On the Haustoria of *Pedicularis vulgaris*, Tournef.

BY

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With five Figures in the Text.

INTRODUCTION.

SO far as it has been possible to ascertain, the only account of the haustoria of *Pedicularis* is due to Leclerc du Sablon,¹ who described, in 1887, the development and structure of these organs in *Pedicularis sylvatica*. The writer does not mention the existence of 'phloeotracheides' in the haustoria; indeed the conception of phloeotracheides in root haustoria did not arise till much later (1910), when Benson² demonstrated their presence in *Exocarpus*, and put forward the suggestion that they existed in all root parasites.³ The following piece of work was undertaken with the object of ascertaining whether such elements existed in the haustoria of *Pedicularis*, and the results may therefore be of use in supplementing those of du Sablon.

METHODS.

The material was fixed in acid alcohol, and was subsequently preserved in 70 per cent. alcohol. Microtome sections were used; the most satisfactory double stain for these was found to be cotton red and aniline blue.⁴ Stains of suitable strength were found by adding 100 c.c. of 80 per cent. alcohol to $\frac{1}{2}$ gram. cotton red, and 1,000 c.c. of 80 per cent. alcohol to 2 gram. aniline blue and 1 c.c. picric acid. The sections were placed for twenty-four hours in cotton red, washed with 80 per cent. alcohol, and then placed in aniline blue

¹ Leclerc du Sablon: Recherches sur les organes d'absorption des plantes parasites (Rhinanthées et Santalacées). Ann. des Sc. Nat. Bot., 7^e sér., 1887.

² Benson, Margaret: Root Parasitism in *Exocarpus* (with Comparative Notes on the Haustoria of *Thesium*). Ann. Bot., vol. xxiv, 1910, p. 671.

³ Benson (l. c.) describes phloeotracheides as lignified cells which are lined with protoplasm but contain no nuclei. Their end walls are absorbed as in open tracheides. Embedded in the matrix lining the walls are a number of granules which probably consist of hydrolysed cellulose which has been deposited as amyloextrin. Their function is to collect and act as a pathway for the hydrolysed products of solution of the host cells. In the case of *Exocarpus*, which is subject to drought conditions combined with much isolation, these elements are supposed to act as a filter, since, by the precipitation of the granules, the ascending sap is less charged with dissolved carbohydrate.

⁴ The instructions for the use of this combination were kindly given me by Miss Bancroft.

for fifteen to twenty minutes. By this method the walls of the xylem elements become clearly differentiated red, whilst dense protoplasmic contents of the parenchymatous cells of the roots, and the phloetracheides, to be subsequently described in the haustoria, take up the blue stain; the nucleus stains deeply with the blue stain, but the nucleolus takes up the red stain, and appears as a bright red spot in the nucleus.

GENERAL MORPHOLOGY OF THE ROOTS AND HAUSTORIA OF
PEDICULARIS VULGARIS.

As du Sablon has not described the haustoria in any great detail, for the sake of simplicity a general account of their morphology and structure will be given, followed by a more detailed account of the histological nature of the conducting elements in the haustoria.

The material consisted of some roots of *Pedicularis vulgaris* preying on roots of *Calluna* and on its own roots. A typical root was from 4 to 6 cm. in length; at the upper extremity, adjacent to the stem, it was about 3 mm.

FIG. 1. A. Drawing of secondary root of *Pedicularis vulgaris*, bearing tertiary roots with haustoria. $\times 4$. B. Portion of secondary root showing two-lipped appearance of haustoria. $\times 4$. C. Drawing showing host root entirely embedded in tissue of haustorium. $\times 4$. s.r. = secondary root of *Pedicularis*; t.r. = tertiary root of *Pedicularis*; h. and h'. = haustoria; y.h. = young haustorium; h.r. = host root; f.r. = fine rootlet.

