist by syphoning a nutrient solution (Knop's and cane sugar) through a small hole down the centre of the stick. (figs. 5 & 6). The spiral so formed remained alive for two or three weeks, after separation from the parent stem. At the end of this time, bacterial activity became so pronounced as to cause the death and later the putrifaction of the spiral. There is no means of/

Fig. 7.

Initiation of Haustorium
Section has missed th
prehaustorium.

Hairs of
Epidermis of Host.
(Cucurbita maxima)



Remains of disorganised cortex.

x N.B. cell division
New walls parallel to surface
of Haustorium.
v. p.6.

Fig. 8.

Fig. 9.

x Dermal cell developing as a root hair ("Hyphal cell")

Fig. 9a. (Bower).

of keeping such an experiment sterile.

Underneath this altered area of the epidermis the haustorium proper is initiated. By tangential division in the inner regions of the cortex of the Cuscuta stem, there arises a structure resembling a young root in all respects, except for the fact that it does not possess a root-cap. (fig. 7). This structure is the haustorium, which is in fact a modified root, both from the point of view of its origin (endogenous) and of its functions (anchoring and absorbing). As the young haustorium grows, it penetrates the tissues overlying it, and enters the host, following the path prepared for it by the prehaustorium. It soon overtakes the prehaustorium and growing through it pushes its remains on all sides. These, along with the remains of the disorganised cortical tissues,(of both parasite and host) remain as a deeply staining mass all along the sides of the "shaft" of the haustorium.(fig. 8). Once inside the host tissues the haustorium advances, partly by the force exerted by its growth, partly by dissolving its way through the host cell-walls. Certain "hyphae" (Sykes."Annals of Botany" 1911) are developed from the dermal tissue of the haustorium. (fig. 9). They are developed in greatest numbers at the tip of the haustorium, but they also occur on the shaft. These hyphae are modified root-hairs (cf. Bower,"Botany of the Living Plant" page 192) (fig. 9a) and the fact that they occur in largest numbers at the tip, may be explained by the absence of a root-cap from the modified root which/

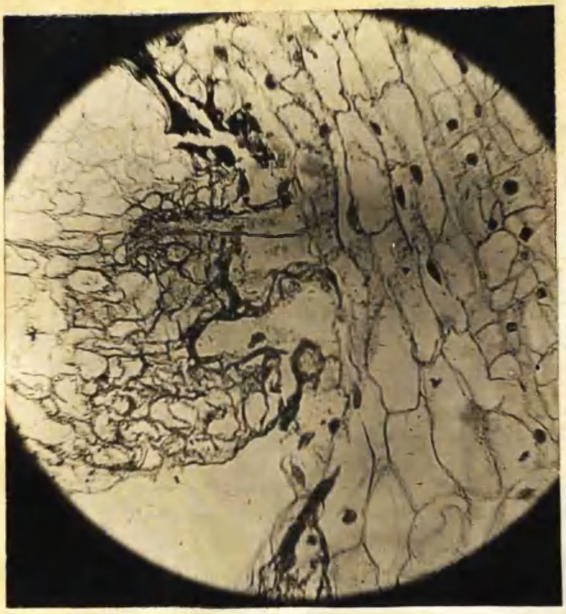
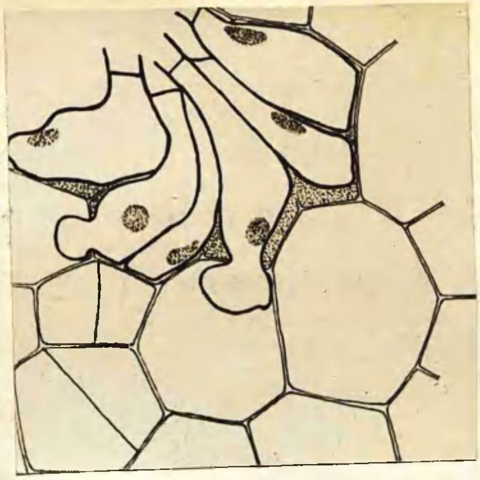


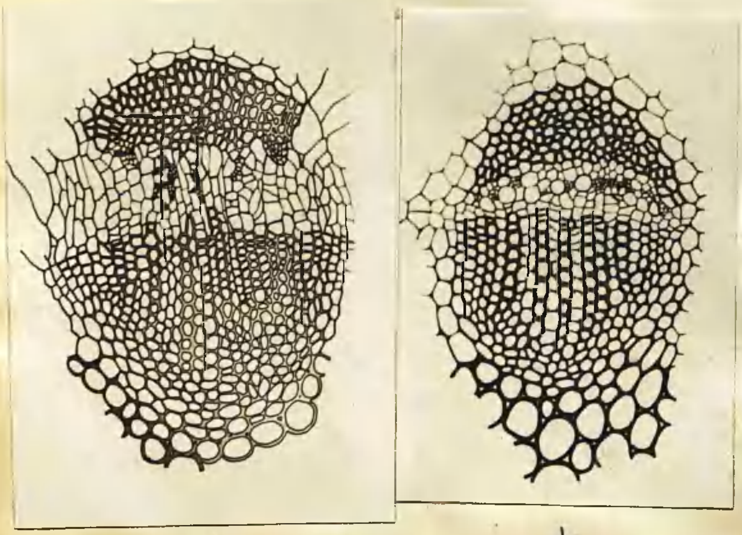
Fig. 10. "Hyphae" (root hairs)



NB. entry into host. cells by solution of. cell-wall. No sign of. Pressure.

Fig. 11.

Fig 12.

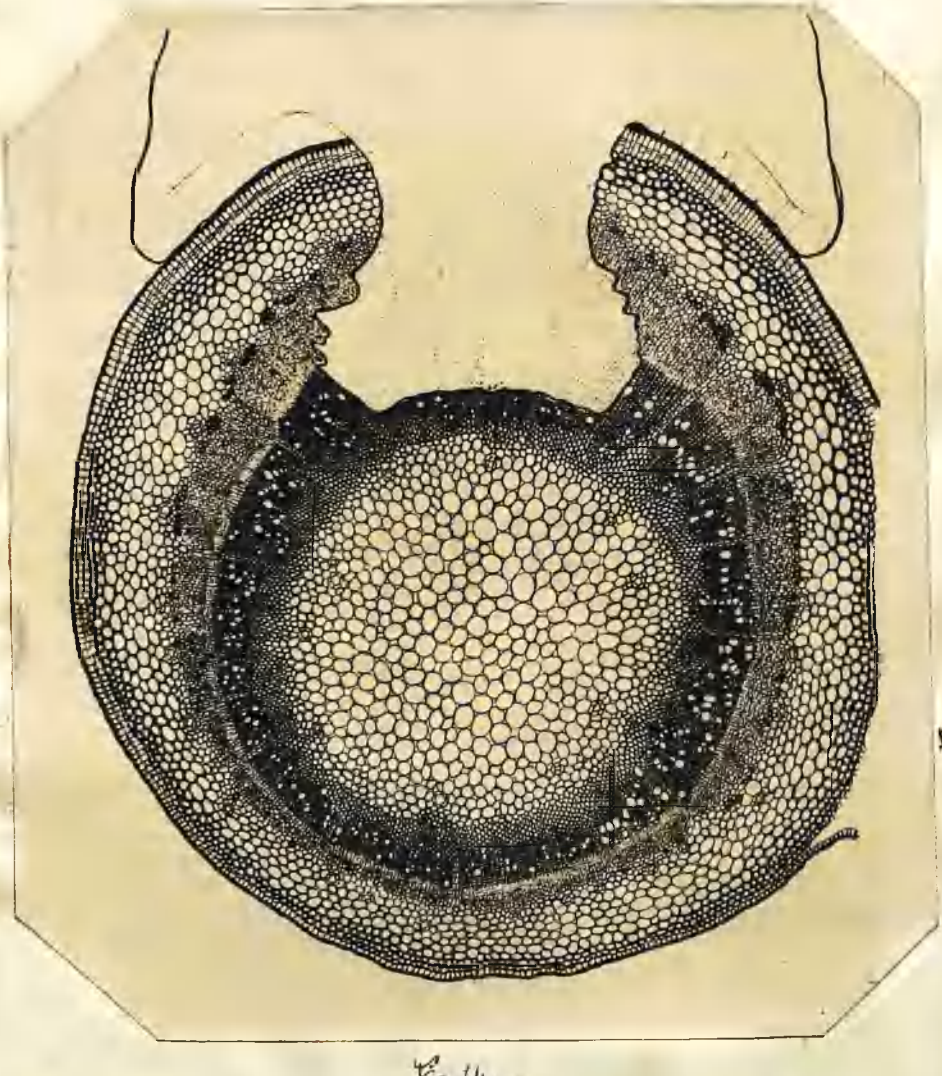


Drawn from a Preparation in Edinburgh Royal Botanic Gardens.

a. b.

Fig. 13.

Vascular bundles of Chrysanthemum.
"a" beside an entering haustorium. "b" the bundle diametrically opposite "a" i.e. non infected side of stem.



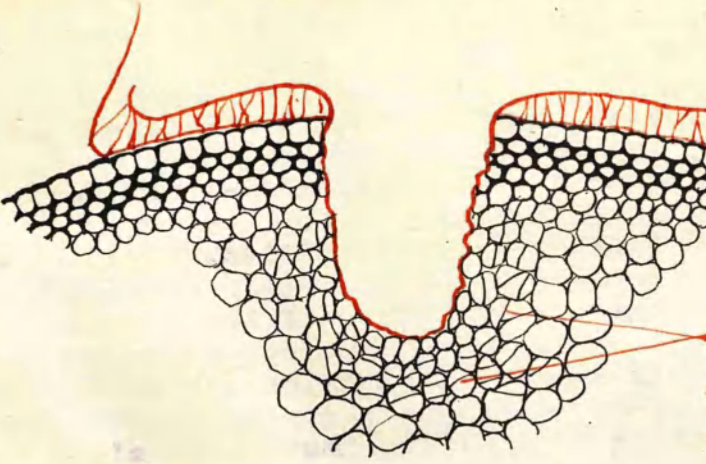
Drawn from a preparation in Edinburgh Royal Botanic Gardens.

Fig 14.

Cuscuta reflexa on Ivy. N.B. increase in all tissues in vicinity of Haustorium.

which constitutes the haustorium. The hyphae are root-hairs, not only in respect of their origin, but also from the point of view of their structure and their function. They are thin-walled, possess large nuclei, and secrete an enzyme which enables them to dissolve their way through the cell walls of the host. (figs. 10 & 11). They are also capable of absorbing nutritive materials from the host tissues, for when the haustorium is unable to reach the vascular tissues of its host the parasite can still grow.

It is the generally accepted belief however that the parasite haustorium must attach itself to the conducting system of its host. Before considering the manner in which this connection is brought about, we shall first of all consider how the parasite reaches the vascular system of its host. As the haustorium enters the host certain changes are wrought in the host tissues. The irritation set up by the entry of the haustorium stimulates all the cambial regions in its immediate vicinity to increased activity. The cork cambium starts to produce extra layers of cork all round the shaft of the haustorium. (figs. 12&31). It also produces extra phelloderm which increases the width of the cortex, to such an extent in some stems that the haustorium never reaches the vascular bundles at all. (fig. ~~32~~36). Both interfascicular (fig. 19) and intrafascicular (fig. 13) cambiums are stimulated and extra phloem and xylem are produced. The result is an increase in the cross sectional area of all the tissues in the region of the haustorium. (fig. 14). When Cucurbita maxima is the host an interfascicular cambium is initiated, linking/



N.B. Cell-divisions parallel to surface of Haustorium.

Fig. 15.

Fig. 16.

Showing expansion of Haustorium in the Cortex, Cambium and Pith of Host.

linking up the normally isolated bundles in the region opposite the entering haustorium. (Fig. 19)

Besides this increase in the activity of already existing meristems, other meristematic activity becomes manifest. The parenchymatous ground tissue starts to divide, division walls appearing parallel to the outer surface of the haustorium. (fig. 15 & fig. 8). Obviously this cell division is ~~due to~~ influenced by the pressure exerted by the increasing bulk of the haustorium since the new cell-walls are laid down at right angles to the direction of such pressure.

