On the Histological Relations between *Cuscuta* and its Host.

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With Plates XLIX-LI.

INTRODUCTORY.

THE questions concerning the origin of protoplasmic connecting threads in plant tissues have long excited much interest. At present we are confronted with two main conflicting theories, namely, that of Strasburger,¹ who has hitherto maintained that connecting threads owe their origin to the boring out of the cell-walls by the protoplasm (the formation of 'plasmodesmic pseudopodia'), and that held by Gardiner² and previously suggested independently by Russow² and Kienitz-Gerloff², who regard connecting threads as derived primarily from spindle fibres, and as therefore only present when cell-wall formation follows on nuclear division. It is obvious that if we knew whether connecting threads are ever formed between cells or tissues which are not genetically continuous, we should be a step further towards a decision between these theories. On this point a large amount of evidence will no doubt be necessary, but it occurred to me that a good beginning might be made by a careful histological investigation of the haustoria of parasites, in order to determine whether sieve plates are ever formed in compound walls separating the cells of the host from those of the parasite. The work of previous authors³ on parasite haustoria tends to support the former of the two theories, but recent improvement in histological methods now makes more minute examination possible.

Material of *Lathraea squamaria* and a species of *Orobanche* was preserved and examined, but both were found to be eminently unsuited to this kind of histological work. Various species of *Cuscuta* growing on

¹ Strasburger, 1901 and 1902.

² Gardiner, 1900 and 1907; Russow, 1883; Kienitz-Gerloff, 1891.

³ Peirce, 1893 and 1894; Strasburger, 1901.

various hosts were also studied; of these *Cuscuta europaea* on the Hop, *Cuscuta reflexa* on *Begonia* and *Ficus*, and an unnamed variety growing on *Solidago* were not found to be very useful; the best material was obtained from *Cuscuta europaea* growing on *Vitis*, and *Cuscuta reflexa* growing on *Salvia* sp. The former, growing out of doors in the Cambridge University Botanic Garden, was collected in July and October, the latter in June and July from a plant growing in the greenhouse.

Most of the more important results were obtained from *Cuscuta reflexa*, a perennial species growing on *Salvia*, and as the histology of the phloem in the latter genus had not been studied, it became necessary in the course of the work to make some investigations on its sieve tubes; these are recorded in the first part of the paper, while the second part deals with the histology of the parasite *Cuscuta*, particularly with the development of its sieve tubes. The investigation of the phloem of these two plants is of some interest in itself, since it is the first time that the phloem of so small a plant as *Salvia* or that of a parasite has been studied by recent methods. In the third part, which is of more interest to the general reader, an attempt is made to give some account of the manner in which the haustorium penetrates the host, and deals especially with the origin of the sieve tubes in the haustorium and the development of connexions with the sieve tubes of the host. The facts brought to light afford important evidence both on the value of sieve tubes for conduction, and on the efficiency of sieve plates; the paper closes with a short discussion of these matters, and of the conflicting theories concerning the nature and origin of connecting threads.

I am indebted to Mr. Lynch for kindly aiding me in obtaining material. The work for this paper was begun in the laboratory of the Royal Holloway College, but was chiefly carried out at the Botany School, Cambridge, while holding a Fellowship at Newnham College.

METHODS.

The methods used for preservation and staining were based on those used by Gardiner,¹ Hill,² and the author³ in previous work. The material found best for the minute histological work was preserved in a solution of 0.5 gramme iodine in 0.75 gramme potassium iodide in 100 c.c. of distilled water. The results obtained by the safranin method without a wall stain were confirmed by a study of paraffin microtomed sections stained in ruthenium red, chlor-zinc-iodine, or Delafield's haematoxylin; in some cases the actual sections used for the examination of sieve plates, &c. (and stained in safranin, aniline blue,⁴ and London blue), were afterwards placed in Delafield's haematoxylin, so that the relations of the walls might be

¹ Gardiner, 1898 *a* and *b*.

² Hill, 1901 and 1908.

³ Sykes, 1908.

⁴ Sykes, p. 298, l. c. [Water blue (Hofmann's blue) made up with aniline.]

more clearly understood. The sieve plates could still be located, and the callus could still be stained; it was thus possible to obtain reciprocal preparations of the same element, in the first place with protoplasmic connexions and slime strings well shown, in the second with the walls stained (see Figs. 76-8, Pl. LI).

I. NOTES ON THE HISTOLOGY OF SALVIA (SP.?) (perennial).

(a) The sieve tubes of *Salvia* are found to resemble closely those of *Vitis*¹ in the general outlines of their development. The small size of the narrow terminal sieve plates makes them difficult to investigate, but it has been possible to make out sufficient of their structure for the present purpose, and it is interesting to find so close a resemblance between the sieve tubes of the Vine and other large plants heretofore examined, and those of a small plant like *Salvia*.

Fig. 1, Pl. XLIX, represents a young *terminal sieve plate* in section; it is seen to be unpitted and traversed by a number of fine protoplasmic threads, on some of which a minute swelling is visible at the middle lamella. On the upper surface of the plate faint specks of callus have already appeared at the ends of the threads. The extension of the callus change is seen in the terminal sieve plate in Fig. 2, where each thread is enclosed in a callus rod. Figs. 3, 4, 5, represent other sieve plates in the same and later stages.² Surface views at these stages showed each string to be in the centre of a hole traversing the plate and surrounded by a ring of callus. Shallow pits are usually formed in the young sieve plates, but are not universally present even in the quite mature plate. When present, each pit is always occupied by a single thread or slime string, the method of development being that of Hill's second type.³

All the older sieve tubes in this material were in the stage shown in Fig. 6, where a large mass of callus is seen on either side of the plate.

Lateral sieve plates were rare; they appeared to resemble the terminal sieve plates in all particulars (Figs. 4 and 8). Fig. 7 represents a lateral plate in surface view; the ends of the callus rods are arranged in groups, and the groups are distributed over the plate, collected together in well-defined areas. In one lateral sieve plate (Fig. 8) median nodes were clearly seen separating the two halves of the callus rod; these were also present in the terminal sieve plates, but are not shown in any of the figures.

The *sieve fields* are rather more abundant in the tangential than in the radial walls.⁴ In surface view numerous elliptical depressions are seen in the wall; each depression is a shallow pit, the membrane of which is traversed by numerous fine threads (Figs. 10 and 11). Each thread is bored out and transformed into a slime string enclosed in a separate callus

¹ Hill, 1908.

³ Hill, 1908, p. 274, Text-figs. 10, 11, 12.

² See description of plates.

⁴ Cf. *ibid.*, p. 268.

rod, and a median node is often visible at the middle lamella (Fig. 9, Pl. XLIX). In many cases each depression becomes a compound pit, and the group of callus rods is separated into smaller groups, each group in a small pit, or even each separate rod in a pit of its own (Fig. 9). Callus is deposited later over the heads of the groups (Figs. 10 and 12) and may occur in considerable quantity in the old tubes (Fig. 13).

The sieve fields of *Salvia* are of especial interest in connexion with the current research, since it is found that it is with these sieve fields that the parasitic cells form a junction in order to obtain food materials from their host. No cases of connexion by means of the terminal, and few by lateral, sieve plates have been demonstrated.

(b) My preparations contained numerous well-stained examples of the developing pits in the walls of both the pericyclic fibres and the lignified elements of the xylem. Three such pits in a young pitted vessel are shown in section in Fig. 14; groups of threads are seen to traverse the pit-closing membrane, connecting the pit fillings. In Fig. 15 the pit-closing membranes are seen in surface view, each traversed by a small number of threads.

II. ON THE HISTOLOGY OF CUSCUTA.

(a) The walls of the *cortical cells* of all the species of *Cuscuta* examined were traversed by numerous connecting threads, generally arranged in small groups, each group being confined to a pit, and containing some 6–20 threads, or fewer in the case of the transverse walls. In many cases the pits were again divided into smaller pits (Figs. 16, 17, 18).

(b) The *sieve tubes* of several species of *Cuscuta* have been to some extent described by Mirande,¹ and my investigations have confirmed his account of their gross mature structure as he saw it when they were isolated by maceration. The sieve tubes of *Cuscuta* are much larger than those of *Salvia*.

As in *Salvia*, however, the development of the sieve plates, in the two species which I studied carefully, agrees in all essentials with Hill's description of the development of the sieve plates in *Vitis*,² and is also closely comparable with that of the sieves in the sieve tubes of *Laminaria*.³ Except when otherwise stated the following account, and also the greater number of the figures, are obtained from *Cuscuta reflexa*.⁴

The terminal sieve plates. In the two species examined the terminal sieve plates are simple, each pit containing a single thread or callus rod; groups of threads or callus rods in each pit are, however, occasionally found in the terminal plates of the sieve tubes in the haustorium of *Cuscuta europaea* on the Vine.

¹ Mirande, 1898.

² Hill, 1908.

³ Sykes, 1908.

⁴ According to Solereder, 1908, pp. 1003–5, there are sieve plates in the longitudinal walls of the sieve tubes of the Monostyleae only. But I have found no difference in this respect between *C. reflexa* (Monostyleae) and *C. europaea* (Distyleae).