in diameter, and tapered to a fine point at the penetrating end. The root was irregular in growth and in the method of branching; at the upper end adjoining the stem signs of shrinkage were distinctly obvious on the number of rings present. The haustoria were borne almost entirely on the finer rootlets, although signs of withered haustoria could be detected on the secondary rootlets, and even rarely on the primary root. This points to the parasitic habit being adopted even in the very young stages of the root's growth, although the life of these haustoria developed on the main roots is probably of short duration, since they die down and cease to be functional

with the production of the secondary and tertiary roots. Fig. 1, A, shows a secondary root *s.r.* of *Pedicularis*, which bears tertiary roots, *t.r.*, on which are borne the haustoria *h.* and *h'*. Fig. 1, B, shows a portion of a secondary rootlet bearing haustoria which have ceased to function. The haustoria are scattered irregularly on the roots bearing them (see Fig. 1, A), and have no definite order of development. They are first obvious as small hemispherical swellings on the rootlet (Fig. 1, A, *y.h.*). These increase in size and attach themselves to the host root in such a manner that the host root is always perpendicular to the portion of the parasitic root bearing the haustorium (see Fig. 1, A and C). The tissue of the haustorium grows up and partially encloses the host root; thus a groove is formed in the haustorium which is parallel to the host root and therefore perpendicular to the axis of the parasitic root at this point. In Fig. 1, A and B, *h'*, the groove is distinctly visible owing to the host root being no longer attached—it has probably degenerated or become torn away—whilst in Fig. 1, A and C, *h.*, the haustoria are shown in connexion with the host roots *h.r.* The growth of the haustorium may sometimes be so vigorous that the host root becomes entirely enclosed in its tissues (see Fig. 1, C). The haustorium depicted here is borne on a tertiary root *t.r.*, and is also interesting in that it arises at the place of origin of a finer rootlet *f.r.*

FIG. 2. A. Longitudinal section of tracheidal element of xylem of *Pedicularis*, showing protoplasmic contents and a nucleus. $\times 472$. B. Longitudinal section of elongated parenchymatous elements which function as phloem. $\times 472$. *tr.* = tracheide; *pa.* = elongated parenchymatous element; *p.* = protoplasmic contents; *n.* = nucleus.

Anatomically the roots of *Pedicularis* differ in two important details from the roots of normal Dicotyledons, namely in the complete absence of phloem and in the peculiar nature of the xylem elements. The xylem of the roots, both main and lateral, is composed entirely of tracheides and elongated parenchymatous cells, the latter being present in great abundance. The protoxylem consists of smaller tracheides, both spirally and annularly thickened. The other tracheides are all reticulately thickened, and, even in the oldest roots, still possess protoplasmic contents and often a nucleus. Fig. 2, A, is an old tracheide from a finer rootlet, and is typical of the tracheidal elements of the xylem. Much lignification of the walls of the element had taken place, yet it still showed abundant protoplasmic contents *p.*, and a large nucleus *n.* The place of the phloem in a normal root is taken by

a zone of elongated parenchymatous cells. All roots were very carefully examined for the presence of sieve-tubes, but no trace of any was discovered. Fig. 2, B, shows two of these elongated parenchymatous cells *pa.*, with their dense protoplasmic contents *p.*, and large nuclei *n.*, in longitudinal section. It is probable that transmission of organic food material takes place in *Pedicularis* root by osmosis, as Peirce¹ suggests for *Arceuthobium occidentale*, the complex materials passing from the elements of the host root through the thin walls of the parasitic parenchymatous elements by simple osmotic pressure. Now Benson² has suggested that the phloeotracheides of *Exocarpus* haustoria combine the functions of phloem and xylem. It seems probable that the tracheidal elements of *Pedicularis* root behave in much the same way, from the fact of their retention of protoplasmic contents.

This absence of typical phloem elements is not characteristic of all root parasites. Barber³ has demonstrated the presence of sieve-tubes in the roots, though not in the haustoria, of *Olex scandens* and *Santalum album*; Peirce has shown that they exist in the roots and in the haustoria of *Arceuthobium occidentale*; and Benson has demonstrated their presence in the roots but not the haustoria of *Exocarpus*. Stephens,⁴ however, failed to find any sieve-tubes in the roots of *Striga lutea* on which the haustoria were borne, and suggested that the transference of organic food might take place by osmosis. In the case of *Pedicularis* this seems to be most probable, especially in view of the nature of the xylem elements.

THE HAUSTORIUM.