This meristematic activity has two important consequences; (1). To bring about the cell division the host plant must necessarily rush plastic materials to these various regions, and undoubtedly some of this becomes available to the parasite. (2). The newly formed cell-walls being thin are easily penetrated by the modified root-hairs (hyphal cells) produced from the dermal cells of the haustorium. Thus a median longitudinal section through the haustorium shows that its general shape is governed by these meristematic activities on the part of the host; it reaches its greatest width in the cortex, the cambium and the pith of the host. (fig. 16). In these regions its extra width is due to greater development of hyphal cells in these regions. It is significant that in each of these regions the hyphal cells not only meet with least resistance to their growth but also have at their disposal all the food materials they/

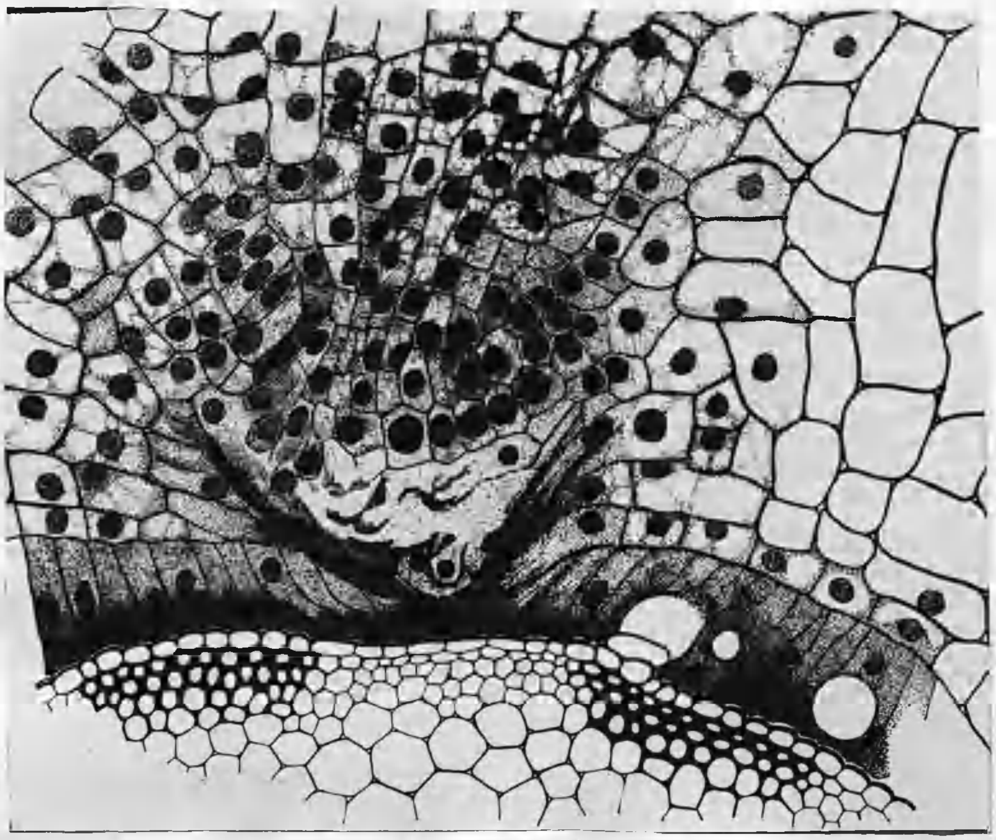


Fig 17.

Cuscuta reflexa on Cucurbita maxima. showing initiation of Haustorium. Haustorium will enter host stem between two collenchyma groups Section, not quite median, does not show "prehaustorium."

they require for the nutrition of the parasite.

The behaviour of the penetrating haustorium varies with the arrangement of the tissues in the host stem. The above description holds for most herbaceous stems. The later stages in the progress of the haustorium through the host tissues, more especially the actual establishment of connection with the vascular supply, are difficult to follow in such a stem owing to the fact that the vascular ring is practically always uninterrupted. It was therefore necessary to find a host in which the vascular bundles were separate from one another. Cucurbita maxima was chosen. In this stem the bundles, besides being separated from one another, are also bicollateral. It therefore seemed that this host would offer a good opportunity to study the behaviour of the haustorium towards the phloem of the host.

The distribution of the tissues in the outer regions of the host stem determines the place of entry of the haustorium, viz- always between two collenchyma groups of the outer cortex. (fig. 17). This is due to the fact that the prehaustorium more successfully attacks the thin walled parenchyma cells between the collenchyma groups and there makes the passage for the haustorium proper. Once within the cortex the pressure exerted by the haustorium causes cell division; this activity is never sufficient to cause any marked hypertrophy in the stem of Cucurbita. There must however be a rush of food material to the dividing cells and doubtless/

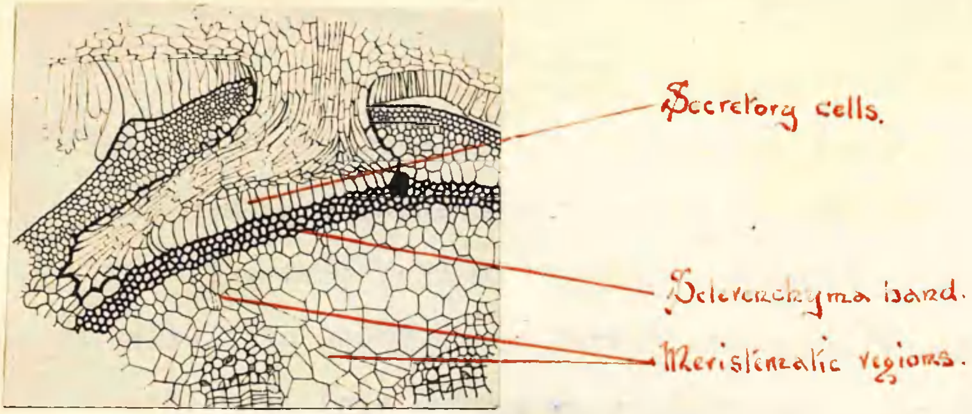


Fig 18 a.

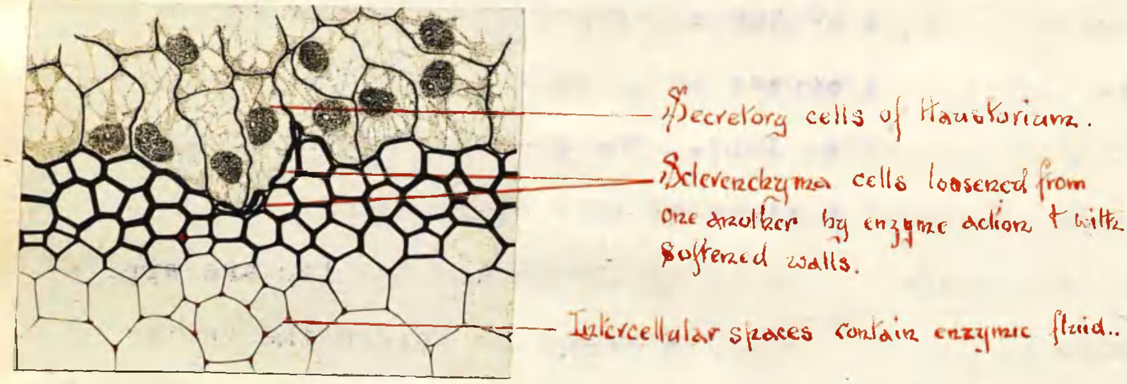


Fig. 18 b.

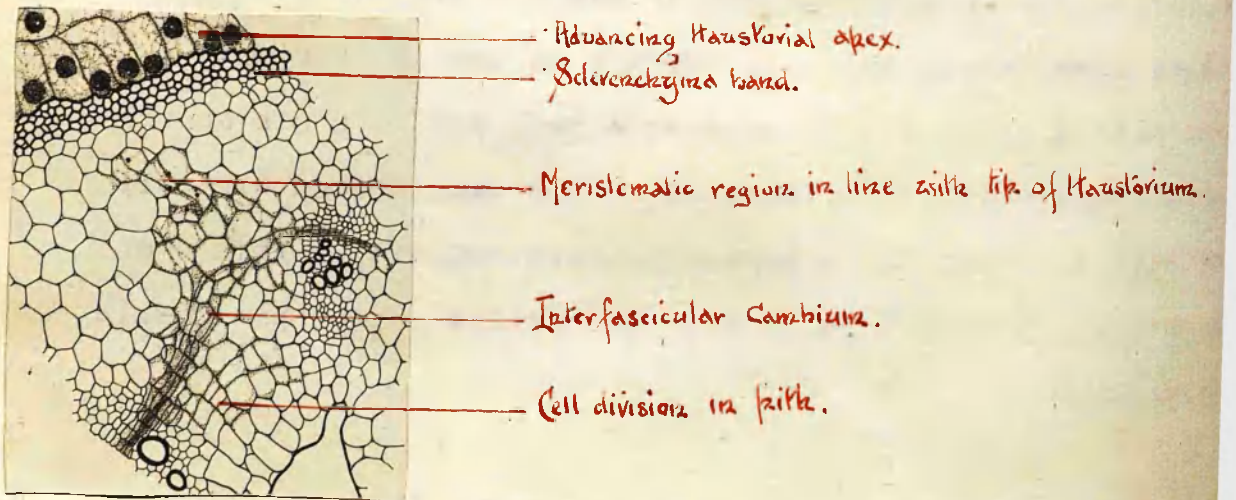


Fig. 19.

All above Cuscuta reflexa on Cucurbita maxima.

doubtless the parasite benefits by it.

Midway across the cortex the haustorium meets an obstacle in the shape of a well defined band of sclerenchyma. When the haustorium meets this obstacle it brings to bear on it all the secretory epidermal cells at its distal end. These are large papillate thin walled cells, with dense protoplasmic contents and large nuclei. (figs. 18a & 18b). They penetrate the sclerenchyma layer by enzyme action. The enzymes secreted by these cells first attack the middle lamellae loosening the sclerenchyma cells from one another. (fig. 18b). Later they seem to attack the lignin in the cell walls of the sclerenchyma cells for the walls become so soft that they appear to be easily pushed in by the advancing haustorium. (fig. 18b). The pressure of the growing haustorium completes the rupture of this obstruction.

While these secretory cells of the haustorial tip are applied to the outside of the sclerenchyma band, and before the latter has been ruptured, certain changes are taking place in the tissues of the host within this band. The most noticeable of these is the initiation of interfascicular cambium between a pair of host bundles immediately opposite the tip of the haustorium. Fig. 19 shows that another region of active cell-division has appeared at right angles to this interfascicular cambium and directly in line with the tip of the advancing haustorium. At this stage the intercellular spaces in the conjunctive parenchyma within the sclerenchyma/

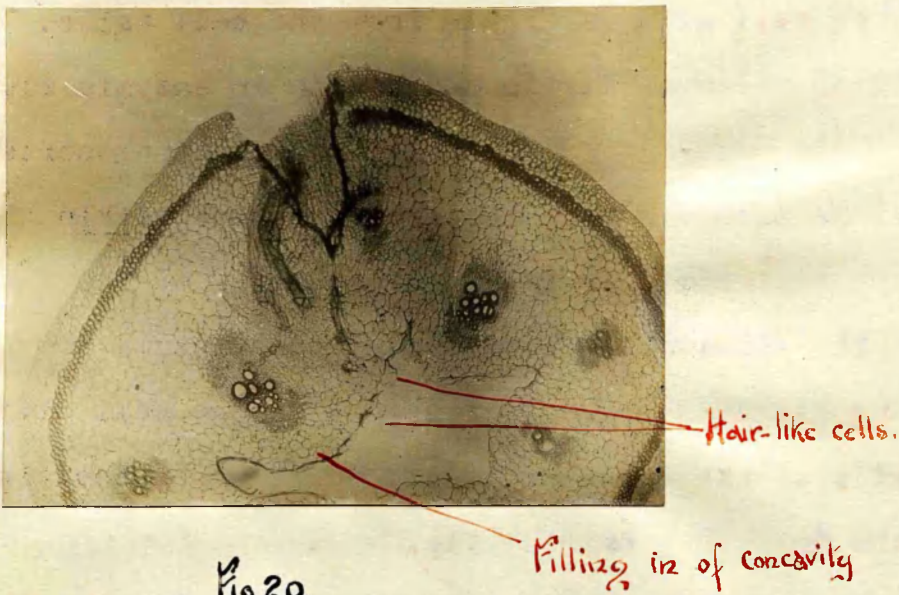
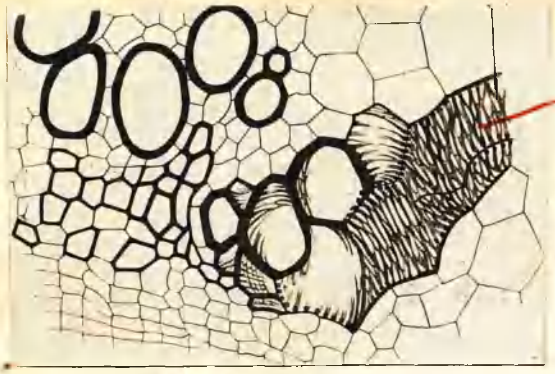


Fig 20.

sclerenchyma ring and opposite the haustorium, show the presence within them of some solution which stains with the usual lignin stains. The probable explanation of this is as follows. The enzymes which aid in breaking down the sclerenchyma layer filter in to these intercellular spaces carrying with them in solution pectic substances from the middle lamellae which they have dissolved, as well as some lignin from the cell walls. This penetrating solution of lignin and pectin in enzymic fluid acts as a chemical stimulus upon the cells of the inner cortex. Cell divisions also occur in the ground tissue within the ring of vascular bundles. This causes hypertrophy of the tissues of the pith. The concavities surrounding the fistula on the side of the entering haustorium are filled in by these cell divisions, and the cells of the limiting layer, abutting on the fistula, grow out into the hollow as hairs. (fig. 20).