In the youngest stage the transverse wall of the young sieve tube is traversed by a number of faintly staining threads, on which a median thickening is sometimes visible.¹ The wall is commonly unpitted. In Fig. 19 the pitting is more marked than is usual in so young a transverse wall, and the threads are exceptionally crowded. The threads soon stain more darkly, and at the same time specks of callus appear at their ends, very speedily spreading along them (Fig. 20). Owing to the small dimensions of the plates, it is difficult to follow the details of this process, but it can be seen that at the next stage each thread stains very darkly with protoplasmic stains, and is enclosed in a tube of callus. In a few cases a median nodule² has been distinguished on the callus rod, which is thus seen to be separated into two plugs. (Cf. Fig. 20 B.) Even at this stage the sieve plate is only very slightly pitted; as a rule a single thread or slime string is found in each pit. Fig. 21 shows groups of strings occurring together in small depressions, and is taken from a sieve tube of *C. europaea*.

The formation of callus next spreads over the region in between the pits, and the sieve plate is now fully mature (Figs. 22 and 23). In surface view the perforations are easily demonstrated, each pore being lined with callus and traversed by a single slime string (Figs. 25 and 26). In the material of *C. europaea*, preserved out of doors in October, some accumulation of callus had taken place over the sieve plates, but very little was present in greenhouse material of *C. reflexa* in October (Figs. 24 and 27). In *C. reflexa* growing on *Ficus* in the greenhouse in November, large masses of callus had accumulated. Mirande³ has also figured still larger masses of callus in other species.

Lateral walls of the sieve tubes. Lateral sieve plates were only rarely found; in them all the phases in the development of slime strings and callus rods appear to be similar to those in the terminal sieve plate. Fig. 27 represents a lateral sieve plate, against which a large accumulation of callus has taken place.⁴ Short strands of cells with sieve plates on their transverse walls are occasionally found connecting two strands of sieve tubes; such a connecting element is shown in Fig. 28.

Groups of threads appear to be equally numerous in the tangential and radial walls of the young sieve tubes.⁵ Sometimes each group contains very few threads, usually in a small pit (Fig. 30, *C. europaeus*); sometimes a large group stretches across the sieve-tube wall, forming a wider 'sieve field' (Fig. 29, *C. reflexa*).

The development of the threads in the lateral walls, each into a slime

¹ Cf. Hill, *a* and *b*, 1901; 1908. Sykes, 1908.

² Cf. Hill, 1901 *b*, Figs. 20 and 21, Pl. XXXIII; 1908, Figs. 34, &c., Pl. XVIII.

³ Mirande, p. 88 and Fig. 7.

⁴ From *C. europaeus* on *Vitis*, October; cf. Peirce, 1893, p. 294.

⁵ For a more detailed description of the distribution of pores in the lateral walls, see Mirande, pp. 85-7, and Figs. 6 and 7.

string enclosed in its callus rod, is similar to the development of the threads in the terminal sieve plate; the only difference is that the perforations are here much finer.

Each fully formed slime string thus becomes enclosed in a very minute callus rod which is only very slightly bored out (Figs. 30 A and 37 A, Pl. XLIX).

The median thickenings are found to be peculiarly conspicuous on the young threads in the lateral walls (cf. Figs. 19 and 31); a median node is also often clearly visible on the mature callus rod (Figs. 32 and 39). In Fig. 31 A a very early stage of callus formation is seen, and in one group the change has proceeded as far as the middle lamella from one side, but has not taken place at all on the other side of the middle lamella.¹

In the walls of the sieve tubes which abut on a companion cell, numerous small pits usually occur, and in these pits groups of threads are found. In many cases that half of the thread which is on the sieve-tube side of the wall has undergone development into a short slime string enclosed in a callus rod, while the half on the side of the wall which belongs to the companion cell has remained unchanged² (Figs. 19, 24, 41, and 42).

In the summer material very small accumulations of callus were sometimes formed over the pits in the lateral walls, but in the material preserved in October much larger masses were present, which often extended over a considerable portion of the intervening wall. Figs. 35 and 39 represent large groups of slime strings in the lateral walls of two sieve tubes, over which small pads of callus have been deposited; Fig. 38 shows in surface view a wall in which many small groups occur, and a small pad of callus has been deposited over each group; Fig. 40 represents a wall inside which the callus forms an almost continuous layer. The pencilled lines in the blue callus indicate the 'paths' above the slime strings, through which continuity with the pores is for a long time maintained.³

Sieve tubes of the haustorium. The sieve tubes of the haustorium are composed of very short elements, and sieves are numerous in all their walls. It appears that any parenchymatous cell may become organized as a sieve tube, but companion cells are by no means universal.

The histology of the haustorial sieve tubes corresponds in nearly all respects with that of the sieve tubes of the main stem. It has already been mentioned that the threads or slime strings in the transverse plates are commonly arranged in groups. As a rule, the callus rods traverse the entire thickness of the wall which separates the phloem elements. Callus appears to be formed earlier in the haustorium than in the main stem; in *Cuscuta reflexa* large masses of callus were already

¹ Hill, 1901 b, Fig. 18, Pl. XXXIII, and p. 589; Hill, 1908, Figs. 23, 24, &c., Pl. XVII, and pp. 281, 367; Sykes, 1908, Figs. 14 and 15, Pl. XIX, and pp. 307, 316.

² Hill, 1901, pp. 600-1; 1908, pp. 279-80; Sykes, 1908, p. 317.

³ Hill, 1901; 1908.

present in the haustorium in October, but were not formed in the sieve tubes of the main stem till November (Figs. 44 and 45). On the transverse plates the callus is sometimes nearly all collected on the parasite side of the plate (Fig. 45); in other cases, a continuous layer of callus lines all the walls of the elements of a sieve tube of the haustorium. Here, as in other cases, the callus is apparently deposited by the protoplasm.¹

It is interesting to find that the haustorial sieve tubes do not terminate at the level opposite the phloem of the host, but are continued down the axis of the haustorium into the host pith (*C. reflexa* on *Begonia*, *C. sp.* on *Solidago*, &c.).

Some attempt was made to determine the number of threads present in the longitudinal walls of a short young sieve tube of the haustorium (Fig. 43). The two groups, A and B, were made up of 11 and 16 threads respectively. The two groups together measured $11.2\ \mu$ across, the whole cell being $24.4\ \mu$ across at this point and $64.4\ \mu$ in length. From these numbers some estimation may be made of the large number of threads present in the wall of such a cell.

III. ON THE RELATIONS BETWEEN HOST AND PARASITE.

A. Outlines of the Development of the Haustorium.

The broad outlines of the development of the young haustorium in *Cuscuta* and its manner of penetrating the host have been described to some extent by Peirce.² A sucker-like organ first arises from the epidermis of the mother stem and adheres firmly to the host plant; its formation is then followed by the ingrowth of the true haustorium, which has originated endogenously, mainly from the cortical region just outside the pericycle, and seems very properly regarded as morphologically an adventitious root.³ The cells of the sucker, or 'prehaustorium', dissolve their way into the host plant, partly by pressure, partly by the excretion of a ferment,⁴ and into the space thus made the haustorium grows, enlarging the opening and becoming surrounded by a mass of compacted dead cell-walls.

The haustorium grows at its tip and finally becomes connected with the bundles of the host plant, its method of growth, either continuing in a straight line towards a single host bundle, or branching into two parts which diverge to join more than one host bundle, varying with the arrangement and size of the bundles of the host.⁵ These variations in form do not concern us here.

The following more detailed account is derived in great part from

¹ Hill, 1901 *b*, pp. 597-600; 1908, pp. 277-8; Sykes, 1908, pp. 316-17.

² Peirce, 1893, pp. 295 ff., and 1894, pp. 99 ff.

³ Ibid., 1893, p. 305.

⁴ Ibid., 1894, pp. 99-106; the invading cells were found to have the power of corroding starch grains.

⁵ See *ibid.*, 1893.

C. reflexa parasitic upon *Salvia*, with corroborative evidence from *C. europaea* on *Vitis*. These hosts were found to be the most favourable for histological work; on the one hand their cell-walls are not so thin or their tissues so parenchymatous as, e. g., in *Begonia* or *Impatiens*, and on the other hand their cortex and pith are fairly free from the numerous crystals, fibres, stone cells, &c., which make the use of the freezing microtome so difficult with, e. g., the hop. In both cases, too, the compacted mass of dead cell-walls which at an early stage surrounds the haustorium is very soon absorbed; in some hosts attacked by *Cuscuta* they are hardened, and form an almost insuperable barrier to histological investigation.¹

The ingrowth of the haustorium is mainly due to the superficial cells covering its tip, which undergo a remarkable series of changes. They become greatly elongated,² and each forms a hypha-like element of very large dimensions. They have all the features characteristic of secretory cells: their walls are at first very thin, especially at the tip; their protoplasmic contents are very dense, and their nuclei are exceedingly large. In many cases the diameter of the nucleus of an invading hypha was found to be greater than the diameter of the whole cell invaded.