Du Sablon⁵ has described briefly the anatomical development and structure of the haustorium, but for the sake of continuity and clearness a short account of the development will be given here. The haustorium arises in the hypodermal tissue of the cortex. The hypodermal cells of the cortex and the cells of the piliferous layer elongate enormously, and radial walls are formed in them. Tangential walls then follow rapidly in the elongated cortical cells, the cells of the piliferous layer, in contact with the host root, still continuing to divide by radial walls. Some of the outermost of these cells, that is, those farthest away from the surface of contact of the haustorium with the host root, elongate enormously, so that they have the effect of clasping the host root and acting as suctorial organs. Meanwhile division still continues in the cortical tissue, the endodermis even taking part in the division. Thus there

¹ Peirce, G. J.: Dissemination and Germination of *Arceuthobium occidentale*. Ann. Bot., vol. xix, 1905, p. 99.

² Benson, Margaret, l. c., p. 673.

³ Barber, C. A.: Studies in Root Parasitism—The Haustoria of *Santalum album*. Mem. Dep. Ag. Ind., Bot. Ser., vol. i, 1906-7. Studies in Root Parasitism—The Haustoria of *Olex scandens*. Mem. Dep. Ag. Ind., Bot. Ser., vol. ii, 1907.

⁴ Stephens, E. L.: The Structure and Development of the Haustorium of *Striga lutea*. Ann. Bot., vol. xxvi, Pt. II, 1912.

⁵ Leclerc du Sablon, l. c.

is formed in the developing haustorium a mass of small-celled tissue, the 'nucleus', using the terminology of former writers;¹ this is bounded by the elongated palisade-like cells of the piliferous layer on the side adjacent to the host root, and by a cortex a few cells in thickness on its flanks. The haustorium penetrates the host root by means of the palisade-like piliferous cells, which grow straight forward into its tissue, dissolving the cortical cells through which they pass, and living on their contents, and eventually reaching the xylem elements of the root. After applying themselves by their tips to the elements of the host xylem, some of them become thickened in an annular or reticulate manner, still retaining their contents. Meanwhile a change has been taking place in the parenchymatous cells adjacent to the xylem elements of the mother root opposite the position of the haustorium. These become thickened in a reticulate or annular fashion and form a mass of tracheidal cells, which, however, still retain dense protoplasmic contents. Then a single row of the small cells of the central mass or 'nucleus', connecting the tracheidal penetrating cells with the mass of the tracheides adjacent to the xylem of the mother root, become lignified and thus tracheidal connexion is set up between the parasitic and host xylems. So much has been described by du Sablon, but little has been said by him about the internal anatomical structure of the mature haustorium, or the orientation of its internal conducting elements beyond mention of the fact that the penetrating cells are lignified in one plane only.

The orientation of the conducting tissue of the haustorium bears a definite relation to the orientation of the host root. It has already been said that the haustorium always attaches itself to the host root in such a manner that the latter is always perpendicular to the portion of the parasitic root bearing the haustorium (see Fig. 1). Hence if a median longitudinal section of the haustorium be made, in such a plane that a longitudinal section of the parasitic mother root is obtained, a transverse section of the attached host root will be made. Conversely, if a median longitudinal section of the haustorium be made in such a plane that a transverse section of the mother root is obtained, a longitudinal section of the host root will result. Always bearing in mind the orientation of the host root with regard to the parasitic root, and with the help of a few diagrams it is a simple matter to understand the internal structure of the haustorium. Fig. 3, A, represents a median longitudinal section of the haustorium taken in such a plane that a longitudinal section of the mother root and transverse section of the host root are obtained. The haustorium is seen to consist of a central mass of small-celled tissue *n.c.* Adjacent to the vascular strand *v.s.* of the mother root is the plate of tracheidal cells *t.p.*, and running directly from this to

¹ Barber, C. A., l. c.; Fraysse, A.: Contribution à la biologie des plantes phanérogames parasites. Montpellier: Société Anonyme de l'Imprimerie Générale du Midi, série A, No. 515, 1906; Benson, Margaret, l. c.; Stephens, E. L., l. c.

the host root *h.r.* is a single strand of tracheidal elements *t.c.* This strand may be one, two, or three cells in thickness when cut in this plane, but is rarely more, and most often consists of a single row of cells. Fig. 3, B, shows a portion of the same haustorium in detail; the relative sizes of the cells *n.c.*