These regions of cambial activity mark out the path of the haustorium after it has passed through the sclerenchyma layer. The new cells formed in the tissues of the host are thin-walled and have received food materials for their formation. They therefore constitute not only the path of least resistance for the advancing haustorium, but also the region of most abundant food supply.

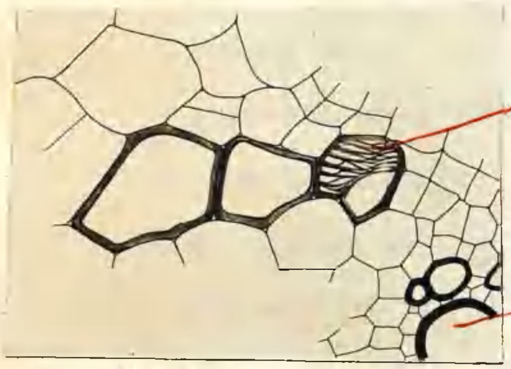
The modified root-hairs arising from the dermal cells of the haustorium reach their fullest development in the Cucurbita host only in the interfascicular cambium. They grow along the inner region/



Lignified Hypha attached to Host-Xylem.

Fig 21.

Diag 1.



Lignified Hypha passing thro' host tissues. N.B. cells (tracheids) fill host cells.

Host Xylem.

Fig. 22.

Diag 2.

Cells of conjunctive parenchyma of Host. N.B. cell-division

Lignified Hyphae entering Haustorium. N.B. absence of Sieve-tubes.

Remains of disintegrated cells.

Fig. 23. Trans. sect. of Haustorium.
Tang. sect. of Host.

Diag 3.

Lignified hairs Entering Haustorium.

Fig 24. In the series of sects. thro this Haustorium the tracheid strand in the shaft was not complete.

Diag 4.

region of this cambium by dissolving the cell-walls and thus they come in contact with the xylem of the host. (fig. 21). THEY NEVER ATTACH THEMSELVES TO THE PHLOEM EITHER ON THE OUTSIDE OR ON THE INSIDE OF THE BICOLLATERAL BUNDLE.

*When such a hair has reached a xylem vessel its cells (it has already become septate) enlarge until they completely fill the host cells they have penetrated. The cells of the hair then become lignified, lignification beginning in the cell immediately in contact with the xylem vessel and proceeding backwards. (fig. 22). The result is a string of tracheids extending from the host xylem back to the haustorium. These tracheids are reticulately thickened. THEY ARE NOT ACCOMPANIED BY ANY PHLOEM EITHER IN THEIR JOURNEY THROUGH THE HOST TISSUES OR WHERE THEY ENTER THE HAUSTORIUM. (fig. 23). The manner in which thickening and lignification takes place, viz. from the connection with the host xylem backwards to the haustorium, seems to indicate that the materials which enable this change to be wrought have been derived from the xylem of the host. Serial sections longitudinally through a haustorium show such lignified hairs stretching from the host xylem to the haustorium before any xylem tract has been established in the shaft of the haustorium. (fig. 24). The cells of the shaft of the haustorium in its central region are differentiated into tracheids from the bases of these lignified hairs backwards, and similar differentiation forwards from the xylem at the base of the haustorium completes the xylem connection between host and parasite.

* See diagrams opposite

NB. This is not a trans sect of the stem but a longitudinal.

Fig 25.

Sieve plates in red.

(Peirce)

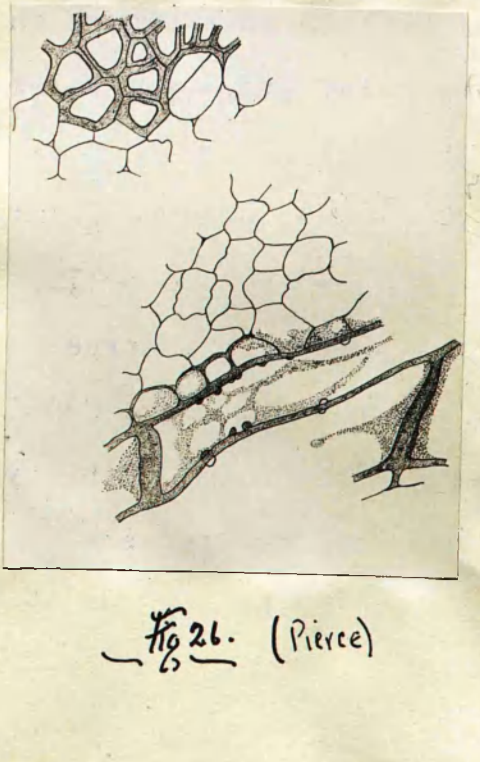


Fig 26. (Pierce)

THERE IS NO SIGN OF SIEVE TUBES IN THE HAUSTORIUM.

With regard to this last statement it will be well to examine the description of the intimate connection between parasite and host given

(1) by Peirce "Annals" 1893.p. 299.

(2) by Thoday (Sykes) "Annals" 1911 p.p. 662-663.

Peirce states:- " If now a <u>cross section</u> of the Cuscuta stem be made through a haustorium we find in the centre the thick walled lignified cells of the xylem, bounding the xylem on either side are the cambial layers, and beyond these are the two phloems consisting of sieve tubes and their companion cells. There is never at any time a radial structure. The phloems lie right and left of the xylem in a transverse section of the parasite stem". After such a careful description of the condition of affairs in the haustorium he shows later in his article the drawing reproduced as figure 25. It will be seen that in this figure the two phloems come off from the parent stem above and below the xylem strand instead of left and right of it.

In another place ("Annals" 1893.p. 298) he points out that the cambiums between xylem and phloem are one cell wide or at most two; and later he shows a figure with a large indefinite number of cells between xylem and phloem. (fig. 26).

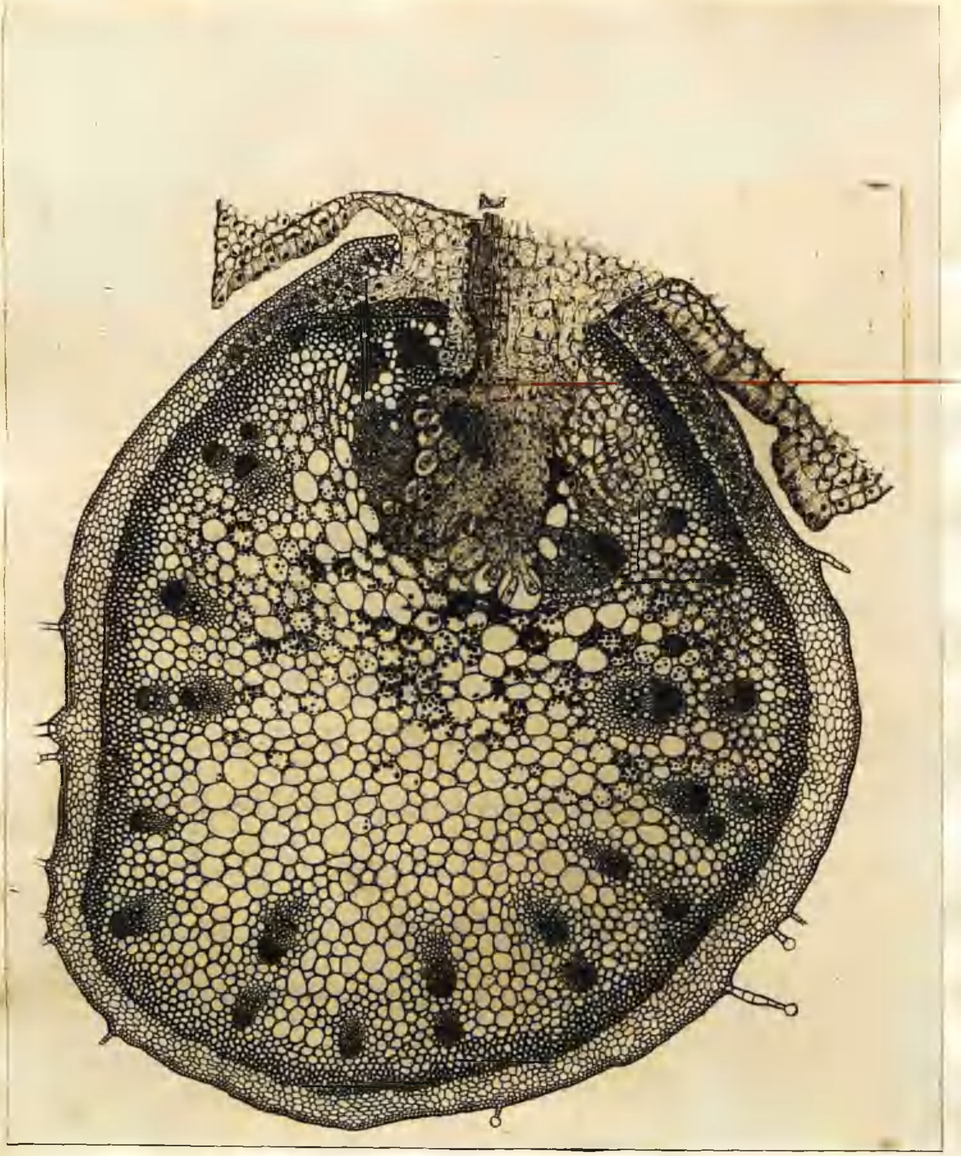
With regard to the intimate connection of the xylem of the haustorium with the xylem of the host he states:-
(page 300) " The xylem elements of the haustorium apply themselves directly/

directly to the xylem elements of the host; that is; those cells of the haustorium (consisting so near its apex of central cylinder mainly with little or no cortex) which come by solution of the intervening cells of the host into contact with the ducts quickly differentiate into tracheids".

(page 302) " When the proximity of the bundles of the host makes it possible for the haustorium to apply itself to two bundles the single strand of xylem divides into two near the tip each of which unites with the xylem of a host bundle".

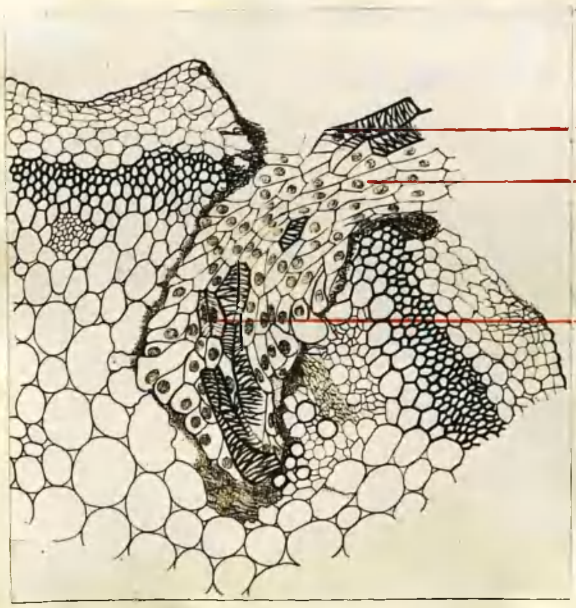
(page 302) "When it unites with three bundles we have a second division of the xylem. Since the third bundle with which the haustorium unites is small and considerably removed from the surface of the stem of the host only a small amount of food is taken from it and the conducting tissue is weak. The xylem already bifurcated in order to unite with the two larger outer bundles sends a feeble strand of tracheids from each of the adjacent sides of its branches; probably also two feeble strands of sieve-tubes and companion cells are sent out from the two phloems but no callus plates are shown by the aniline blue test".

Thoday (Sykes) states:- (loc. cit.) " The hyphae of the central core at the tip of the haustorium develop sometimes as sieve tubes in the host pith. The hyphae immediately surrounding the central core become applied to the xylem elements of the host, The peripheral hyphae of the haustorium become applied to the walls of the functional phloem and develop as strings of short sieve tubes." The Author apparently recognises as a sieve tube any cell with a pitted wall through whose pits slime strands/



A connection such as this can only be explained in the manner set forth in this thesis.

Fig. 27. Cuscuta reflexa on geranium.



N.B. nucleus still present in tracheid.

Only nucleated cells (no sieve tubes) accompany the tracheids.

Tracheids which have not yet lost their nuclei.

Fig. 28. as above (27).

strands stretch irrespective of the presence or absence of a nucleus in the cell A mature sieve element never contains a nucleus.