Cell-division occurs at first chiefly in the cells immediately behind the hyphal cells,³ but as the tips of the hyphae grow inwards their hinder portions become also subdivided, their elongated apices remaining, however, unicellular throughout all the young and growing stages. As they extend further into the host plant it is common to find, in the tip of a single hypha, from two to five of the large characteristic nuclei (Figs. 46 and 47, Pl. XLIX); these unicellular and multinucleate elements may branch at an early stage, but it is not until later that they become subdivided transversely and longitudinally almost up to the tip, each of the nuclei then being surrounded by a cell-wall.

From each hypha a strand of cells is thus developed; the further development of the different strands depends on their position with regard to the tissues of the host. The end of the invading haustorium in the cortex of the host may be compared with a brush of hairs, separated somewhat from one another in the early stages. In *C. reflexa* on *Salvia* and in *C. europaea* on *Vitis* the central hairs (hyphae) push straight through the vascular cylinder into the thick-walled pith of the host; they do not become subdivided for some distance from the tip, and generally remain small and undifferentiated. In a few cases, however, strands of sieve tubes were found to be developed from them even in *C. reflexa* in the empty, innutritious

¹ This is still more strikingly the case in plants attacked by *Lathraea squamaria*, where the mass of dead cell-walls stains with lignin stains.

² Cf. Peirce, 1893, esp. Figs. 15, 16, 18, Pl. XIV; Heinricher, 1894 (*Lathraea*), p. 325, Fig. 1, Pl. IX, and Fig. 1, Pl. X; Solms Laubach, 1868, Figs. 2, 5, 6, Taf. XXXV; Leclerc du Sablon, 1894 (*Melampyrum*), Figs. 3, 5, &c., Pl. I.

³ See Peirce, p. 304, &c., and Fig. 5 G, Pl. XIII.

pith of *Salvia*,¹ and such strands were quite common in *C. reflexa* in the juicy pith of *Begonia*.

The hyphae immediately surrounding the central core become applied to the xylem elements of the host; the strands of cells to which these hyphae give rise become organized as strands of reticulately pitted tracheides and are connected with the xylem of the main stem of the parasite. Concerning the details of the development of the xylem connexions I have little to say; Peirce has given some descriptions of the mature state in his paper, and my observations, as far as they go, do not differ from his to any important extent. The hyphae apply themselves firmly to the xylem elements of the host; and the thin walls at their tips, which are at first undifferentiated, later become lignified, thick and thin areas being developed which correspond to the thick and thin areas of the host wall.

The peripheral hyphae of the haustorium (outer hairs of the brush) do not extend so far into the host plant, but many of them push their way straight through the older layers of the host phloem (Fig. 60, Pl. L, is an example of a parasite hypha seen boring through a host sieve tube), and, making for the functional and developing sieve tubes from which the most nutriment can be obtained, become applied to their walls and form intimate connexions with them. It is generally found that in the phloem the haustorium expands considerably (especially in *C. europaea* on *Vitis* and *C. sp.?* on *Solidago*). At the surface of the host the haustorium is circular in section; it becomes oval or lozenge shaped in the cortex of the host, the long axis of the oval being parallel to the length of the host stem. When it reaches the phloem it expands laterally and may again become roughly circular in section. Contact is thus made with a large number of sieve tubes outside the region originally pierced by the shaft of the haustorium. When a connexion has been made, the applied hypha becomes subdivided to form a strand of cells from which a string of short sieve tubes is developed; these are connected by other short sieve tubes in the shaft of the haustorium with the phloem in the parasite stem (Figs. 62-4). It is the development of the phloem connexions and of the strings of sieve tubes with which I am mainly concerned.

Some of the separate hyphae on the outer edge of the brush have got no further than the cortex, others have pierced a little deeper, but only as far as the old disused sieve tubes. It is not possible to determine how far these have still the power to work further into the functional phloem, but it seems most likely that at a certain stage their development stops, the total number of connexions being then adequate to the needs of the parasite. Occasionally a hypha after reaching the old phloem turns back, bending sharply on itself, and returns into the cortex. Such hyphae presumably are unable to find food in the old phloem, and seek it in the

¹ Cf. also Peirce, 1893, p. 309, for development in an innutritious pith.

more nutritious cortex, where they were occasionally found applied to a secretory cell. The hyphae in the cortex are smaller and shorter and have smaller nuclei.

Finally, in the fully developed haustorium, the brush of loose hairs has become a tissue of closely compacted cells, a few on the extreme periphery of the brush alone remaining separate from one another. It must be clearly realized, however, that the tissue owes its origin to the fusion of separate strands of cells, and that therefore all the cells composing it are not genetically connected with one another. Some of the longitudinal walls have originally formed the walls of separate invading hyphae, and have become fused together later; these walls afford an excellent opportunity for the investigation of the question which forms the main object of this paper, viz. whether connecting threads are formed between non-genetically connected cells.

B. *Histology.*

We are now in a position to consider in detail the manner in which the young invading hyphae make their way through the cortex and pericycle of the host, and through the old disused sieve tubes, form connexions with the functional sieve tubes of the host, and, finally, give rise each to a strand of sieve tubes which conveys the food products absorbed from the host to the main parasite stem.

Fusion of lateral walls of invading hyphae to form a tissue. The tips of the invading hyphae are for some time separated from one another, but later, when the more advanced of the hyphae have been joined by those which lagged behind, they become closely applied to one another. Their adjoining walls are then fused together so closely that all sign of their separate origin is lost. Fig. 51 A, Pl. XLIX, represents small portions of the longitudinal walls of two adjacent hyphae near their tips. The section was stained with London blue, and the blue colour in the figures indicates the distribution of the bluish-green colour so characteristic of callus and substances like it. The inner and outer superficial layers of the walls of both hyphae were stained blue. Apparently the blue colour is characteristic of various substances produced by the hydrolysis of ordinary cellulose;¹ these, being mucilaginous, facilitate the fusion of the walls. The softening is a temporary process and is lost when its object is accomplished. In Fig. 51 B the two adjacent walls have fused, and the wavy blue line marks the still visible softening along the line of fusion. In Fig. 51 C the line of fusion no longer stains blue, but can still be clearly seen (see also F, Figs. 76, 77, 78, Pl. LI). As in Fig. 51 A, Pl. XLIX, the inner layers of the walls stain blue; in some cases even larger portions of the wall may be temporarily softened. Since the hydrolysis of the outer layer is probably affected by the ferment

¹ See Sykes, 1908, p. 315.

secreted by the protoplasm, it is easy to understand that the ferment may change other parts of the wall on its way outwards.

Just behind the fusing tips, cell-divisions are now taking place in the hyphae. Fig. 49 represents a transverse section of a hypha which has been divided into three cells; the newly formed cell-walls are packed with connecting threads, but there are no connecting threads in the outer fusion walls. *No connecting threads have ever been seen in the fusion walls separating adjacent hyphae* or adjacent strands of cells formed from these hyphae. In quite mature haustoria it is often very difficult to make out the boundaries of the original strands, but whenever the preparation is sufficiently good it is clear that, whereas sieve tube areas are common in the walls subdividing the hyphae, they are not formed on their original longitudinal walls (see Figs. 62 and 64, Pl. L; *w* = original wall).

These facts are perhaps the most interesting outcome of this investigation, since it would appear that here is at least one incontrovertible case in which the distribution of connecting threads is clearly coincident with the distribution of genetically connected cell-walls, and does not extend to walls associated with one another by later growth.

Behaviour of the wall at the tip of an invading hypha. It has already been stated that the tip of an invading hypha is at first covered by a thin, very soft and plastic wall with which the protoplasm is closely in contact.¹ The plasticity of the wall in this region is illustrated by Figs. 46 A and 46 B, in which hyphae are shown on their way through the walls of cortical cells; the invading element makes a clean hole in the cortical wall, and squeezes its way through the hole. It is often much contracted in this process, expanding again when it reaches the cavity of the cortical cell; later the hole is enlarged and the hypha regains its original shape. At the edges of the hole, host and parasite are almost from the first so firmly cemented together that it is difficult to ascertain at exactly what point one wall begins and the other ends.² In preparations stained with Delafield's haematoxylin the common portion of the wall takes the stain more deeply, and is thus to a certain extent distinguishable.

As the hyphae approach the central cylinder their end walls become conspicuously swollen and mucilaginous, and at the same time still more plastic. Fig. 50, Pl. XLIX (less magnified than Fig. 46 B), represents two adjacent hyphae passing through the pericycle; the wall of the right-hand element is slightly swollen at the tip.

The thick-walled cells of the pericycle in *Salvia* must offer some considerable resistance to the passage of the hyphae. Cases have been met

¹ Peirce also suggested that the end walls are not quite solid; 'kept in partial solution by the enzyme they are secreting,' 1894, p. 114.

² Cf. Peirce, 1894, pp. 113-14, and Figs. 8 and 9, Pl. VIII. It is this firm union which even at an early stage prevents the haustorium from being pulled out of the host tissues.

with again and again in which the pressure of a hypha has bulged in a thick-walled cell to the extent of causing its two longitudinal walls to touch each other, obliterating the cavity between them. Sooner or later, however, the solvent action of the hypha dissolves even the thick walls of these elements. In Fig. 52, Pl. L, are shown two invading hyphae which have penetrated for some distance into the pericycle; a portion of the wall of the last cell penetrated (F, Fig. 52) is still visible in the space between their tips. The next pericycle cells are in their turn about to succumb, and the wall of the cell on the right is already considerably bulged in, and is dissolved as far as the middle lamella.