FIG. 3. A. Diagrammatic median longitudinal section of haustorium in a plane of a longitudinal section of the mother root and transverse section of host root. $\times 57\frac{1}{2}$. B. Detailed drawing of a portion of haustorium represented in A. $\times 223\frac{1}{2}$. C. Diagrammatic obliquely longitudinal section of root of *Pedicularis* attacked by two haustoria, *h* 1 and *h* 2, and bearing two haustoria, *h* 3 and *h* 4, which are attacking roots of *Calluna*, *c* 1 and *c* 2. $\times 44$. D. Portion of haustorium, *h* 1 in detail. $\times 223\frac{1}{2}$. *t.p.* = tracheidal plate; *t.c.* = tracheidal connexion; *n.c.* = cells of 'nucleus'; *c.c.* = cortex of haustorium; *v.s.* = vascular strand of parasitic root; *h.r.* = host root; *p.t.* = penetrating tracheides; *d.r.* = dead remains of host root; *xy.* = xylem of host root.

of the 'nucleus', and those *c.c.* of the cortex, and the difference in density of their protoplasmic contents are shown. The cells of the tracheidal plate *t.p.* are in all stages of differentiation; some still have completely unthickened walls, whilst others have become lignified to a considerable extent. The strand of tracheidal cells *t.c.* connecting the thickened tracheidal cell *p.t.* of the penetrating piliferous layer with the elements of the tracheidal plate is not complete owing to the fact that the section was cut in a slightly oblique direction. The black line *d.r.* represents the crushed remains of the cortical tissue of the host root.

Fig. 3, C, *h. 1* represents a median longitudinal section of a haustorium, cut in such a plane that a transverse section of the mother root, from which the haustorium arises, is obtained. In this plane the central mass of small-celled tissue is seen to be surrounded only by a very few layers of cortical cells, *c.c.*, and nearly all the cells of this central mass have become lignified

in a reticulate or annular manner. Similarly the majority of the penetrating piliferous cells have become lignified. The blackened circle *v.s.* represents the vascular tissue of the mother root, now cut in transverse section; the tracheidal plate is the cross-hatched portion *t.p.* and the portion marked by parallel straight lines represents the lignified elements of the 'nucleus' and penetrating piliferous layer, which connect the parasitic and host xylem. Fig. 3, D, represents half of this haustorium in detail; the tracheides *p.t.* which have been differentiated from the penetrating cells of the piliferous layer are at one end in direct communication with the xylem elements *xy* of the host root *h.r.*, and at the other with the elements *t.c.* of the tracheidal connexion which have been differentiated from the small-celled tissue of the 'nucleus'. These again are in direct communication with the elements *t.p.* of the tracheidal plate, and are practically indistinguishable from them, except for the larger size of the latter.

Before proceeding to construct the anatomy of the mature haustorium from the sections cut and just described, and from other serial sections, a fuller description of Fig. 3, C, will be given, as this represents rather a unique case of attack. The section is a slightly oblique longitudinal one of a root *h.r.* of *Pedicularis*, which is attacked in two places by haustoria, *h. 1* and *h. 2*. Meanwhile it has itself produced two haustoria, *h. 3* and *h. 4*, which are attacking two roots of *Calluna*, *c. 1* and *c. 2* respectively. The root *r.* of *Pedicularis* acts as host to the two haustoria *h. 1* and *h. 2*, and hence, since it is itself cut in longitudinal section, these two haustoria are cut in the plane of section which gives a transverse section of the mother roots at the point of origin of the haustoria. Again, the root *h.r.* acts as the mother root of the two haustoria *h. 3* and *h. 4*, whose host roots are respectively *c. 1* and *c. 2*. Here, since the mother root *h.r.* is cut in longitudinal section, the two host roots *c. 1* and *c. 2* are cut in transverse section and the plane of section of the haustorium is the same as that shown in Fig. 3, A. Hence, here in one figure there are represented, typically by *h. 1* and *h. 3*, the two planes of section of a haustorium, which give the two principal views of the anatomy just described.

From Fig. 3, A and C, *h. 1*, it can be seen that the differentiation of the palisade-like elements of the piliferous layer takes place in one plane only, the plane of section of the haustorium represented in Fig. 3, C, *h. 1*. This is also true of the cells of the 'nucleus' which become differentiated for conduction. The tracheidal plate, however, is not elongated in one direction, but is disc-like in shape, varying in thickness, but generally about three or four cells deep. Thus the mature haustorium consists of tracheidal elements arranged in a row, varying from one to three elements in thickness, and running in a direction parallel to the length of the host stem; these are surrounded by an elliptically shaped mass of small-celled tissue, the 'nucleus', the long axis of the ellipse being represented by the row of tracheidal

elements. The cells of the 'nucleus', and also the row of tracheidal elements, are in direct communication with the cells of the tracheidal plate, which is adjacent to the vascular tissue of the parasite, and all food material drawn from the host has to pass through this disc on its way to the parasitic root. The whole of this central tissue of the haustorium is surrounded by a cortex, which in most places is from four to six cells deep.