These two descriptions are very far from agreeing with one another, either in regard to the anatomical structure of the haustorium or in regard to the establishment of connection with the host.Peirce seems to suggest that the connections established with the vascular bundles of the host are foreordained by the arrangement of these bundles in the host stem. This is by no means the case since from a single coil of the parasite as many as half a dozen haustoria may enter the host stem, and of these no two may make the same connections with the host bundles. Thoday (Sykes) on the other hand seems to hint that the manner in which connection with the host tissues is established depends on the arrangement of the tissues in the haustorium. Neither description can explain such a connection as is shown in fig. 27.

The shaft of the haustorium consists essentially of thin-walled, NUCLEATED, prosenchymatous cells, their direction of elongation being parallel to the long axis of the shaft.(fig. 27). From these ordinary thin-walled living cells the tracheids are differentiated. All stages in thickening and lignification may be observed. It is only when the changes in the cell-wall have been completed that the cells lose their nuclei. (fig. 28). The differentiation of tracheids proceeds from cell to cell along the/

the axis of the haustorium both from the tracheids at its base forwards and from the bases of the lignified hyphal cells (root hairs) backwards.

If we remember that the xylem is a dead tissue and is therefore incapable either of branching or of attaching itself to the vessels of the host, but that such connection is established by the modified living root-hairs or hyphae, and that lignification of these hyphae backwards from their point of contact with the host vessels establishes the uninterrupted union of the xylems of host and parasite, we ~~shall avoid such a mistake~~ can explain every manner of xylem connection we may meet.

That this method of establishing continuity between the xylem of the host and that of the parasite is not peculiar to Cuscuta is shown by McLuckie's work on Loranthus celastroides and on Notothixos incanus.

With regard to Loranthus he states:- ("Botanical Gazette" vol. LXXV No. 4, June 1923.p. 358) " In the (host) xylem the haustorial cells in contact with the vessels differentiate into short reticulate tracheids, connecting up with those in the main part of the root by the differentiation of the intervening cells into tracheids also".

And again he says:- (p. 353. loc. cit.)

" The cells of the central core at the base of the haustorium are meanwhile differentiating into short, reticulately thickened tracheids charactistic of most of such parasites. Later, when the apex has reached the vessels of the host and applied itself to their walls, the haustorial cells in actual contact differentiate into tracheids, those immediately behind do so also, and so connection is established between the basal series of the haustorium and those apical tracheids in contact with the water tissues of the host".

With regard to Notothixos he states:-("Proc.of the Linn. Soc. N.S.W. XLVII pt. 4.1922.p. 574)

" When the haustorial tissue taps a number of vessels of the host branch, certain cells of the peripheral layer differentiate into short reticulate tracheids which link up with others already formed in the central shaft of the Sucker".

In neither plant has MacLuckie succeeded in demonstrating the presence of sieve tubes.

The changes brought about in the host tissues.

Certain of these changes have been mentioned already in connection with the penetration of the haustorium and the establishment of the vascular continuity between parasite and host. We have noted that the active cell-division which brings about these changes results in a flow of plastic material to the region of the host in which the parasite's haustorium is embedded and doubtless much of this plastic material is appropriated by the parasite. In this appropriation of food material from the host the active organs concerned are the hyphae or root-hairs which grew out from the surface of the haustorium.

When the changes in the host tissues are so extensive as to cause hypertrophy visible on the exterior of the host, this may have been brought about in either of two ways.

Fig 29. Hypertrophy of Fuchsia stem.

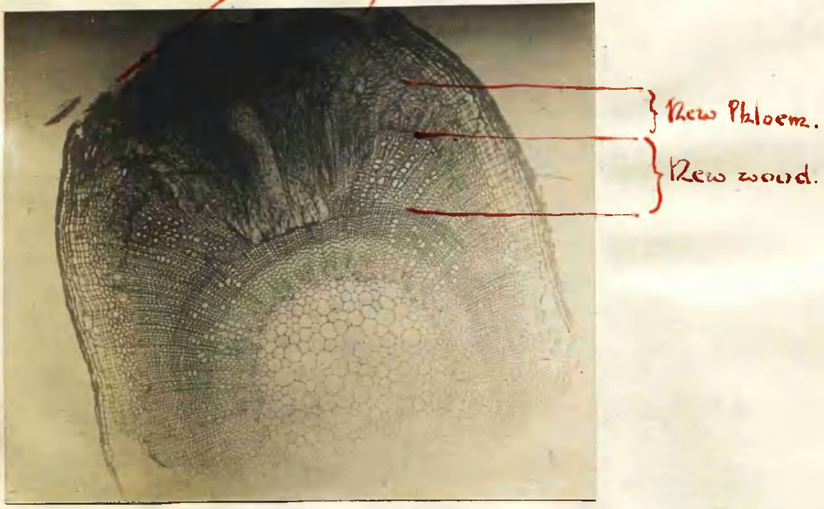


Fig 30. NB. Width of cork not increased near haustorium.

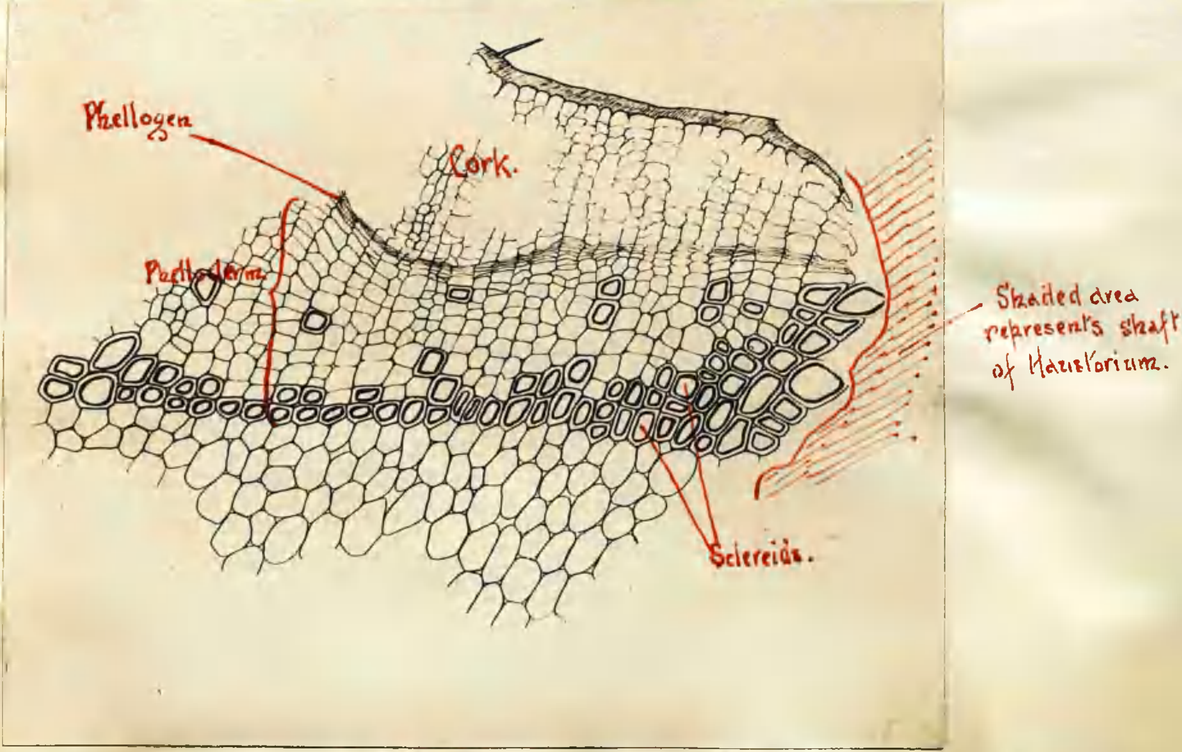


Fig 31. Phellogen activity in Geranium stem on infected side.

(1) In the case of Fuchsia the change in the host is visible in the form of a rupture of the outer tissues of the stem, a slit running upwards and downwards from the point of entry of the haustorium, narrowing as it leaves the haustorium, and ending 3 or 4mm. from the haustorium. This splitting of the outer tissues is due to an increase in the xylem and in the phloem in the vicinity of the haustorium without a corresponding increase in the tissues outside viz- the cortex and the cork. (figs. 29 & 30).
(2) In the case of geranium no splitting of the outer tissues takes place, the increase in the cortex and more especially in the cork being far more pronounced than that in the vascular tissues. In fact the whole of the warty looking structure which is developed round the place of entry of the haustorium is the result of marked activity on the part of the cork-cambium. Not only are the layers of cork considerably increased in number in consequence of this activity, but many layers are added to the cortex (phelloderm). The first formed layer of phelloderm has all of its cells transformed into sclereids, the next formed layer may undergo a similar change. Fewer and fewer sclereids are produced in succeeding layers, but in the radial rows of cells immediately abutting on the shaft of the haustorium sclereid formation continues. (fig. 31). On the side of the host stem opposite the haustorium cork formation is normal, i.e. the number of layers of cork produced is much less, and so also with the phelloderm. The first formed layer of phelloderm in this region of/

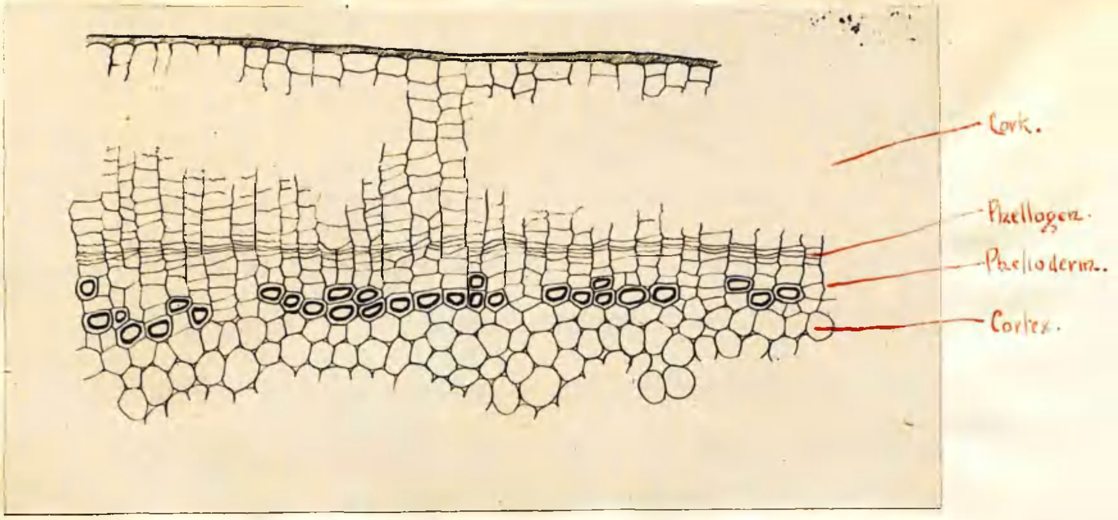


Fig 32. from non-infected side of same section as 31.

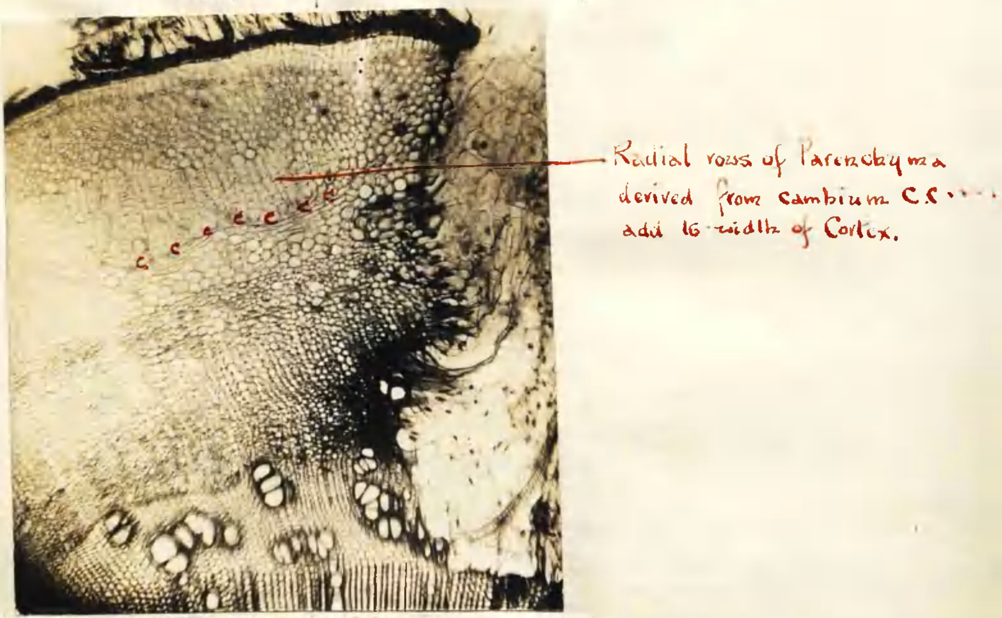


Fig 33.