Occasionally when an invading hypha has made an entry into the cavity of a thick-walled cell it turns and for a short time pursues its course longitudinally in the cavity of the host cell, following the path of least resistance and widening the cavity by its pressure.

The wall at the tip of an invading hypha becomes more and more swollen and mucilaginous as it penetrates the pericycle and reaches the disused phloem; the inner layers of the wall now commonly stain with London blue or water blue, and are evidently softened in the same way as has been described in the lateral walls of adjacent hyphae which are about to join with one another.¹ Occasionally even in the inner layers of the pericycle (Fig. 53) the tip of the hyphal wall is sufficiently hydrolysed to stain blue; this is of some importance, since it makes it appear certain that the blue-staining substance is the product of some activity of the hyphal cell itself (probably of a hydrolysing ferment), and is not due to an interaction between the parasite and the old sieve tubes of the host, which contain much blue-staining callus. The same conclusion is suggested by the fact that it is the *inner* layers of the wall which first undergo the change. Fig. 55 shows a very early stage in which only two minute patches of blue-staining substance have yet been produced (see also Figs. 56, 58, &c.). Only a few cases were seen in which hydrolysis in the walls of the hyphal tips had gone far enough for them to stain with water blue,² but the less hydrolysed state which stains with London blue was common even in hyphae in the outer zones of the old host phloem.

Sometimes the blue staining substance occurs at first only in patches (Fig. 61); later it generally extends throughout the inner layers. A thin outer layer of unstained cellulose is visible until the invading cell reaches the functional phloem (Figs. 56, 58, &c.). Then, on the edge of the functional phloem, there is a short stage in which the whole wall at the tip of the hypha stains blue. Being transient, this stage is not very often seen. Figs. 59 and 60 represent hyphae just getting to this stage; in Fig. 59 two small blue patches are seen in the outer layers as well as the large swollen mass within. Fig. 60 represents a transverse section through

¹ *Ante*, p. 664.

² Sykes, 1908, p. 315.

the tip of a hypha making its way straight through the wall of a host sieve tube ; the inner and outer layers of its wall both stain blue.

In two of the elements shown in Fig. 57, and probably also in the left-hand element in Fig. 65, the blue stain is taken by the entire thickness of the much swollen wall at the tip of the hypha.

When the hyphae have penetrated well into the functional phloem these swollen blue-staining tips are very rarely met with, though occasionally irregular masses of blue mucilaginous-looking substance are found, apparently in the cavity of the hyphae (see Figs. 62 and 67).

Formation of junctions between the tips of the hyphae and the sieve areas of the host. It is by no means an easy matter to ascertain exactly what does occur when the tip of a hypha forms a junction with a sieve area of the host. The accumulated mass of evidence seems, however, to demonstrate conclusively that *the formation of a junction is effected by the application of the naked protoplasm of the hyphal tip to a functional sieve plate or sieve field of the host.* The swollen and mucilaginous parasite wall is entirely dissolved away in the region immediately over the sieve area.

Before proceeding to give the evidence on which this conclusion is based it may be well to state that it is opposed to that reached by Peirce and Strasburger. Peirce¹ demonstrated the fact that the haustorium forms junctions with the phloem as well as the xylem of the host ; having described the sieve plates between host and parasite, and having seen callus on either side of their plates, he stated his view that half of the 'compound' sieve plate is derived from the host wall and half from that of the parasite. Strasburger² came to a similar conclusion. He could not demonstrate any simple protoplasmic connexions between other cells of the host and parasite, a fact which he attributes to absence of near relationship between the two ; he states, however, that open communication is established in the pores of the compound sieve plates, and he enumerates the facts among other evidence possibly in favour of his view that protoplasmic communication may be established between non-genetically connected tissues.

When the junction sieve areas are carefully examined by suitable methods, the most obvious fact concerning them is that *they resemble exactly in appearance and dimensions, and in every detail, the lateral sieve plates or sieve fields already described in the respective hosts, Salvia and Vitis.* The junction sieve areas are certainly no thicker than those in the undisturbed host phloem, as they would almost necessarily be if they owed their origin to a fusion between the host sieve area and the thick swollen wall of the tip of the parasite hypha. The presumption is therefore that these are not

¹ Peirce, 1893, p. 301 and p. 314, Fig. 13, Pl. XIV. The account given by Peirce of his observations and the figures given by him are by no means conclusive. This is partly due to his researches having been conducted on alcoholic material. His figures by no means preclude the possibility that in the formation of the junction sieve plate, one or other of the host and parasite walls is absorbed.

² Strasburger, 1901, pp. 601-2.

compound sieve plates, but are derived from the host wall only, and are utilized in their original condition by the parasite for its own convenience.¹

We are at once confronted with the question as to what is the ultimate fate of the portion of the wall of the parasite intervening between host sieve area and parasite protoplasm, since it does not form part of a 'compound sieve plate'. There are obviously two possibilities: the food material may pass through the soft and plastic terminal wall, or the wall may be dissolved and the naked protoplasm apply itself to the host sieve area.

It has already been stated that after the parasite hyphae have penetrated into the functional phloem, thick mucilaginous blue-staining tips are no longer to be found. Some change in their nature must therefore have taken place. When an invading cell is applied to a young or mature sieve plate, in nearly all cases an unstained area is found between the parasite protoplasm and the sieve plate. Since it is the essence of the methods employed in this investigation that they demonstrate protoplasm, slime strings, callus, &c., but leave the cell-wall unstained, it is not easy in such cases as Figs. 76 and 77, Pl. LI, to decide whether this unstained area (between the parasite protoplasm and the sieve area J) be wall or space. It was not found practicable to use a wall stain conjointly with safranin and London blue, &c., and in preparations in which wall stains were employed by themselves it was very difficult to locate the junction sieve areas. In a few cases, however, this method led to useful results. Fig. 72, Pl. L, is an example of a junction plate between parasite and host, stained in Delafield's haematoxylin. Between the parasite protoplasm and the sieve field there is a large unstained area (*sp*) which is here undoubtedly a space, and must have been caused by the solution of the parasite wall in this region. *x, x* mark the termination of the unaltered portion of parasite wall. In Figs. 76 and 77, Pl. LI, also similar knob-like endings are labelled *x, x* and suggested a similar interpretation even when examined without a wall stain. The same preparation was later stained in haematoxylin, and is drawn in Fig. 78, where the relations of the walls are clearly demonstrated.² It was then quite clear that the unstained area here also is a space, and *that the intervening parasite wall must have been absorbed.*

In Fig. 78, at R, R, are shown small remnants of the parasite wall which have apparently not been dissolved with the rest.

The formation of a space on the parasite side of the sieve area is no

¹ It appears to be always with the longitudinal wall between two sieve tubes that junctions are effected; at any rate in *Salvia* no satisfactory cases were observed in which a junction was made with the wall between a sieve tube and a companion cell; in *Vitis* there was some evidence that such junctions may occasionally be developed.

² In such preparations, stained with haematoxylin, after having been examined by the usual methods for demonstrating the structure of the sieve areas, the walls stain quite sharply, notwithstanding the processes employed to slightly swell them, and the termination of the parasite wall round the hole which is formed over the sieve area is perfectly clear.

doubt due to artificial shrinkage of the protoplasm. It was most pronounced in preparations which had at any stage been placed in alcohol (Fig. 72, Pl. L); it is probable that the protoplasm in this region is easily shrunk, having only recently come to occupy its position against the sieve area, consequent on the solution of its own wall. In some preparations there was hardly any sign of shrinkage, e. g. in Fig. 68.

There can be little doubt that the *mucilaginous change described at the tips of the parasite hyphae is preparatory to dissolution*. The actual disappearance of the blue mass is rapid and is difficult to detect. Fig. 71 probably represents one of the last stages in its solution, the blue line being a last remnant of the mucilaginous mass. Several other cases, none of them very clear, were also met with, in which irregular 'blobs' of callus separated the parasite protoplasm from the junction sieve area. Figs. 62 and 67 were drawn from two rather curious cases, in which a relatively large mass of blue mucilaginous substance probably represented the dissolving tip of the wall. Apparently the protoplasm had already crept past the jelly-like mass and applied itself to the junction sieve plate.

C. Functional Efficiency of the Arrangement.

It is probable that the orientation of the hyphae which make connexion with the host phloem is significant from the point of view of the efficiency of the junctions.