One of the haustoria examined exhibited a peculiar arrangement of the conducting tissue, which was interesting in so far as it showed a modification in the direction of economy of conduction elements. A median longitudinal section of a haustorium of *Pedicularis* had been cut in the plane giving a transverse section of the host root, hence the type of section illustrated in Fig. 3, A, was shown. One of the

cells, Fig. 4, *p.t.*, of the piliferous layer, adjacent to a xylem element of the host root, had become thickened in the usual way, and still retained its contents. The cell *t.c. 1* of the conducting tracheidal strand which was adjacent to this element *p.t.* was elongated to an abnormal extent, and in a direction perpendicular to that of the axis of the haustorium, and therefore perpendicular to the normal direction of elongation of these elements. The remaining elements of the tracheidal strand were of the normal form. The solution absorbed by the element *p.t.* from the host xylem element *xy* passes into the element

FIG. 4. Detailed drawings of a few cells at the penetrating end of a *Pedicularis* haustorium showing unique arrangement of haustorial tracheidal element *t.c. 1*. $\times 326\frac{2}{3}$. *xy.* = host xylem element; *p.t.* = cell of piliferous layer tracheidally thickened; *t.c. 1*, *t.c. 2* = cells of tracheidal connecting strand; *n.c.* = cells of 'nucleus' adjacent to elongated element *t.c. 1*. The arrow denotes the direction of the longitudinal axis of the haustorium.

t.c. 1, whence it can be passed into each one of the cells *n.c.*, and also the cell *t.c. 2*. Hence this phenomenon would appear to be a unique effort on the part of the haustorium towards economy of conducting material.

It has already been mentioned that the parasitic root preys on other roots of the same or a different plant of *Pedicularis*. When such was the case no difference in the structure of the haustorium arose. Barber¹ has shown that where *Ola*x attacks itself marked differences occur in the structure of the haustoria; all the vascular tissues of the mother root are continued down the entire length of the haustorium, and at the penetrating end enter into connexion with similar elements of the host root, the connexion being of the nature of a fusion. No such difference was found to exist in haustoria of *Pedicularis* in cases of self-attack, but the method of

¹ Barber, C. A. : Mem. Dep. Ag. Ind., Bot. Ser., vol. ii, 1907.

attack was precisely similar to that on *Calluna* root. As has been already mentioned, Fig. 3, C, represents in *h. 1* and *h. 2* two haustoria of *Pedicularis* attacking a root *h.r.* of the parasite. From the figure it can be seen that these two haustoria were similar in structure to the two haustoria, *h. 3* and *h. 4*, which were attacking roots of *Calluna c. 1* and *c. 2*.

There can be little doubt as to the morphology of the haustorium. That it is not a lateral root is evident, firstly because the haustoria arise indiscriminately, without any regard to sequence, on the surface of the lateral rootlets—in one case figured (Fig. 1, C) a haustorium had arisen actually at the point of origin of a lateral rootlet; and secondly, because the seat of origin is in the hypodermal layers of the root. They must therefore be regarded merely as superficial outgrowths of the roots formed for the purpose of extracting food material from foreign roots.

MINUTE STRUCTURE AND HISTOLOGY OF THE TRACHEIDAL ELEMENTS OF THE HAUSTORIUM.

So far no account has been given of the minute structure of the elements composing the conducting tissue of the haustorium, beyond the fact that when lignification has occurred, the cells still retain their protoplasmic contents and nuclei. The penetrating cells of the piliferous layer differ from ordinary adult tracheides only in the possession of protoplasmic contents and a nucleus (Fig. 5, A, *p.t.*). Before lignification of the walls sets in, the contents of these club-shaped cells appear to diminish slightly in density, the protoplasm lying along the walls (Fig. 5, A, *p.c.*). No alteration in size of the nuclei is visible. That this slight diminution of protoplasm is not a stage in the complete degeneration of the protoplasmic contents, as would be the case in the development of an ordinary tracheidal cell, is demonstrated by the fact that in quite old haustoria these tracheidal elements are always seen to contain protoplasmic contents.