Fig 34. C. reflexa on Geranium.

of the host stem may contain a single sclereid here and there; these do not occur in the later formed layers. (fig. 32). In some host stems , in transverse section, a distinct cambium is seen to have been initiated in the cortex on either side of the haustorium. This cambial layer is distinct from any previously existing cambium. It occurs between the cambial ring of the stele and the cork cambium. The result of its activity is the production of radial rows of parenchymatous cells which add to the width of the cortex. (fig. 33).

The result of such increase in the various tissues of the host, in the region invaded by the parasite haustorium, is that contact with the conducting strands of the host may fail to be established. In those thicker stems of geranium, such as those shown in figs. 2 & 34, where the warty hypertrophies are pronounced, the haustorium never reaches the vessels of the host. Nevertheless, the parasite grows healthily. In such instances the haustorium behaves more after the manner of a normal root. Its root-hairs (hyphae) develop in a tissue (the cortex) which contains all the food materials necessary for the nutrition of the parasite. These they absorb, and pass on into the parasite stem. The haustorium behaves like an ordinary root, embedded in the soil, but whereas the latter absorbs only water with mineral salts in solution, the former may absorb, not only these, but also plastic materials from the living cells of its host's cortex. Whether it does absorb plastic materials or not, we shall discuss later.

The remarkable activity of the phellogen in geranium may be an attempt to exclude the haustorium (cf. McLuckie on Loranthus celastroides "Bot. Gazette" 1923 p, 367). The attempt is certainly successful in so far as the haustorium is prevented from reaching the conducting system of the host; it is unsuccessful in that it does not prevent the parasite becoming established upon the host or its growing vigorously.

The general increase in the various tissues of the host stem in the region of the invading haustorium presents an important feature in the case of woody host plants viz. the manner of maintaining connection between the conducting elements of host and parasite. If, when the haustorium has reached and connected up with, the host's xylem cylinder, all the host tissues outside the point of connection increase radially one of three things might be expected to happen;-

(1) The shaft of the haustorium may lengthen "pari passu" with the radial increase in the host tissues and so maintain the parasite's connections, both lateral and apical, with the host.

(2) The lateral connections being established by living hyphae (root-hairs) may be maintained by intercalary growth of these hyphae.

(3) The connections with the host may be broken down.

The growing region of the haustorium is situated at its apex as is the case in a normal root (Peirce "Annals" 1893, p. 294 and p. 304). Therefore it would appear that unless the root-hairs/

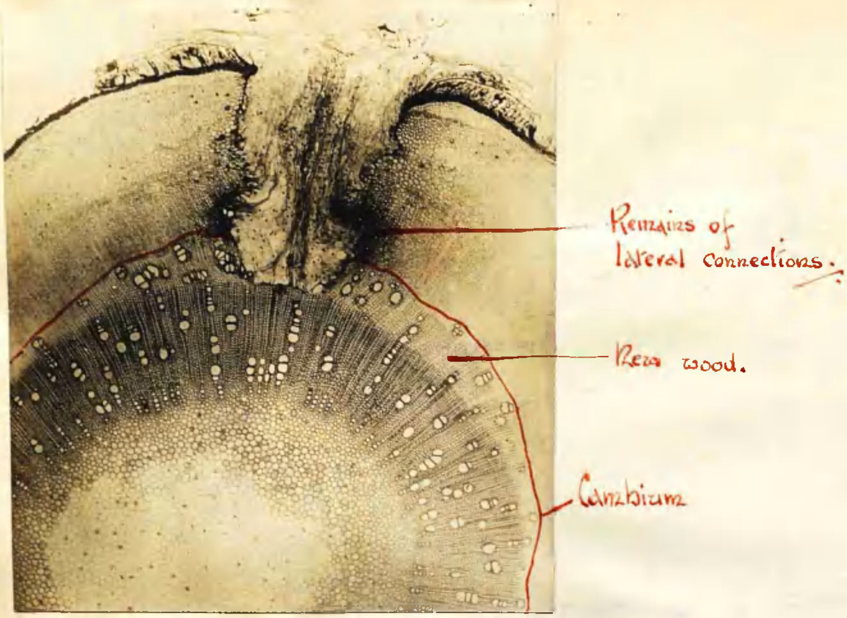
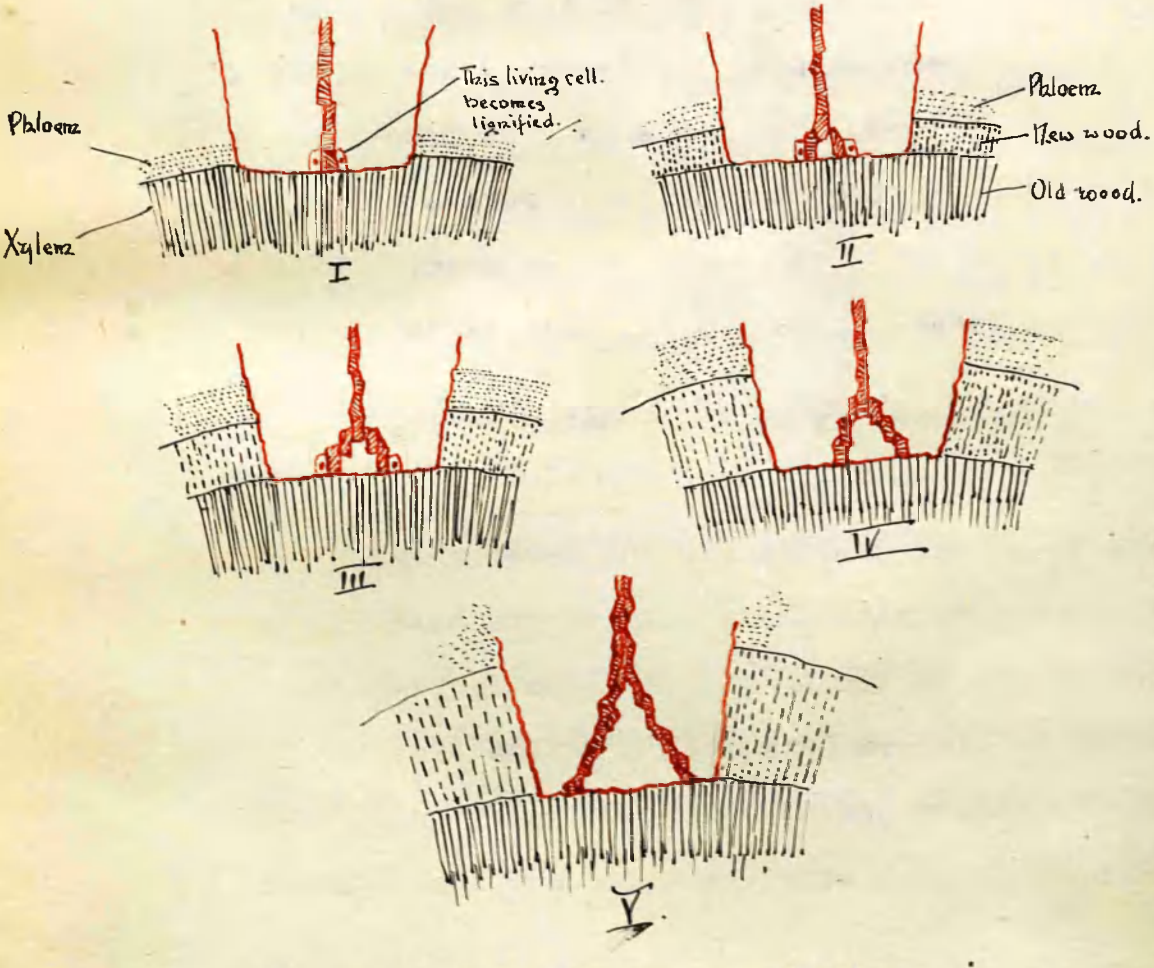


Fig 35.



Diagrams to illustrate the maintenance of the xylem Connection.

Apex of Haustorium in Red.

Host tissues in black..

root-hairs which arise from the sides of the shaft of the haustorium can adapt themselves by intercalary growth to the changing position of the host tissues in which they are embedded their connections must be broken. The apex of the haustorium is in contact with the wood of the host and direct communication between host and parasite xylems has been established through a strand of tracheids. Obviously this strand of tracheids (which are dead elements) cannot lengthen to keep pace with the growing host tissues. Rupture of the xylem connection is prevented by the addition, to the distal end of the tracheid strand, of elements from the apical growing region of the haustorium. A living parenchyma cell alongside the terminal tracheid of the haustorium is differentiated into a tracheid and so the xylem connection is maintained. Fig. 35 shows the breakdown of the lateral attachments of the haustorium in such a woody stem. The diagrams on the opposite page show the manner in which the xylem connection between parasite and host is maintained.

Observations on the problem of the parasite's nutrition.

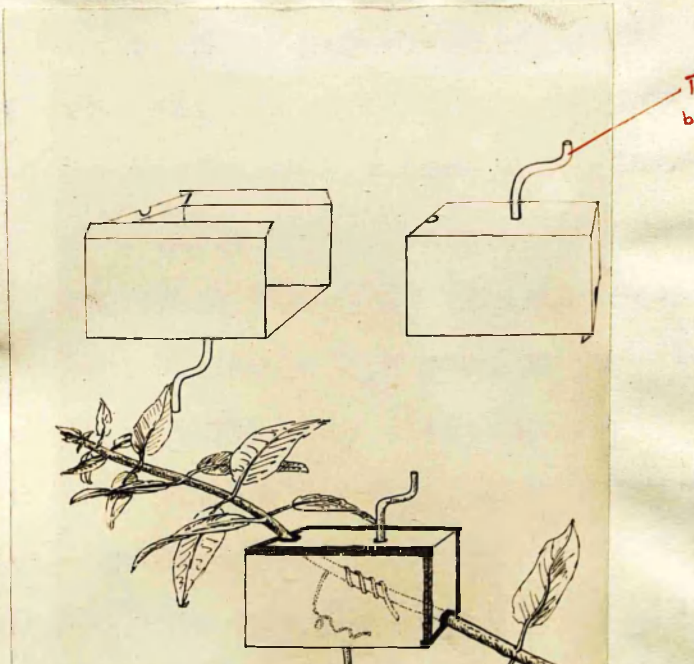
We have seen that Cuscuta reflexa never makes a definite sieve-tube connection with the phloem of its host, nor does it possess sieve-tubes in its haustoria. Its carbo-hydrate supply must therefore be elaborated by means of the small amount of green colouring matter present in its tissues or it must receive it from its host through some channel other than a normal phloem.

Haustorium has not reached host stele but derives all its food from cortex. It is furnished with a central strand of tracheids.

Fig 36. Cuscuta reflexa on Geranium

The plant bears no leaves; its outer surface is covered by a distinct, though thin, cuticle; neither this species nor any other species of the Cuscutaceae is possessed of stomata, (Ad. Chatin, Anatomie comparee des Vegetaux, Plantes parasites, Paris 1892). Therefore it would appear that, although it does possess a small amount of green colouring matter in its cortical cells, this cannot functionate in the elaboration of carbo-hydrate, since the necessary supply of carbon-dioxide is probably unobtainable by these cortical cells. One is forced then to consider the possibility of its obtaining its carbo-hydrate from its host. In those cases in which the haustorium does not reach the conducting strands of the host (page 17) (also fig. 36) the necessary carbo-hydrate may be obtained from the living cells of the host's cortex by means of the root-hairs (hyphae) developed from the dermal tissue of the haustorium.

In those cases where a definite connection is established with the vascular bundles of the host the parasite obtains its water and mineral supply from the host's xylem. While its carbohydrate may be derived from the same source or from living host cells by means of its unlignified hyphae(root-hairs). The fact that a root-hair (hypha) when it comes in contact with a xylem vessel becomes lignified at its distal end, i.e. the part in contact with the vessel, and that lignification proceeds backwards along its length, seems to suggest that the materials necessary for lignification (ligno-celluloses) may have been obtained/



Tube for ventilation.
bent to exclude light.

Fig. ~~36~~ 34.

obtained from the sap carried in the wood vessel.