It has already been stated that the haustorium widens out when it reaches the phloem, its transverse section becoming much greater than before. As the hyphae enter the old phloem of the host they also change their direction slightly, and, instead of running in a straight line with the long axis of the haustorium, they twist a little obliquely and finally turn outwards at an angle with the long axis, thus coming into contact with sieve tubes which have not been interrupted by other ingrowing elements. In the functional and young phloem the invading hyphae turn still more, often twisting repeatedly so that their course is difficult to follow under the microscope, and they never remain long at the same focus. Finally, the tips of many of them run nearly at right angles to their original direction, that is, almost parallel with the host sieve tubes (see Figs. 59, 68, and 70, Pl. L, Figs. 77 and 78, Pl. LI, &c.). The advantage of this change of direction is clear when it is remembered that it is always with the *lateral* sieve fields (or occasionally with the lateral sieve plates) that junctions are effected. The hypha may be said to lay itself alongside the host sieve tube; it is thus able to bring as large an area as possible into contact with a sieve field. At the same time it runs the least risk of injuring the sieve-tube wall, since it avoids bringing to bear on it the terminal pressure, which we have already seen to be sufficiently great to bulge in even the thick wall of a pericycle cell.

It is not, of course, possible to be quite clear as to whether the lateral twisting of the end of the hypha always takes place before contact with a sieve area is actually made (as appears to be the case in Fig. 68, Pl. L), or whether in some cases it is after the formation of a junction has begun that the hypha continues its growth in a lateral direction in order to avoid terminal pressure and not to injure the junction plate.

However it is brought about, lateral contact is so common that it would seem probable that even the few cases in which the extreme tip appeared to be utilized, e. g. Fig. 76, Pl. LI, are probably to be accounted for by the plane of the section passing through the heel of the slipper-shaped end. Such an arrangement as is seen in Fig. 76 would be obtained by taking a section at right angles to that of the adjoining element in Fig. 77, passing through the left-hand end of the junction sieve area.

Even in the element drawn in Fig. 77 the extreme tip really extended further at another focus for some distance beyond the point shown in the diagram.

These facts naturally raise the question whether, after a junction has been formed with a sieve area in the wall of one sieve tube, the hypha ever goes on to form a junction with other sieve tubes. As my methods do not admit of cutting sections in series, it is not possible to deny absolutely that this ever happens. If it does occur, it must be only on the extreme periphery of the haustorium, where the invading elements are less closely packed together. There could, however, be no advantage to the parasite in forming junctions with a second series of sieve tubes if, in order to do so, it would be necessary to make holes in the sieve tubes already attacked, and thus probably to destroy their efficiency. It may well be that the further growth of the hyphae depends on the composition of the phloem in the host. In *Salvia* the phloem consists largely of sieve tubes, and it would thus be almost necessary after the formation of a junction to bore through a sieve tube in order to reach others. In other hosts, such as *Vitis*, where the phloem contains much parenchyma, the hypha might conceivably make its way from one sieve tube to another by way of intervening parenchymatous cells, thus to a less extent disturbing the sieve tubes. No sign of any such second junction plate has, however, been found even in *Vitis*, nor any sign of a re-formation of the dissolved portion of the wall of the hypha, nor any other adaptation to protect the naked area of parasite protoplasm, such as would probably be necessary in the neighbourhood of the disused sieve plate. Several hyphae may apply themselves laterally to the same sieve tube, but apparently each hypha only forms one such lateral connexion during its course. The arrangement would thus be similar to that prevalent among the hyphae which form junctions with the xylem. These, having made one junction, become lignified, and of course lose the power of further growth. We may conclude that the development of the invading hyphae

ceases when an adequate number of connexions has been established between host and parasite.

The formation of single lateral connexions has probably the additional advantage that it disturbs to the smallest possible extent the mechanics of the sieve tubes. It appears to be necessary that the connexion should be established with a host element whose wall is otherwise uninjured, though occasionally another element of the same tube may have been pierced by an invading hypha. No connexion has ever been found between a parasite hypha and a sieve area in the wall of an element which has been broken through by other hyphae on their way further into the host. That is to say, at least one transverse sieve plate always intervenes between a broken place in a sieve wall and a junction sieve area.

It is generally accepted that the substances translocating in the sieve tubes are under considerable pressure;¹ in consequence of this pressure their contents flow out laterally through the sieve fields as well as terminally through the sieve plates. In the special case, when the sieve tube has been interrupted by the growing shaft of the haustorium, the translocating substances will all the more attempt to find some lateral outlet, and, as in the normal case, will flow gently through the lateral sieve fields into the trap laid for them by the invading hyphae. The actual passage of food material would thus appear to be more a passive than an active process, due mainly to filtration from an enclosed space under pressure. Under these conditions a very close connexion between the parasite and host protoplasm in the pores of the sieve area would not be necessary. I have no conclusive observations to demonstrate how far the parasite protoplasm penetrates the pores of the sieve plate or establishes connexion with the slime strings of the host or with the protoplasm enclosing them. The ease, however, with which the protoplasm of the parasite shrinks away from the junction plate is very evident, and one may conclude from this fact, with some degree of probability, that the two are never very closely connected. Evidence that this connexion is, nevertheless, sufficient for all requirements has been obtained by Mr. Mangham,² who has seen in microchemical preparations indications of the actual passage of sugars from host to parasite.

IV. GENERAL OBSERVATIONS.

A. *The efficiency of sieve tubes.* The contrast between the behaviour of the parasite hyphae in the cortex and the phloem affords evidence of the efficiency of the sieve tubes and sieve areas for conduction.

¹ As shown by the work of Fischer, Sachs, &c. See Mangham, 1910, p. 265.

² I am indebted to Mr. Mangham for his kind permission to mention his observations. The methods employed were those indicated in his paper in *Science Progress*, 1911, and by means of which he obtained the results communicated to the Brit. Assoc. at Sheffield, 1910.

In the cortex the parasite hypha bores straight through the wall into the cavity of the cell, without apparently taking any account of the presence of connecting threads; in the phloem, on the other hand, it makes connexion with the unchanged sieve area. The junction is effected in such a way as to disturb as little as possible the mechanics of the sieve tube, and the hypha thus secures a long-continued supply of food.¹

The adaptation of the unchanged sieve area to the purposes of the parasite points to the great efficiency of the multiperforate septum² of which the sieve area is composed. In the cortex of the host the connecting threads appear to be inadequate for bringing a supply of food to the hyphae. Even those hyphae which finally extend freely into the cortex of the host seem always to make a hole in the wall of the last cortical cell attacked. These facts may be regarded as affording further evidence in favour of the view that while connecting threads seem to be of value rather for the conduction of impulses (stimuli) than of food,³ the slime strings of the sieve areas afford an excellent medium for the translocation of food substances.

It would be of interest to know what would occur if an invading hypha made contact with the wall between a sieve tube and a companion cell of the host, i. e. with a wall crossed by connecting threads bored out only on the sieve-tube side as far as the middle lamella. Unfortunately no satisfactory cases of this kind have been observed.⁴

B. Callus. Substances which stain with callus stains are not all identical. I have already shown that in the seaweeds⁵ there are various states of hydration of the cell-wall, in which it stains with one or other of the callus stains; in the least hydrated condition it is affected by London blue alone. 'Callus' is thus a collective term which applies to several different states of hydration, if not actually to more than one chemical substance.⁶

In the haustorium of *Cuscuta* also, there are several substances which stain with callus stains and which play an important part in the history of the parasite. There is the ordinary callus in the sieve plates which stains with all the callus stains and which, as has been made clear by recent work, is due in the young sieve plate to the hydrolysis of the cellulose wall by a ferment, but is added to in the later stages by accumulations of callus directly deposited by the protoplasm.⁷

¹ It would be of interest to know what would occur if an invading hypha made contact with the wall between a sieve tube and a companion cell of the host, i. e. with a wall crossed by connecting threads bored out only on the sieve-tube side as far as the middle lamella. Unfortunately no satisfactory cases of this kind have been observed.

² See Hill, 1901 *b*, p. 604.

³ Hill, 1908, pp. 281-3; on the other hand, Gardiner, 1898 *a*, p. 111 (food and impulses).

⁴ See p. 668, footnote 1.

⁵ Sykes, 1908, pp. 315-17.

⁶ Cf. Mangin, 1892.

⁷ Hill, 1901 *b*, pp. 597-600, and 1908; Sykes, 1908.

Again, there is the blue-staining mucilaginous substance which helps to fuse together the lateral walls of the separate invading hyphae during the process of the formation of a compact tissue.¹ This only stains with London blue, and does not show in preparations in which water blue only has been used. It is probably less hydrated than the sieve-tube callus.

Still more important is the substance formed from the tips of the walls of the invading hyphae, on their way to apply themselves to the host sieve areas. It is this blue-staining substance in the tips which dissolves at the junction sieve plate by a process which is perhaps best described as mucilaginous degeneration of a limited area of the cell-wall. Sometimes this substance stains with water blue, more often with London blue only, but it has none of the bright, refractive appearance of ordinary callus. Both here and in the lateral walls the mucilage is clearly derived from the already formed cell-wall, probably by the hydrolytic action of a ferment in the hyphae.