The elements of the tracheidal connecting strand and the tracheidal plate differ from each other only in size, the elements of the tracheidal plate being larger than those of the connecting strand. They both alike differ from the penetrating tracheidal cells of the piliferous layer, in that their protoplasm exhibits a number of granules, which stain bright blue with aniline blue. These elements, which will be called the 'phloeotracheides', differ only from those of *Exocarpus*, described by Benson,¹ in the possession of a nucleus. Otherwise they possess every characteristic of phloeotracheides. As Benson emphatically states that the phloeotracheides of *Exocarpus* were devoid of nuclei these cells were very carefully examined. In the majority of cases nuclei were found, and nowhere could any sign of degeneration of the nucleus be perceived. It is therefore concluded that the normal condition

¹ Benson, Margaret, l. c., p. 671.

in *Pedicularis* is for these cells to possess nuclei. Fig. 5, B, represents an optical section of a phloeotracheide which shows spiral thickening *l.*, and dense protoplasmic contents with granules *g.*, and a nucleus *n.* Fig. 5, C, shows two of these cells in transverse section, one of which has included the nucleus *n.*, and the other not. In Fig. 5, D, is depicted a fairly large phloeotracheide of the tracheidal plate in obliquely transverse section. The nucleus was not included in this section.

Previous records of these granules in tracheides have been made by Heinricher¹ and Benson.² Heinricher pointed out their presence in the con-

FIG. 5. A. Detailed drawing of cells of penetrating piliferous layer of haustorium, one of which, *p.t.*, has become lignified. $\times 472$. B. Detailed drawing of optical section of cell of 'nucleus' which has become lignified. $\times 472$. C. Transverse section of cells of nucleus which have become lignified. $\times 472$. D. Obliquely transverse section of element of tracheidal plate showing protoplasmic contents and granules. $\times 472$. *p.t.* = penetrating tracheidal element; *p.c.* = unlignified penetrating elements of piliferous layer; *p.c.* = protoplasmic contents; *g* = granules in protoplasm; *l.* = lignification; *n.* = nucleus of cells.

ducting cells of *Lathraea haustoria*, and figures some of these cells in Taf. IX, Fig. 7, and Benson describes them in *Exocarpus*, and considers that phloeotracheides are characteristic of all root haustoria, though they are arranged in different ways in haustoria of different plants. She considers the presence of the granules to be due to the deposition of the surplus of hydrated cellulose contained in the elements at the time of their lignification. In all the lignified conducting cells of this species of *Pedicularis* examined, not

¹ Heinricher: Anatomischer Bau und Leistung der Saugorgane der Schuppenwurz-Arten. Cohn's Beiträge z. Biol. d. Pflanzen, Band 7, ii, 1898.

² Benson, Margaret, l. c., p. 671.

only of the haustoria, but also of the roots, the persistence of the protoplasmic contents is a unique adaptation to the absence of phloem, the xylem elements being thereby enabled to conduct both organic and inorganic food material.

SUMMARY AND CONCLUSION.

1. *Pedicularis vulgaris* is a root parasite capable of attacking both the roots of other plants and of itself.
2. Haustoria of *Pedicularis vulgaris* were examined in detail and their anatomical structure has been described. The structure was found to be identical both in the case of attack of a foreign root and of itself. In this respect *Pedicularis* differs from *Olex*, which Barber has shown to vary in structure in the case of self-attack.
3. The haustoria were found to possess phloeotracheides, which, however, differed from those described by Benson for *Exocarpus* in being nucleated.
4. The xylem tracheides of the roots and of the piliferous layer of the haustoria were found to possess abundant protoplasmic contents.
5. Phloem was found to be absent from both the roots and the haustoria of *Pedicularis vulgaris*. This phenomenon was concluded to be correlated with the retention by the xylem tracheides of their protoplasmic contents. In the roots the place of the phloem is taken by elongated parenchymatous cells.
6. *Pedicularis vulgaris* being a root parasite is characterized by less highly differentiated haustoria than is found in stem parasites. The conducting cells are not specialized for the conduction of either organic or inorganic materials, but are capable of conducting them both indiscriminately.

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