With a view to determining whether carbo-hydrate was obtained from the host's xylem, an attempt was made to grow Cuscuta upon wood alone. A stem of willow had all its tissues outside of the cambium removed by peeling. The parasite formed a close spiral around the peeled stem. After a time its connection with the parent parasite stem was severed. The part twined around the wood continued to grow, and it was prevented from grasping any other nutritious host by being provided with non-nutritious supports in the form of ordinary gardener's stakes. This plant grew, but whether its growth was due to the using up of the plastic materials in the withering basal part of its stem (Peirce "Annals" 1894 p. 58) or to the fact that it received these materials from the wood of the willow was doubtful. Attempts to grow Cuscuta upon peeled stems of Fuchsia were also successful. These experiments do not prove that the plastic materials travel in the host wood since it may be that the green colouring matter, though small in amount, is capable of supplying the carbo-hydrate necessary for the parasite's growth. A piece of Cuscuta which had gripped a peeled stem was enclosed in a light tight box (fig. ~~36~~ 37.). At the end of a fortnight flower buds had developed from the parasite stem. In this experiment the green colouring matter, which is regarded by most authorities as insufficient for the plant's requirements even when exposed to sunlight, is altogether prevented from functioning. Therefore since/

since the parasite was able to grow under such conditions one might conclude that it had received the necessary carbo-hydrate supply from the wood of its host. Examination of the haustoria of such plants shows that they differ very markedly from normal haustoria.

In such abnormal haustoria (at least in the few examined so far) development appears to have proceeded only so far as the formation of the "prehaustorium". The cells of the "cushion" are closely applied to the surface of the wood, in some cases causing an inward bulging of the outer walls of the wood vessels. The "prehaustorium" has penetrated to a depth of some six or eight cells from the surface usually along a medullary ray. Whether such an attachment is sufficient to enable the parasite to withdraw the necessary nutriment for its needs I should hesitate to say and I prefer to leave the consideration of this question (viz. the growth of the parasite upon wood alone) until I have had an opportunity of examining many more cases than so far I have had time for.

Since as we have noted the stem of Cuscuta possesses no stomata, and is covered with a definite cuticle, and since its shape is such that it exposes to the air an exceedingly small amount of surface in proportion to its bulk, its transpiratory activity must be feeble. How then does it convey the necessary plastic materials to its growing apex? One can easily reverse the direction of flow of the sap in this plant (cf. Dixon "The Transpiration Stream" 1924 p. 59). Fig. 38 shows a stem of Cuscuta/

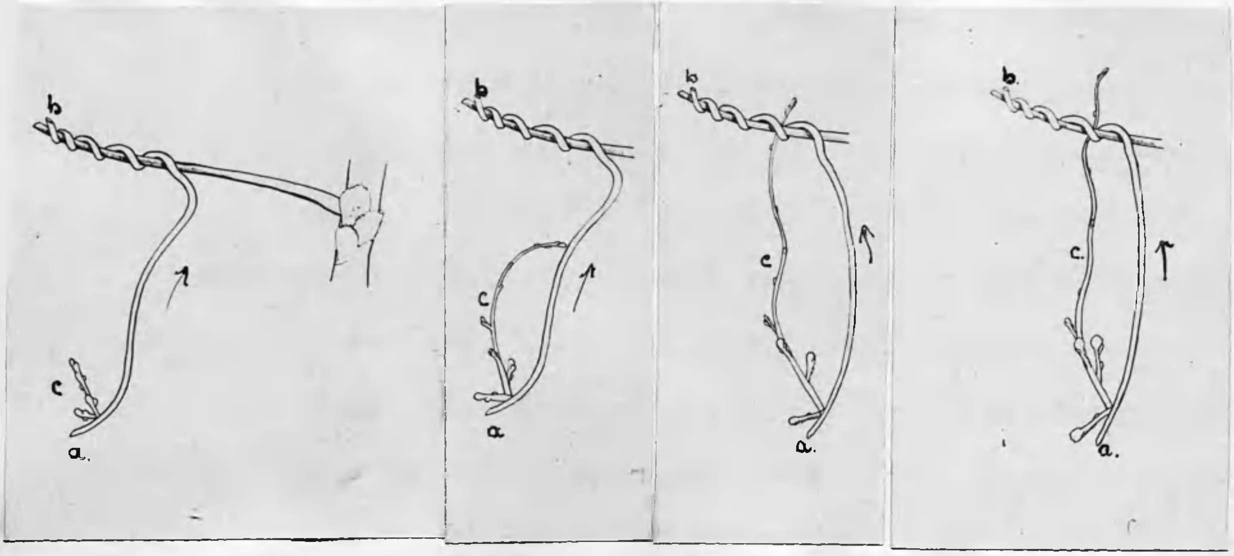


Fig 38.

Cuscuta which has gripped the petiole of a geranium leaf. The normal direction of its growth and of the flow of its sap is indicated by the arrow. It was severed at the points "A" and "B" (the bud "C" continued to develop). Its supply of food materials must have come from the host petiole and must have been carried in a direction exactly opposite to the normal. If we suppose (see Dixon "The Transpiration Stream" 1924. P. 73) that the wood of the parasite stem is "a specialised reservoir of liquid food-stuffs", and that movement of this sap is towards a sink, created by loss of water (transpiration) from a particular region, then it is a necessary corollary of such a theory that the solutes (including carbo-hydrates) will move in this solution to make good loss created by their excessive consumption at any point. The developing apices of the branch "C" will withdraw carbo-hydrates from the "reservoir of liquid food-stuffs" and consequently there will be a movement of the food-stuffs (by diffusion) in the stem "A" "B" in the direction opposed to the normal sap flow.

STUDIES IN IRREGULAR NUTRITION.

No. 2.

A. The Haustorium of Cassytha sp.

B. The Haustorium of Lathraea clandestina L.

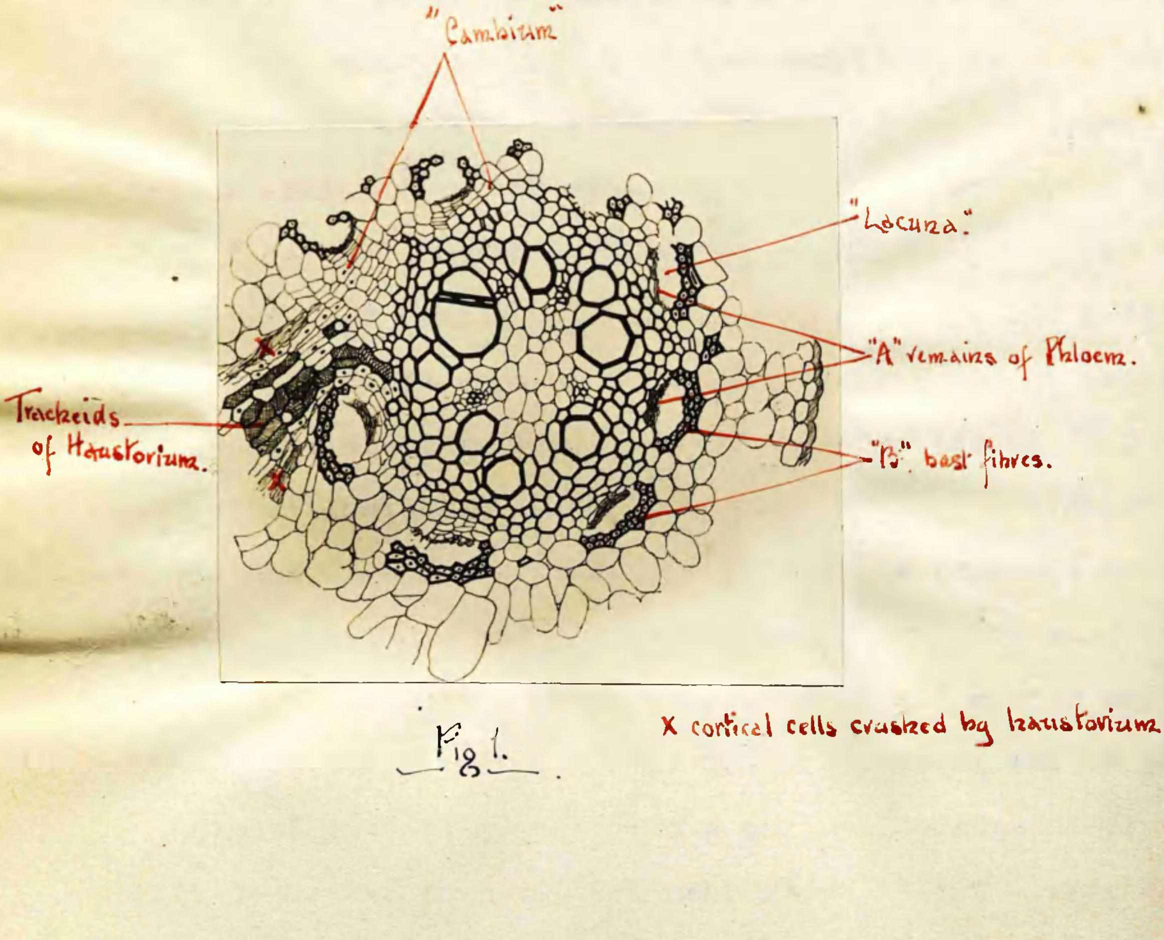


Fig 1.

X cortical cells crushed by haustorium

A short note on the Haustorium of Cassytha.

The material for this examination was collected in Australia by Professor Bower to whom I am indebted for its use.

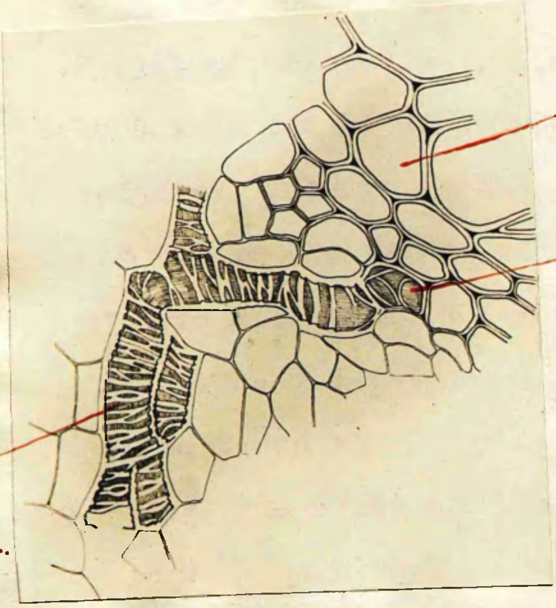
The material so far examined is all parasitic on itself. Undér such circumstances I find that one of the entwined stems develops haustoria. This observation is directly opposed to that of Chatin who, as far as I have been able to determine, seems to be the only investigator who has published any work on this genus. (Ad. Chatin, "Anatomie Comparée des Végéteaux, Plantes parisites 1892. P. 35 and P. 40). He holds that when this parasite coils its stems around one another no haustoria are formed although a normal "cushion" is formed holding the stems together. He also states that this parasite shows an aversion to living on species which are closely related to it. In the material which I have examined both stems produce a "cushion" by modification of their epidermal cells over the region of contact, and one of the stems sends what appears to be a normal haustorium into the tissues of the other.

Sections across the stem of this plant show a very striking peculiarity of the phloem. All of the sieve tubes and companion cells have disintegrated leaving a hollow tube running lengthwise through the stem. Their broken down remains line the inner side of this tube. These appear in sections as a darkly staining mass, (A. fig. 1) on the inside of what Chatin calls the lacunae (loc. cit.). These lacunae are bounded on the outer half of their circumference by a well defined band of bast fibres (B. fig. 1), these,

hese bast fibres owing to their resistant nature have undergone o disintegration.

According to Chatin this disappearance of the phloem and the consequent formation of lacunae are characteristic of all the species of the genus except C. triflora where a normal phloem is found only in the young condition. The other tissues of the stem are normal. The epidermis is protected by a well developed cuticle and is interrupted by numerous stomata. The cortex consists of five or six layers of ordinary parenchyma cells with a well developed aerating system. Its cells contain some few chloroplasts. The lacunae, varying in number according to the thickness of the stem, are distributed at regular intervals in a circle within the cortex. On their inner sides they abut directly (without the intervention of a cambium) upon the xylem which forms a continuous ring around the pith. The protoxylem groups are half as numerous as the phloem groups (lacunae) Fig. 1.

The base of the haustorium is situated between a pair of lacunae. It seems therefore to be root-like in its nature. The cell divisions by means of which it seems to have been initiated spread on either side of its base between the lacunae and the wood as far as the second lacuna on either side of the base. This cambium which thus appears between the phloem groups and the xylem on the haustorial side of the parasite stem adds no new functional phloem to the insides of the four disintegrated phloems, nor does any phloem leave the stele and enter the haustorium. The tissues of the haustorium/

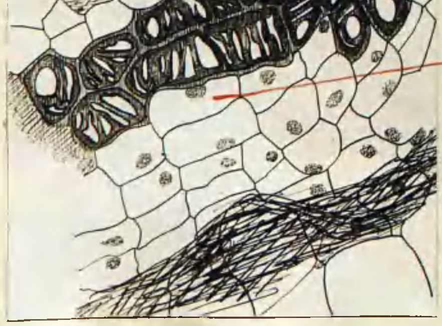


Wood of parent stem.

"A"

Tracheid strand in Haustorium.

Fig. 2.



Note position of Nuclei in cells next tracheids.