A substance staining with callus stains is found in still another form as granules, which often accumulate to form large blue-staining masses, very conspicuous, especially in the old haustoria. These granules are bright and refractive, staining both with water blue and London blue. Very few, if any, were found in the haustoria of *C. reflexa* or *Begonia*, but they were common in *C. europaea* on *Vitis*, and still more numerous in *C. reflexa* on *Salvia*. They never occurred in the main stem, but were found both in the sieve elements and in the parenchymatous cells of the haustorium, chiefly where it abutted on the pericycle and phloem of the host. They did not appear in the early stages of the growth of the haustorium, but increased in number later. In *C. reflexa* on *Salvia* they were particularly numerous in the part of the haustorium near the pericycle of the host and were found also in the haustorial cells which had invaded the cortex and pith. They even occur, though then generally small in size, in the tips of the invading hyphae (Figs. 68, 73, Pl. L). In the old decayed haustorium they were very numerous, often swelling during the processes of staining, &c., and making the preparation obscure. Occurring in the midst of the protoplasm without relation to the cell wall, they must be formed by direct deposition from the protoplasm itself² (Figs. 73, 74, 75).

They are probably of the same nature as the granules recently described by Dr. Benson in the 'phleotracheides' of *Exocarpus* and *Thesium*,³ which also stain with water (aniline) blue. In these plants the granules apparently never attain the great size of those in *Cuscuta*. It has already been suggested that they are due to the deposition of the hydro-

¹ *Ante*, pp. 664, 665. Cf. the 'callus' which unites the separate members of a tetrad of pollen grains, by the solution of which the four grains are set free. Mangin, 1892.

² Cf. Hill, 1901 *b*, p. 599, and Fig. 26, Pl. XXXIII.

³ Benson, 1910, pp. 673 ff.

lysed products of the cellulose which is continually being absorbed by the parasite as it burrows through the cell-walls of the host. In this connexion it is interesting to notice the absence of granules in *Cuscuta* growing on the thin-walled *Begonia*, and their great number in the same species of *Cuscuta* growing on *Salvia*, with its thick-walled pith and pericycle. Heinricher's¹ examination of the smaller and more compact granules in *Lathraea*² led him to describe them as 'amylo-dextrin'. These granules have no very close resemblance to the more irregular masses in *Cuscuta*, and it is not known whether they stain with callus stains. They are present both in tracheides and parenchyma; their reactions resemble to some extent those in *Cuscuta*. Both turn a darkish brown with iodine in potassium iodide, the colour fading later, and both lose their refractiveness on swelling. With sulphuric acid there is a great deal of swelling and degeneration into mucilaginous drops.³

It appears probable that the granules and masses thus occurring in so many parasite haustoria are at any rate of allied nature. In *Cuscuta* their absence at an early stage even when growing on *Salvia* suggests that at first all the cellulose dissolved by the ingrowing haustorium is needed by the parasite, and is converted into soluble form and translocated; later, as the hyphae reach the functional phloem, and richer supplies of food are at their service, the hydrolysed cellulose is deposited in the form of these blue-staining granules and masses. Their accumulation at a later stage must to some extent choke the old haustoria.

C. *The origin of connecting threads.* It has been suggested independently by Russow⁴ and Kienitz-Gerloff,⁵ and the view is strongly supported by Gardiner,⁶ that the connecting threads found throughout plant tissues are present *ab initio* in the young cell-wall. Their origin is regarded as connected with the spindle fibres found between the dividing halves of the nucleus, which are so to speak 'imprisoned in the young wall'.⁷

On the other hand Strasburger⁸ remains the chief exponent of the view that connecting threads, though often appearing in the young tissues, owe their origin to the formation of 'plasmodesmic pseudopodia', processes growing out from the protoplasm and boring through the young cell-wall. On this view the development of protoplasmic connexions need not be confined to genetically connected cells.

It will not be easy to obtain direct developmental evidence such as would be conclusively in favour of either of these two views. To find

¹ Heinricher, 1894, p. 349, and 1901, p. 725.

² Cf. Heinricher, 1894, pp. 343 ff.

³ Kienitz-Gerloff, 1891.

⁴ Gardiner, 1898 a, p. 110; see also Hill, 1908, pp. 282-3.

⁵ Strasburger, 1901, pp. 493 ff. and 1902, pp. 52-3.

⁶ Ibid., Fig. 7, Pl. IX.

⁷ Russow, 1883.

⁸ Gardiner, 1898 a, 1900, 1907.

such evidence research must go back to the developing cell plate, of which our knowledge is at present so meagre.

The presence or absence of connecting threads between non-genetically connected tissues is, however, at any rate a strong indirect argument for or against the view that their formation is intimately connected with the genesis of the cell. Strasburger apparently expects to find such threads¹ at least between cells of the same or of sufficiently closely allied plants.

When working on the histology of *Macrocystis pyrifera* and *Laminaria saccharina*² I tried to find out whether connecting threads were developed in the septa formed between the tips of the invading cortical hyphae and the longitudinal walls of the primary pith filaments. It was, however, not only very difficult to distinguish these septa, but I had no young material adequate for their study.

We are also still ignorant as to what happens in the case of sliding growth and grafts.³

But the present investigation has, I believe, made it clear that in two cases in which cells not genetically connected are brought into contact later, no connecting threads are formed. In the one case, that of the approximation of the separate invading hyphae to form a tissue, the adjacent longitudinal walls fuse together, but no connecting threads are ever developed in them.

Now this is a case of fusion between the young thin cell-walls of cells which belong, not to different plants, however closely allied, but to the same plant. The fusing cells are, moreover, in an identical stage of development, so that if ever the formation of connecting threads were to be expected between cells not genetically connected it would be here.

The other case, that of fusion of part of the tip of a hypha with a host sieve area, has formerly been described as resulting in a fusion sieve plate, the slime strings of which would, one supposes, be derived from both host and parasite. But I have been unable to find any evidence that this is so. The junction sieve area is merely the intact sieve area of the host sieve tube; the parasite wall immediately overlying it first becomes swollen and mucilaginous and then is completely dissolved away.

It would seem that the application of naked protoplasm to a bored-out wall would be especially favourable to the formation of 'plasmodesmic pseudopodia' which should project into the wall and fuse with the host protoplasm. Yet not only is there no sign of the development of such processes, but the parasite protoplasm is probably not even very closely applied to the junction sieve area. The junction between the sieve tubes of *Cuscuta* and its host therefore afford no argument in favour of Strasburger's hypothesis. Indeed, the two cases, taken together, may be regarded as a strong argument against such a view.

¹ Strasburger, 1901.

² Sykes, M. G., 1908.

³ Gardiner, 1898 a, p. 310.

V. SUMMARY.

1. The development of the sieve plates and sieve fields in the phloem of *Salvia* and *Cuscuta* is found to agree in all essentials with *Vitis* (Hill) and *Laminaria* (Sykes). It is interesting to find the same type of development in the comparatively large sieve tubes of the climber *Vitis*, in the minute sieve tubes of a small plant like *Salvia*, in a non-chlorophyllaceous parasite, and in a seaweed. In every case the connecting threads in the young transverse wall of the sieve tubes are each bored out to form a single slime string enclosed in a tube of callus.

2. The outlines of the development of the young haustorium in *Cuscuta* are described. The invading haustorium is compared with a brush of hyphae; the central hyphae push into the pith or fuse with the xylem of the host; the ones next surrounding these fuse with the sieve tubes; the peripheral ones remain in the cortex. The main mass of the originally separate hyphae form in the mature haustorium, by lateral fusion with one another, a compact tissue.

3. Each hypha composing the tissue becomes subdivided into a number of cells forming a strand. When the tip of the hypha is connected with a sieve tube of the host, this strand of cells is developed into a strand of short sieve tubes. Connecting threads and sieves are numerous in the subdivision walls, but are never formed in the fusion walls between the originally separated hyphae—that is, they are only formed in those cell-walls which are genetically connected.

4. The wall at the tip of the invading hyphae becomes more and more mucilaginous as it approaches the functional phloem. In the inner layers of the pericycle it is sometimes sufficiently hydrolysed for some of its inner layers to stain with callus stains; this hydrolysis spreads till it affects the entire thickness of the wall at the tip.

5. Preparatory to the formation of a junction with a host sieve tube, an invading hypha lays itself more or less alongside the sieve-tube wall, so that the two come into lateral contact. The mucilaginous wall of the parasite where it touches a sieve area is then absorbed, and the naked protoplasm of the hypha applies itself to the sieve area of the host. It is nearly always with a sieve field, occasionally with a lateral plate, that the junction is made; the junction sieve plates and sieve fields in all cases exactly resemble those of the host under normal conditions.

6. The protoplasm of the parasite is easily shrunk away from the sieve area, and is probably never closely fused with the host protoplasm. The translocation of food substances from host to parasite would appear to be of the nature of passive filtration, the contents of the sieve tubes, forced by internal pressure, escaping through the lateral sieve fields into the parasite. This arrangement probably disturbs as little as possible the

normal mechanics of the sieve tubes of the host and ensures for the parasite a long-continued supply of nutriment.

7. The facts accumulated afford evidence on three interesting theoretical questions:—

A. That the parasite takes so much trouble to make use of the host sieve fields as they are, and not to disturb the mechanics of the sieve tubes, is important testimony in favour of the functional efficiency of sieve tubes in general and sieve fields and sieve plates in particular.

B. Various cases of hydrolysis of the cell-wall have been demonstrated; not only are substances staining with callus stains formed in the ordinary way in the sieve tubes, but they occur in the fusing longitudinal walls of adjacent hyphae, in the dissolving walls at the tips of the hyphae, before junctions with the phloem are developed, and in the form of granules or masses of varying size in many of the cells of the old haustorium. Hydrolysis has not proceeded to the same extent in all these cases. In the first three places the hydrolysed substance is produced from already formed cell-wall; in the last place it is laid down directly by the protoplasm, and probably owes its origin to the superabundance of cellulose absorbed by the parasite.

The haustorium of *Cuscuta* thus provides us with unmistakable cases of the formation of callus, both by direct deposition and by changes in already formed wall.

C. Connecting threads are not found in the fusion walls between adjacent hyphae. Also the wall at the tip of a hypha is not burrowed through by connecting threads or slime strings when a junction with a sieve area is to be formed; but instead the whole area of the parasite wall abutting on the sieve fields is absorbed. These facts militate against Strasburger's theory of the origin of connecting threads through boring out by the protoplasm, and may be regarded as indirect evidence in favour of Gardiner's view that connecting threads only occur between genetically connected cells, their origin being associated with the processes of cell-division.

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DESCRIPTION OF PLATES XLIX-LI.

Illustrating Mrs. Thoday's paper on *Cuscuta* and its Host.

The lenses used were Swift's 3 mm. objective of 1.4 N.A., Zeiss 2 mm. objective of 1.4 N.A.; Zeiss oculars $\times 6$, 8, 12, and 18. Unless otherwise specified the preparations were stained by the safranin method followed by treatment with London blue. The blue colour in the figures represents substances staining with London blue.

PLATE XLIX.

I. *Salvia* sp.

Fig. 1. Young terminal sieve plate in longitudinal section, traversed by fine connecting threads. At the upper end of some of them a faint callus change is already discernible. $\times 500$.

Fig. 2. Terminal sieve plate in which each thread is enclosed in a callus rod, and is situated in a minute depression. A number of fairly deep pits are visible in the radial wall; in each pit a group of fine callus rods are visible. $\times 800$.

Fig. 3. Terminal sieve plate at about the same stage, but more deeply pitted, and with slime strings more bored out. $\times 1,000$.

Fig. 4. A lateral plate, similar to the terminal plate in character. $\times 500$.

Fig. 5. A terminal plate in which the formation of callus has extended over the part of the wall in between the pits. $\times 500$.

Fig. 6. An old terminal sieve plate, with a large deposit of callus on either side. The majority of the sieve tubes in the material were at this stage. $\times 500$.

Fig. 7. Lateral sieve plate in surface view. $\times 1,000$.

Fig. 8. Lateral sieve plate in section; in each pit is a single slime string surrounded by a callus rod, which is interrupted at the middle lamella by a median node. $\times 1,000$.

Fig. 9. Sieve field in section. The wall is profusely pitted; each slime string has its own callus rod; the median nodes are clearly shown. $\times 1,500$.

Fig. 10. Ditto. Shows more uniform pitting; each pit is occupied by a group of callus rods. Most of the plates to which the haustorial cells apply themselves resemble this figure. (London blue only.) $\times 750$.

Fig. 11. Surface view of sieve fields. The small figure shows a few of the slime strings, each traversing a hole in the wall, and surrounded by a tube of callus. $\times 800$ and $1,500$.

Fig. 12. Sieve field; in which the formation of callus has extended over the areas of wall between the threads. $\times 800$.

Fig. 13. Sieve field over which large masses of callus have been deposited. $\times 800$.

Fig. 14. Longitudinal section of wall of developing xylem element, showing the pit-closing membrane in section, traversed by a group of threads. $\times 1,500$.

Fig. 15. Wall of the same. M = pit-closing membrane with ends of threads in surface view; P = pit in section showing pit filling. $\times 1,000$.

II. *Cuscuta*.

(Preserved June or July unless otherwise mentioned).

Fig. 16. Radial wall of cortical cell of *C. reflexa*, showing the connecting threads traversing the pit-closing membranes. $\times 1,500$.

Fig. 17. Longitudinal wall of cortical cell of *C. europaea*. $\times 1,000$.

Fig. 18. Cortical cell of *C. reflexa* in section, showing the groups of threads traversing the pits in the longitudinal walls seen both in surface view and in section, and also the much smaller groups in the transverse walls. $\times 1,000$.

Fig. 19. Longitudinal section of sieve tube and companion cell from the main stem of *C. reflexa*. The threads in the transverse wall are arranged in groups and are still unaltered. In the right-hand longitudinal wall (between two sieve tubes) the wall surrounding them has become changed into callus, in the left-hand one (between sieve tube and companion cell) the change has only occurred in the sieve-tube side of the wall. cc. = companion cell. $\times 1,000$.

Fig. 20. Terminal sieve plate of sieve tube of main stem of *C. reflexa*; each thread has given rise to a slime string enclosed in a callus rod. Fig. 20A illustrates the stages in the development of the slime strings as seen in longitudinal section. $\times 1,000$. Fig. 20B is part of an old transverse plate in longitudinal section, showing the fully developed callus rods interrupted at the middle lamella by a well-marked median node. $\times 1,500$.

Fig. 21. A sieve tube from the main stem of *C. europaea*, showing a case in which the strings are arranged in groups and not distributed uniformly. $\times 600$.

Fig. 22. Sieve tube and companion cell from main stem of *C. reflexa*. The surface of the wall in between the individual callus rods is now coated with a thin layer of callus. In the wall between sieve tube and companion cell the callus change appears only to occur in the sieve-tube side of the wall. cc. = companion wall. $\times 1,000$.

Fig. 23. Fully developed sieve plate as Fig. 22; slime strings more bored out. $\times 1,000$.

Fig. 24. Old sieve tube from *C. europaea* (preserved in October), showing accumulation of callus on one side of sieve plate and over the sieve-tube end of the groups of strings in the longitudinal wall between sieve tube and companion cell. cc. = companion cell. $\times 600$.

Fig. 25. Surface view of a transverse sieve-plate from the haustorium of *C. reflexa*; the callus rods are evenly distributed and each contains a single slime string. $\times 1,500$.

Fig. 26. Part of an old transverse sieve plate from the main stem of same, showing the callus change extending to the wall between the rods. $\times 1,500$.

Fig. 27. Lateral plate from sieve tube of *C. europaea* (preserved in October), showing accumulation of callus. $\times 750$.

Fig. 28. *C. reflexa*. A and B = sieve tubes of two separate groups, separated by parenchyma and connected by transverse connexion D. The longitudinal wall of A is traversed by numerous groups of minute callus rods. $\times 500$.

Fig. 29. Surface view of longitudinal wall of sieve plate of *C. reflexa*, showing groups of connecting threads, some of which are beginning to be bored out. $\times 600$.

Fig. 30. Surface view of sieve field on longitudinal wall of sieve tube of *C. europaea*. The slime strings are arranged in little groups, and each string is enclosed in a minute callus rod (shown in Fig. 30 A). $\times 600$.

Figs. 31 A and B. Stages in development of the lateral sieve fields (*C. reflexa*) seen in section. $\times 1,000$.

Fig. 32. Longitudinal wall of a mature sieve tube of *C. reflexa*, showing well-marked pits, each traversed by a group of slime strings. Median nodules well defined. $\times 1,500$.

Fig. 33. Ditto, showing a larger sieve field. $\times 1,000$.

Fig. 34. Single pit more highly magnified.

Fig. 35. Longitudinal wall from sieve tube of *C. europaea* (preserved in October), showing accumulation of callus over each pit. $\times 500$.

Fig. 36. Surface view of lateral sieve fields in *C. reflexa*, showing spread of callus change. $\times 500$.

Fig. 37. Ditto, smaller fields and callus change further advanced. $\times 500$.

Fig. 38. Ditto, showing large accumulation of callus over the ends of the small sieve fields. $\times 500$.

Fig. 39. Longitudinal section of sieve field from a sieve tube of *C. europaea* (preserved in October), showing remarkably large median nodules and considerable accumulation of callus. $\times 1,000$.

Fig. 40. Longitudinal wall of sieve tube of *C. reflexa* in section, showing large accumulation of callus on the sieve-tube side of the wall. 'Paths' through callus. $\times 1,000$.

Fig. 41. Wall between sieve tube and companion cell (*C. reflexa*), showing callus change on sieve-tube side of wall only. $\times 1,000$.

Fig. 42. Ditto, *C. europaea* (October). $\times 800$.

Fig. 43. Short element of sieve tube from haustorium of *C. reflexa*. Each thread has its own callus rod; at *c* a small accumulation of callus has taken place. (Greatest length of cell = 64.4μ ; A-B = 11.2μ ; the group A consists of eleven threads; the group B of sixteen.) $\times 500$.

Fig. 44. Short element from haustorium of *C. reflexa*, showing accumulations of callus. $\times 1,000$.

Fig. 45. An exceptionally large mass of callus in old haustorium, nearly filling cell. $\times 1,000$.

Relation of Host and Parasite.