Fig 3. In the shaft of the Haustorium.

haustorium occupying the space between the crushed cortical cells (x. fig. 1) of the parasite stem consist of elongated parenchyma cells those towards the centre having been lignified and reticulately thickened link up with the xylem of the parent stem. Nowhere throughout the length of the haustorium could I distinguish a slightest trace of phloem. The condition of affairs in the shaft and in the base of the haustorium is represented in fig. 2. The only specialised tissue of the haustorium is the strand of reticulately thickened tracheids linking up with the xylem of the parasite stem at (A) fig. 2. At the distal end of the haustorium the strand of tracheids makes a similar connection with the xylem of the host stem. This strand of tracheids may be several cells wide in the shaft of the haustorium. All the other cells which accompany the tracheids in the base, the shaft and the apex of the haustorium are ordinary thin-walled nucleated parenchyma cells, elongated somewhat in the direction of the length of the haustorium. From the appearance of the tracheids (their general shape etc.,) one would conclude that they had arisen from ordinary thin-walled, living parenchyma cells, such as those which accompany them, by reticulate thickening and lignification of their walls.

The haustorium of Cassytha in its fully developed condition resembles that of Cuscuta. The connection between host and parasite is a xylem-xylem connection through a strand of tracheids. This would indicate that the only materials absorbed by the parasite from its host are those carried in the xylem viz. water and dissolved salts/

salts (plastic material?). In the language of the text-books Cassytha is merely a "water parasite". In this parasite (cf. Cuscuta) the cortical cells contain a small amount of chlorophyll. This chlorophyll may quite well functionate in the elaboration of carbo-hydrate since unlike Cuscuta this plant is possessed of stomata and a well developed aerating system. The chlorophyll containing tissue is here capable of acquiring the necessary carbon-dioxide for photosynthesis. If however Professor Dixon be correct in his suggestion that the plastic materials are transported in the xylem this parasite may receive more than merely water and mineral salts through the simple strand of tracheids which links up its xylem with that of its host.

3. The haustorium of Lathraea clandestina,L.

Fig 1.

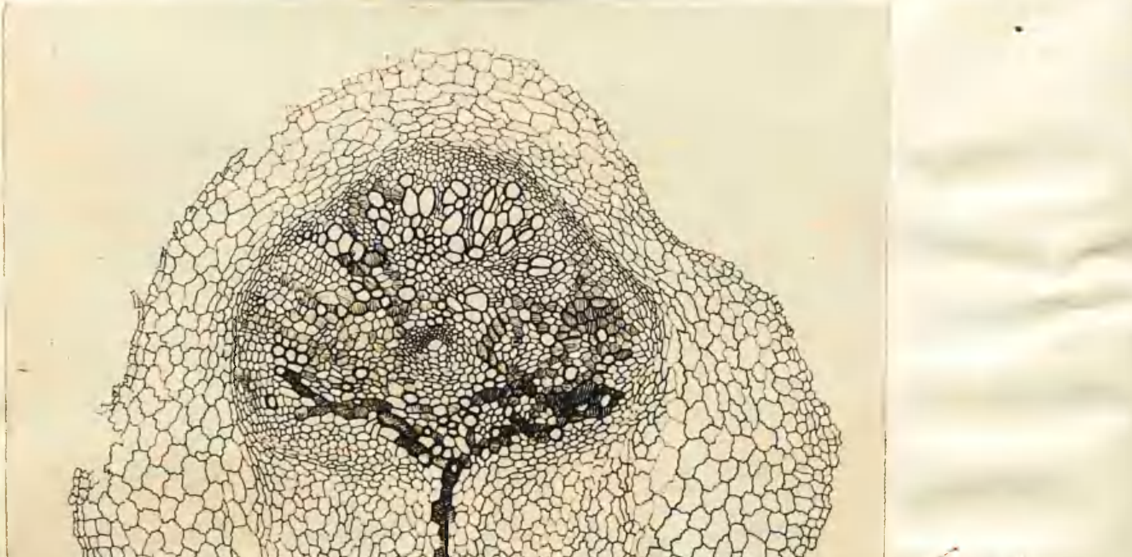

Tracheid strand.
Parenchyma cells elongated parallel to surface of separation.

Fig 2.

The Haustorium of Lathraea clandestina.

The haustoria of this holoparasite are developed in large numbers upon the roots of its hosts. They are hemispherical swellings which terminate rootlets, or occur as lateral outgrowths upon rootlets.(fig. 1.cf. Chatin Anatomie Comparée des Vegeteaux, Plantes parasites p. 90). Viewed macroscopically they appear to sit upon the host root and to fit closely to it. Sections through the haustorium show that the part in contact with the host root is conical or funnel shaped and that its apex penetrates to the host WOOD. The conical or funnel shaped part of the haustorium seems to have made its way through the outer tissues of the host root chiefly by pressure, since it is always separated from the uninjured host tissues by a well marked layer of compressed cells of the cortex and outer tissues of its host. This layer of compressed host cells is of considerable width, stains deeply in microscopic preparations, and IS NOWHERE PENETRATED BY ANY PART OF THE PARASITE HAUSTORIUM, except where at the extreme apex of the cone of the haustorium connection is established with the WOOD of the host. (cf. Bowman "Trans. Linn. Soc. vol. XV1.1833 p. 405). At this point one or two cells of the haustorium actually enter the host wood and from this point a single strand of tracheids runs straight through the haustorium to link up with the conducting strands of the parasite root. (fig.2). These tracheids are reticulately thickened, lignified cells, communicating in many instances with one another through the solution of their end walls. Except for this strand of tracheids the haustorium consists of nothing but parenchymatous cells. Those immediately abutting on the tracheids are in no way different from the others.(fig. 3). THERE IS NO TRACE OF PHLOEM.

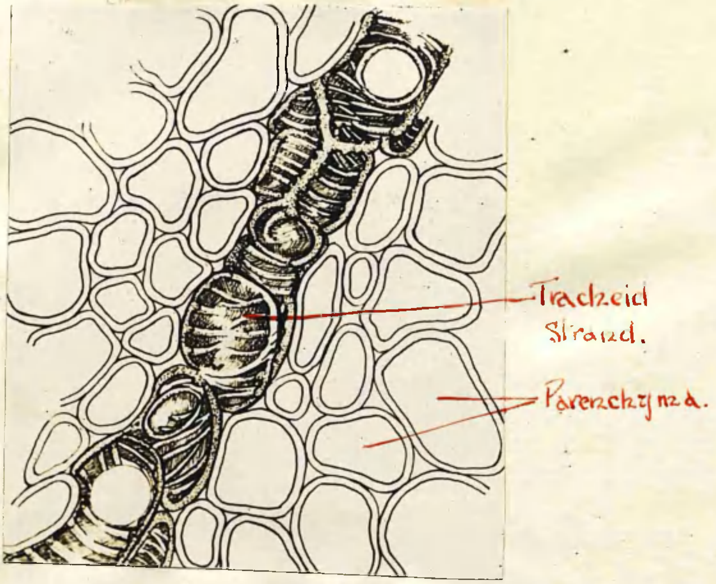


Fig. 3.

The Haustorium of Lathraea appears to be an annual organ in the sense that it never persists for longer than a single year. Bowman (loc.cit. pp. 407 and 408) has collected a certain amount of evidence in support of this view but I think an observation which he makes earlier on in his work (p. 405) and which he does not use to support the view is by far the weightiest argument in its favour viz. the haustorium penetrates "to various depths into the alburnum but never into the solid woody fibre". In all the material I have examined the tip of the funnel shaped part of the haustorium, i.e. the part which is intimately connected with the wood is never sunk deeper than the current year's growth of wood.

The surfaces of the host roots always show innumerable scars indicating the attachments of haustoria which have perished. These scars are never deeper than the current year's wood. A section through such a scar shows that the exposed surface of the host's tissues has been covered by a protecting layer of wound cork (cf. Bowman loc. cit. p. 408 and fig. 5). In further support of this view one finds that the haustoria are more numerous in Spring (April) than in Winter (November). (N.B. I have not yet had an opportunity of examining haustoria collected in Winter and do not therefore know if they differ in any respect from those collected in Spring).

Here we have a holoparasite whose haustorium like that of so many (all?) root parasites has no trace of phloem (Benson "Annals" 1910 p. 672. "no true phloem occurs in the haustoria of any so far described root parasite"). The parasite must therefore transport ALL its food materials through the strand of tracheids. We shall see that the parenchymatous cells which constitute the bulk of the haustorium are not adapted to aid to any great extent in such transport. The name "Phloeotracheids" has been suggested for such tracheids to signify that they do the work of both phloem and xylem (Benson loc. cit.). There is no need to coin a new name for these tracheids since we shall see that they perform the same work as do the xylem vessels of the host root.

The Nutrition of Lathraea clandestina.

The food materials transported through the haustorium are obviously carried in the strand of tracheids. The parenchyma cells which accompany the tracheids are not even elongated in any very marked degree in the direction of transport (figs. 2 & 3). In any study of the nutriment of this parasite the region which requires special consideration is the surface of contact between haustorium and host. On the haustorial side of this surface the parenchyma cells are elongated parallel to the surface. One would not therefore suspect such cells of playing any important part in the removal of material from the host. On the host side of the surface there lies a mass of compressed cells of the bark and cortex of the host. This layer of compressed cells is NEVER penetrated by any outgrowth from the haustorium. The apex of the conical part of the haustorium comes in contact with the wood and here the distal end of the tracheid strand is prolonged into the tissues of the wood. We see then that the only part of the surface of contact at which the haustorium connects up with uninjured host tissues is at this point in the wood. The cells of the haustorium which/

Fig. 4.

Disintegrated cells of Host. This layer is continuous thro' phloem + Cortex of Host.

Fig. 5.

× Compressed vessels of Wood.

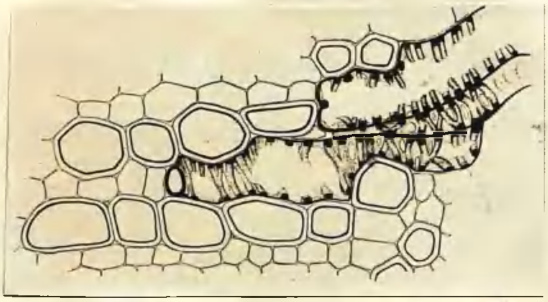


Fig 6. Cuscuta reflexa on Salvia sp.

Fig 7. (Bowman).

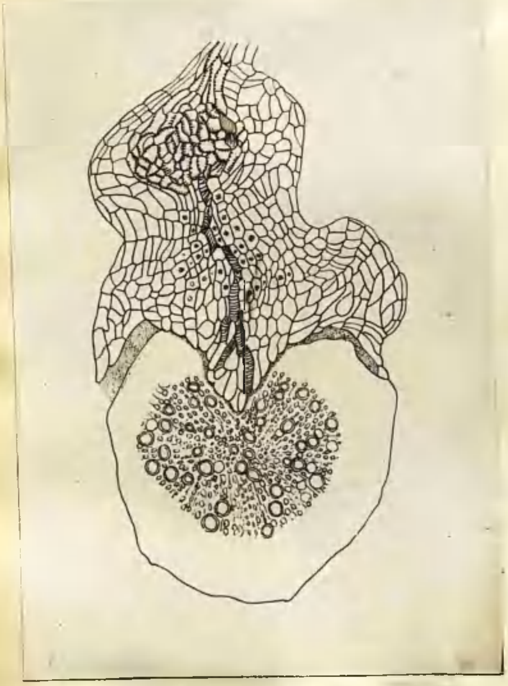


Fig 8. (Benson)

which bring about the actual junction with the host must have done so when they were living thin-walled cells, otherwise one cannot explain the manner in which the wood vessels of the host alongside of these cells are crushed (fig. 4.X.) or the way in which the tip of the strand of tracheids fits so exactly into the space which it occupies (figs. 4 & 5 and cf. fig. 6).

Bowman (loc. cit.) shows this point of contact with the wood in the illustration reproduced as fig. 7, though he does not stress the point in his description. Benson (loc. cit.) also neglects the point in her description of Thesium, although she too shows a drawing (fig. 8) which brings out the same point. Chatin (loc. cit.) p. 91 describes the parenchymatous tissue of the haustorium as covering over the "vascular cone". The most important point in the consideration of this haustorium (far more important than its structure) is this point of union with the undamaged tissue of the host WOOD combined with the fact that the compressed host tissues outwith the wood are NEVER penetrated by the haustorium. Benson (loc. cit.) suggests that the haustorium has consumed the wedge of host tissue which previously occupied the place which is later filled by the conical part of the haustorium. She regards the haustorium as a "filter" which strains the food materials passing through it from the host to the parasite. There is no need for such a suggestion. Arguing from the structure of the haustorium and its connection with the host, we may conclude that the parasite withdraws from its host the materials carried in the host wood.