Fig. 46 A. Tip of invading hyphal cell from haustorium of *C. europaea*, making its way through the cortex of *Vitis*. It has already two large nuclei. $\times 800$.

Fig. 46 B. A similar cell of *C. reflexa*, passing through the longitudinal wall of a cortical cell of *Salvia* and boring a clean hole in it. At the edges of the hole the two walls are fused together. $\times 500$.

Fig. 47. (Figs. 47, 48, 49, 51 from *C. europaea* on *Vitis*.) An invading hyphal cell which has nearly reached the host phloem and is four-nucleate. $\times 800$.

Fig. 48. An invading hypha which has reached the phloem of the host. The large size of the nucleus is apparent from a comparison with the dimensions of the transverse section of a host sieve tube. $\times 800$.

Fig. 49. Transverse section of an invading element, which has reached the phloem, taken at some distance from the tip. Longitudinal divisions have taken place to form a strand, and the thin longitudinal walls (*l*) are seen to be packed with connecting threads. $\times 1,000$.

Fig. 50. Two invading cells of *C. reflexa*, near host phloem. The right-hand element has just bored through a host element; its compressed shape may be taken as an indication of the softness

and plasticity of its walls. No connecting threads are present between the two adjoining elements, but they are always found in the transverse walls. A transverse wall is shown in which they have been converted into fine slime strings enclosed in callus rods. $\times 500$.

Fig. 51 A. Parts of the adjoining walls of two invading hyphae, near their tips. The walls are not yet fused together, but their surfaces appear to be becoming mucilaginous and stain with London blue. $\times 800$.

Fig. 51 B. A later stage, in which the adjoining walls are fused; the wavy blue line indicates a line of mucilaginous substance along which fusion has occurred. $\times 800$.

Fig. 51 C. A similar case, in which, however, the fusion line no longer stains with London blue. Faint indications of a blue stain are seen also on the inner edges of the two walls. $\times 800$. (Figs. 51 A, B, C, from *C. europaea* on *Vitis*.)

PLATE L.

(In Plates L and LI the drawings are obtained, unless otherwise specified, from *C. reflexa* on *Salvia*.)

(Here, as also in Pl. LI: H = host element; P = parasite element; HS = host sieve tube; HC = host companion cell; *sp.* = space; *x* = broken or partly dissolved parasite wall; J = sieve plate at junction between host and parasite.)

Fig. 52. Two invading hyphae which have just reached the pericycle of the host (*Salvia*). On the left the host element is merely slightly bulged inwards; on the right the bulging has been carried further, and the wall of the pericycle cell (f_1) has been absorbed as far as the middle lamella. *f* = the remains of the wall of the last fibre, the rest of which has been absorbed. (Stained Delafield's haematoxylin.) $\times 750$.

Fig. 53. A similar invading hypha which has got through the greater part of the pericycle and has nearly penetrated into the phloem. Part of the wall over the tip of the hypha stained with London blue. $\times 500$.

Fig. 54. An invading hypha which has reached the old phloem; the wall at its tip, where it is applied to the host sieve-tube wall, is still unaltered. It appeared at another focus that a continuation of this element went on further into the phloem. (Stained first in safranin and London blue and afterwards in Delafield's haematoxylin.) $\times 600$.

Fig. 55. A somewhat similar case; two adjoining hyphae in the host phloem. In the tip of the left-hand element the inner layers of the thick cell-wall are apparently beginning to be softened and stain in patches with London blue. (Stained as Fig. 54.) $\times 600$.

Fig. 56. Two invading hyphae in which the process of softening the wall appears to have proceeded further, and the inner layer of the wall is swollen up and stains with London blue. $\times 600$.

Fig. 57. Three similar elements which have penetrated still further into the host phloem; in two of them the whole thickness of the wall at the tip now takes the blue stain with London blue. $\times 450$.

Fig. 58. The tip of another such element, a thin outer layer of the wall still unstained. $\times 600$.

Fig. 59. A similar element near a lateral sieve plate (*s*) of the functional host phloem, to which it is very probable that it was about to apply itself. The relations of the walls were almost impossible to make out; it appeared that even at the tip a layer of unaltered parasite wall was still present, but was just being softened so as to stain with blue on the outer surface also. $\times 600$.

Fig. 60. A parasite hypha seen in transverse section making its way at right angles to the old host sieve tubes and going straight through a hole made in one of them. The wall of the hypha stains blue in parts, the section being probably taken near its tip. $\times 500$.

Fig. 61. The surface view of an invading hypha; the wall as yet only stains blue in patches. $\times 600$.

Fig. 62. A strand of sieve tubes derived from an invading hypha. A connexion has been established with a host sieve area and most of the walls subdividing the hypha have become bored out and developed as sieve areas. *w* = original wall of hypha in which no connecting threads or slime strings are found. The relations of the walls of the host and parasite in the region of junction could not be clearly made out; possibly the mass of blue-staining substance may represent the dissolving wall of the tip of the parasite hypha in a last stage of degeneration. (Ditto in Fig. 67.) $\times 600$.

Fig. 63. Part of a strand of sieve tubes from an old and possibly degenerating haustorium. The

arrows pointing to P and H indicate the direction of the ends of the haustorium which belong respectively to parasite and host; the element cut in transverse section belongs to the phloem of the main parasite stem. Callus changes have taken place to an unusually large extent in the longitudinal walls. $\times 600$.

Fig. 64. Strand of sieve tubes from the haustorium of *C. europaea* on *Vitis* (preserved in October). Accumulation of callus had taken place over the sieve areas on the subdivision walls, but none was found on the original walls of the hypha. w = wall of the original hyphal element which has now become subdivided. c = crushed cells on the periphery of the invading strand. It was not found possible to make out the exact relations of parasite and host. x = a thin ridge or broken wall. (Cf. Figs. 68, 76, &c.) $\times 500$.

Fig. 65. Ends of three invading hyphae, closely appressed to one another; the left-hand element resembles Figs. 58, 59, &c.; the right-hand one is applied to a lateral sieve field of the host. x is probably the partially dissolved remains of the parasite wall. $\times 600$.

Fig. 66. An invading hypha in contact with a host sieve tube, of which a lateral sieve field is seen in surface view. $\times 600$.

Fig. 67. Compare Fig. 62. The end wall of the parasite cell beyond x has probably been dissolved, and the blue mass may represent part of its degenerating remains. The naked protoplasm of the parasite is seen extending beyond the blue mass, and would appear to have applied itself closely to the host sieve area. $\times 600$.

Fig. 68. Two invading elements which have turned more or less at right angles to their original course and are now running in almost the same direction as the host sieve tubes. The lower one is as yet unattached; two small blue-staining granules are seen embedded in its protoplasm. (Cf. Figs. 73-5.) The upper element has applied itself to a lateral sieve plate. No cell-wall could be distinguished between the sieve plate and the parasite protoplasm at x. (The preparation was stained first with safranin and London blue; afterwards light green and Delafield's haematoxylin were used successively as wall stains.) $\times 500$.

Fig. 69. From a transverse section of *C. sp.?* on *Solidago sp.?* The tip of an invading parasite hypha is applied to a lateral sieve plate, and no cell-wall appears to be present between the sieve plate and the parasite protoplasm. $\times 600$.

Fig. 70. An empty parasite element whose wall appears to terminate in a ridge at x. J = the host sieve field to which the protoplasm of the parasite element was probably applied. $\times 500$.

Fig. 71. An empty parasite element applied to a sieve field, J. The remains of the wall (stained blue) at the tip x are apparently dissolving. $\times 600$.

Fig. 72. From a paraffin preparation stained only with Delafield haematoxylin. The invading element with its enormous nucleus is applied to the sieve field J. In this case it was fairly clear that the parasite wall terminated on either side of the sieve plate at x. $\times 750$.

Figs. 73, 74, 75. Haustorial cells showing blue-staining masses in various stages of development embedded in the protoplasm. All from old haustoria. $\times 750$.

PLATE LI.

Figs. 76, 77, 78.¹ The ends of three invading hyphae which have formed connexions with sieve areas in the host phloem. Figs. 76 and 77 were obtained from a preparation stained with safranin, aniline blue, and London blue. The preparation was afterwards stained in Delafield's haematoxylin, and Fig. 78 was drawn from the same three elements. The difference in proportion between the same element stained in the two ways is partly due to different foci, and the difference in thickness of the walls to the difficulty in focusing sharply walls which are unstained.

The protoplasm of the parasite cells is only shrunk very slightly from the sieve plate, and it is fairly clear even from Figs. 76 and 77 that no wall intervenes between it and the sieve plate. This is made unquestionable by Fig. 78, the small space remaining quite unstained. In Figs. 76 and 77, x represents what was regarded as being probably the termination of the parasite wall. In Fig. 78 these points are more sharply identified. H = host sieve tube. P = parasite element. J = sieve field of host. W = wall seen obliquely. F = line of fusion between walls of adjoining parasite elements. R = remains of almost dissolved parasite wall. In Fig. 78 the host walls are shaded, the parasite walls left unshaded. Fig. 78 magnified 1,000, Figs. 76 and 77 slightly less.

¹ Fig. 78; D. Thoday *del.*

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