Lathraea clandestina is a holoparasite absolutely incapable of/

Disintegrated outer tissues of Host.

Another fig showing union of Haustorium with wood of Host.

of elaborating carbo-hydrate by means of its underground,white, fleshy scale-leaves. It is in uninterrupted contact with its host only where the distal end of its strand of tracheids is immersed in the host wood. Therefore all of its food material ,water,mineral salts and plastic substances must be derived from the wood of its host and transported through the strand of tracheids in its haustorium. All of these food materials must be carried in the sap of the host wood. The concentration of wood sap seems never to be greater than % (V.Dixon "The Transpiration Stream" 1924 P. 57). In order therefore that the parasite may acquire a sufficiency of plastic material a very large volume of this weak solution must be passed through its tissues. This is probably effected by the glands(hydathodes) in the scale-leaves, and the excess of water which the parasite is compelled to take into its tissue is excreted in the liquid state by these glands. This would account for the fact that in a dry season when the soil elsewhere is crumbly and powdery or hard and baked that in which Lathraea is growing is saturated with water (cf. Groom "Annals of Botany" 1897 p. 385 et seq.,also Darwin "The Movements of Plants" p. 85 footnote.

DISCUSSION.

The foregoing observations on the three parasites, Cuscuta, Cassytha, and Lathraea, lead us to doubt very much the efficacy of the phloem as a carbohydrate-conducting tissue.

Cuscuta is generally regarded as being dependent on its host for more than its water supply alone. Its feeble development of chlorophyll is deemed totally insufficient to supply its carbohydrate requirement. The presence of an uninterrupted cuticle over all of its surface exposed to the air and the total absence of stomata render it extremely difficult for what chlorophyll there is in its tissues to obtain the necessary carbon-dioxide for the photosynthesis of carbo-hydrate. We would expect then, that if the particular function of the phloem be the transport of carbo-hydrate, the haustorium of this parasite would make a very definite connection with the phloem of its hosts. No such definite connection is established. Certainly hyphae grow out from the surface of its haustorium into the phloem of the host, provided the distance separating the two be not too great. These hyphae are no different from the hyphae which grow through the other tissues of the host, either in the nature and amount of their growth, or in their histological structure. In fact such hyphae are generally less strongly developed than those which enter the cortex, the cambium, or the pith of the host. Their connection with the phloem elements (if any special connection ~~is~~ be.. established ?) is short-lived in those host stems, whose width from the stelar cambium to the epidermis is increased in consequence of the irritation set up by the presence/

presence of the haustorium. The materials which such hyphae as penetrate the phloem, absorb, can be obtained from any living tissue of the host plant. Those other hyphae which penetrate the cortex, the cambium and the pith of the host are better developed and more numerous than the hyphae which enter the phloem. (This fact is evident even in the figures of those authorities who lay particular stress on the phloem connections of host and parasite).

We see then,

(1) that the host phloem exerts no pronounced attraction upon the absorbing hyphae of the haustorium, such as we should expect it to do, were the phloem capable of supplying any outstanding need of the parasite;

(2) that those absorbing hyphae which do make their way into the host phloem undergo no structural modification;

(3) that those hyphae display no specialised mode of attachment to the phloem elements of the host;

(4) that what connection there is with the host phloem may be continually ruptured, without the parasite's suffering any apparent inconvenience.

In the haustorium itself we find no trace of a phloem. The two authorities whom we have mentioned as insisting that it is present are not even agreed as to where it is, one holding that it is situated peripherally and distributed radially round the haustorium, the other that it never is radially distributed and that it is separated from the periphery by a distinct cortex.

The stem of Cuscuta is certainly possessed of phloem, distributed as in a normal herbaceous dicotyledon.

We/

We conclude then from our examination of Cuscuta, that the host phloem does not transport any food material of which the parasite stands in any dire need, nor do such materials, as the parasite may withdraw from the host phloem, require the establishment in the haustorium of any specialised tissue for their removal.

Our study of the anatomy of the stem of Cassytha strengthens the view that, as far as transport of material is concerned, the phloem is of no importance. This plant manages to transport all the materials that have to be carried in its stem, in spite of the fact that all of its phloem has ceased not only to function but even to exist. Although, as the result of haustorial formation, a distinct cambium is iniated to the inside of certain of the lacunae (which previously were occupied by phloem) no fresh functional phloem is derived from this cambium. No phloem is present in the haustorium, and all of the materials withdrawn by the haustorium (and these may include carbo-hydrate) are carried to the parasite's stem despite this want.

Even though the chlorophyll present in the cortical tissue of Cassytha ~~does~~ Could elaborate all the carbo-hydrate which the parasite requires, this must be transported from the cortex where it is formed by other channels than the phloem. The presence of stomata in the epidermis, and of intercellular air-spaces in the cortex render it probable that at least some of the parasite's carbohydrate is elaborated by its own efforts. The probable path of transport of this material we shall consider later.

The efficacy of the phloem as a tissue specially designed for the conduction of plastic materials is completely negatived by our study of Lathraea. In this plant too there is no trace of phloem in its haustoria. (This absence of phloem is characteristic of the haustoria of all root parasites, and may probably be the case in stem parasites as well.) The most outstanding feature of the haustorium of this plant is the fact that it never forms any attachment with the phloem of its host. As a matter of fact no part of the haustorium even so much as comes in contact with the host phloem. In our consideration of this parasite we are not troubled with the question of what proportion of its carbo-hydrate is elaborated by the parasite itself. Lathtaea is more wholly dependent on its host for its plastic material than it is for its water and mineral supply, since its own roots may to some extent satisfy this latter want; but its leaves, owing to their underground development and to their total non-possession of the faintest trace of chlorophyll, cannot in the slightest degree contribute to the former want. Obviously the parasite's requirements in respect of carbo-hydrate are satisfied from other sources than the phloem of its host, and further its carbo-hydrate supply is transported through a woody tissue, viz. the strand of tracheids in its haustorium, this being the only conducting channel possessed by that organ.

~~We are forced therefore to the conclusion~~ Our observations indicate that the phloem does not transport the plastic materials required by the various tissues and organs of the plant. Obviously such a highly organised tissue/

tissue performs some special and important function, but it is easier to enunciate what it does not do than to postulate what it may do. Professor Dixon ("The Transpiration Stream") has suggested that the phloem may be a special reservoir in which are contained certain enzymes whose special function is to maintain the sap travelling in the xylem in a state in which its transport is made possible. If such be the case then its function in those haustoria which we have considered is probably taken over by some other tissue.

The haustorium of a parasitic plant is not a highly specialised structure from the point of view of its anatomical organisation. There is no marked development of a specialised tissue to meet each of the various demands made upon it. The main functions which the haustorium is called upon to perform are, attachment, penetration, solution of host tissues, absorption of food materials from the host, and the transport of these into the parasite stem.

The first of these is performed by the epidermal cells of the parasite stem. These cells undergo only very slight structural modification to adapt them to their new role. The second function of the haustorium is performed by a combination of growth and of solution of host tissue. The solution of the host tissue is carried out by the dermal cells of the haustorium. These may be specially modified for this particular purpose, but modification is only carried so far as alteration in size and shape, and in their manner of growth; their walls and their contents undergo no visible change. Such cells contain enzymes which enable them to perform their work./

work.It is highly probable that they contain a large assortment of enzymes,for they are capable of dissolving their way through various types of cell wall.The same cells which perform this function of solution of host tissue are the cells which are called upon to perform the function of absorption.In many cases (e.g.when connection with the conducting elements of the host fails to be established) they are the sole organs of absorption ~~p~~ possessed by the haustorium.The only other organs,and these are the most highly specialised organs possessed by the haustorium, which take part in the absorption of food materials from the host are the tracheids when they establish definite connection with the host wood.The tracheids are the only organs specially set apart for the last of the functions devolving upon the haustorium namely that of transport.

We see then that the division of labour in the haustorium has not resulted to any marked degree in the elaboration of a special tissue for each particular function.All of the tissues are of the nature of "general purposes" tissues,and of the lot the living parenchymatous cells which constitute the great bulk of the haustorium (including its dermal system) are capable of undertaking practically any job.Can these parenchyma cells then not undertake. the work which Professor Dixon has suggested is the particular role of the phloem? There is no scarcity of enzymes in the ~~phloem~~ haustorium.The activity of these enzymes is most marked in the work of the dermal cells,but this does not necessarily mean that these are the only cells in which they occur in quantity.The supply/

ply of enzymes to the dermal cells must be continuous,and must be by way of the ordinary parenchyma cells forming the body of the haustorium.Therefore it is probable that the enzymes,required to keep the sap,travelling in the tracheids of the haustorium, in a state which will allow of rapid and easy movement,may be present in the ordinary living parenchyma cells lying alongside the tracheids.It is significant that the nuclei of these cells are generally closely adpressed to the wall of the cell which abuts upon the tracheid.(v.Cuscuta,fig.23.& Cassytha,fig.3.) According to Haberlandt ("Physiological Plant Anatomy".p.30.et seq.) the nucleus of a cell takes up its position in the cell always at the spot where some particular work is being performed.It would appear then that the parenchyma cells alongside the tracheids have something to do with the work of the tracheids,and it is possible that they take the place of phloem.

[illegible]

Since we have definitely decided that the phloem is not a channel of transport of plastic materials,we must therefore examine the possibility of the xylem doing all the work of transporting all materials,since it is the only other tissue which by its structure is capable of performing any such work.

The haustorium of Cuscuta developes hyphae in all the tissues of its host.These hyphae are absorbing organs and may acquire the necessary carbo-hydrate required by the parasite from ordinary living cells of its host.The experiments in which Cuscuta has been grown upon wood alone are not in a sufficiently advanced state/

state to enable us to reach a definite conclusion regarding the materials carried in the host wood.The fact that the parasite lives in such circumstances even when its chlorophyll is prevented from functioning suggests a possibility of the host's xylem being the path of transit of carbo-hydrate as well as of water.The fact that a hypha of the haustorium is lignified from its distal end backwards when once it has established connection with a wood-vessel of the host,seems to suggest that the ligno-cellulose (carbo-hydrate) employed in the altering and thickening of its walls has come from the sap in the host wood-vessel. The hyphae developed from the dermal tissue of the haustorium are capable of dissolving the lignified walls of xylem vessels, but a hypha which establishes connection with a vessel of its host never attacks the wall of the vessel it attaches itself to. Therefore the ligno-cellulose employed in transforming the cells of such a hypha into tracheids is not obtained from the wall of the vessel to which it is attached.The woody tracheids in the shaft of the haustorium constitute the only specialised conducting tissue possessed by that organ.In the haustorium of Cuscuta the xylem is probably concerned in the transport of plastic materials as well as water.

In the case of Cassytha a similar state of affairs exists in the haustorium,the woody tracheid strand,the xylem,carrying all of the materials derived from the host.In the stem of this parasite the total absence of phloem makes it necessary that the xylem should/

should conduct plastic material as well as water,at any rate if the plastic material is to be moved at any speed,osmotic transfer of such substances through the living tissues of the cortex or the pith being an exceedingly slow process.

We have already considered the possibility of carbo-hydrate elaboration in the cortex of this stem,and in this connection we note that the~~y~~ xylem is produced out into the spaces between (Cassytha fig 1.). pairs of lacunae,i.e. it is in contact with the cortex,and is thus in a position to collect the carbo-hydrate formed in the cortex and to transport it to the regions where it may be required.Undoubtedly the xylem in the stem of Cassytha is the channel of transport of carbo-hydrate.

Our study of Lathraea furnishes us with the most conclusive evidence in favour of regarding the xylem as the tissue in which plastic materials as well as water and mineral substances are transported.The haustorium of this parasite has only one tissue by which the materials withdrawn from its host can be transport- to the parasite root,that is the strand of woody tracheids which traverses the axis of its parenchymatous bulk,in other words the xylem of the haustorium.The amount of conduction which might be performed by the parenchyma cells of the haustorium must be so small as to be entirely negligible.

This parasite is not attached to,is not even in contact with, any undamaged tissue of its host except the wood.It must therefore since it is a holoparasite receive all of its organic food-material/

material from its host's wood. Before it can do so it is necessary that the host wood should be carrying these materials along with the water and mineral matter in its sap.

The study of these parasites shows that the PHLOEM SHOULD NOT BE REGARDED AS A TISSUE SPECIALLY CONCERNED IN THE TRANSPORT OF PLASTIC MATERIALS.

It also ~~shows~~ suggests that the phloem probably does not contain these materials in any greater quantity than any other tissue.

THE TRANSPORT OF ANY MATERIAL, NO MATTER WHAT ITS NATURE, PROVIDED IT CAN BE RENDERED SOLUBLE IN THE WOOD-SAP, AND KEPT IN SUCH A STATE, IS THE WORK OF THE XYLEM.

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