IV. *On Endophytic Adaptation shown by* Erysiphe Graminis *DC. under Cultural Conditions.*

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Received February 24,—Read April 6, 1905.

[Plate 6.]

I. *Introductory.*

I have recently pointed out (1) (2) (3) that if a small wound, removing a patch of epidermal cells, is made on the leaf or stem of certain host-plants, and conidia or ascospores of certain species of the *Erysiphaceæ* are sown on the cells of the internal tissues thus exposed, vigorous infection will take place, and in a few days the surface of the wound will be covered by a mycelium bearing densely clustered conidiophores with ripe conidia.

The fact was somewhat surprising, since the fungi in question are confined normally to the external surface of the epidermal cells. It was desirable to ascertain the details of the growth of the fungus under these abnormal conditions, and to discover to what extent the hyphæ of the mycelium penetrated into the intercellular spaces of the internal tissues, and especially whether haustoria, normal or otherwise, were produced, and if so, in what cells they were formed.

Before describing the experiments carried out with the object of determining these points, and the results obtained, it will be convenient to give first a brief account of our present knowledge of the mycelial characteristics of the *Erysiphaceæ* in relation to their parasitic habit.

Since De Bary's classical work (5) on the family in 1871, the species of the *Erysiphaceæ* have been, until a few years ago, universally regarded as possessing a strictly ectoparasitic habit, the whole of the fungus being supposed to be external to the host-plant, with the exception of haustoria sent into the epidermal cells.* In Harper's work (6) on the development of the perithecium of *Sphærotheca* and *Erysiphe* confirmation was given of the ectoparasitism of the *Erysiphaceæ*.

In 1899 Palla (7) made the discovery that in *Phyllactinia*, one of the genera of

* The statements made by Berkeley ('Gardener's Chronicle,' 1847, p. 779) and Worthington Smith (*loc. cit.*, 1886, p. 621) as to the hemi-endophytic habit of the mycelium of *Oidium Tuckeri* have not been confirmed.

the *Erysiphaceæ*, the hyphæ of the mycelium instead of producing haustoria in the epidermal cells, send branches through the stomata. Each of these nutrient hyphæ ("Ernährungshyphe"), after traversing the intercellular spaces for a short distance, forms a normal haustorium in a cell of the mesophyll tissue. On account of this hemi-endophytic mode of life, the genus *Phyllactinia* has been separated as a distinct sub-family, *Phyllactineæ*, from the rest of the genera, which form the sub-family *Erysipheæ* (see 4).

In 1900 GRANT SMITH (8), in his investigations on the structure and development of the haustorium in the *Erysiphaceæ*, discovered that in one species of the genus *Uncinula*, viz., *U. salicis* (DC.) WINT., the mycelium (which is entirely external to the host-plant) sends haustoria not only into the epidermal, but also into the sub-epidermal cells by means of slender bar-like necks stretching across the epidermal cells. In the case of the other species of the *Erysipheæ* studied by GRANT SMITH (comprising species of all the genera), no departure from the strictly ectoparasitic habit was noticed.*

So far as we know at present then, the species of the *Erysipheæ* are normally strictly ectoparasitic in habit, the hyphæ of the mycelium being confined to the external surface of the epidermal cells (never gaining access to the intercellular spaces of the internal tissues), and sending haustoria, either into the epidermal cells alone, or in the case of *U. salicis*, into the sub-epidermal cells as well.†

II. *Experiments, Methods, etc.*

The general results of infection obtained when conidia or ascospores are sown on internal tissues exposed by a wound have already been described (1) (2). Under these conditions it was found that conidia or ascospores of one "biologic form" of a species were able to infect host-plants of other "biologic forms" of the same species, although these host-plants are normally immune to their attacks. Also, conidia of a certain species which are unable to cause infection on the uninjured epidermis of the old leaves of its host-plant, prove able to grow vigorously on

* GRANT SMITH makes the following observations on a specimen of "*Erysiphe communis* (WALLR.)" on *Geranium maculatum* examined by him:—"At the end of a section, where the scissors with which the pieces of leaves were cut had destroyed the section in part, a haustorium was found in what was clearly a sub-epidermal cell. Its connection with the surface was destroyed, but there is no doubt that it was a normal haustorium in one of these cells. Whether it was due to the chance presence of *Phyllactinia* on this host, whether *Erysiphe* occasionally adopts the practice of *Uncinula salicis*, or whether it was *Uncinula* itself on this host, could not be determined."

† I have recently discovered (see 'Annal. Mycolog.,' vol. 3, p. 82 (1905)) that *Erysiphe taurica* LÉV., in its conidial stage, possesses an endophytic mycelium, the conidiophores being sent up through the stomata. The occurrence of such a form within the *Erysiphaceæ* must be borne in mind, since it is possible that the endophytic adaptation shown by the ectoparasite *E. Graminis* under cultural conditions (described in the present paper) may be of the nature of a reversion.

such leaves when sown on the mesophyll-cells exposed by a wound (3). In the present investigations the fungus used was the conidial stage of *Erysiphe Graminis* DC. on barley and on oats, and with the view of obtaining the most vigorous growth possible under the circumstances, the normal host was used, *i.e.*, conidia were taken from barley and sown on wounded leaves of barley, and from oats on wounded leaves of oats. In each case a young vigorous leaf (usually the first leaf) was cut off from a seedling plant, and a minute piece of tissue was cut out with a sharp razor from the upper surface of the leaf. The wound made (which measured about 2 millims. × 1 millim.) was sometimes shallow, the razor-cut removing scarcely more than the cells of the epidermis, so that in inoculation the conidia were sown on the cells of the upper layers of the exposed mesophyll; sometimes the wound was deeper, the razor-cut extending to, but not through, the lower epidermis, and removing at the deepest part of the wound all or nearly all the layers of the mesophyll, and exposing here and there the inner surface of the cells of the lower epidermis, so that in inoculation the conidia were sown on the cells of the lower layers (often the lowermost layer) of the mesophyll, or even on the interior surface of the cells of the lower epidermis. After inoculation the leaves were placed on damp blotting-paper in a Petri dish. By the sixth to eighth day vigorous infection had nearly always resulted, the surface of the wound bearing patches of clustered conidiophores, more or less powdery with accumulated ripe conidia. By this time the leaf showed signs of dying. The wounded part of the leaf was then cut off, and fixed either in FLEMMING's fluid (the weaker solution), or in chromacetic. The fixed material, after washing, dehydrating, and embedding, was microtomed, and the sections stained with Diamant Fuchsin and "Licht grün."

III. *Results and Conclusions.*

It was seen at once on examining the wounded part of the leaves fixed on the sixth to eighth day after inoculation that the fungus had developed, not merely on the superficial cells of the wound on which the conidia had been sown, but had grown inwards through the numerous intercellular spaces of the internal tissues to a remarkable extent. Where the mesophyll-cells remaining uninjured were several layers deep, the hyphæ had penetrated inwards, winding through the intercellular spaces, until they reached the interior surface of the lower epidermis. Also, hyphæ had extended inwards from the sides of the wound in a direction parallel to the surface of the leaf, so that at some little distance from the edge of the wound, hyphæ were to be found traversing the intercellular spaces between mesophyll-cells and the respiratory cavities lying under the uninjured epidermis. It often happened that a short stretch of vascular bundle had been cut through more or less longitudinally, in such a way that the xylem elements were exposed at the surface of the wound. In such cases it was usually found that hyphæ proceeding from conidia germinating on

the surface of the wound, on cells adjoining the cut ends of the bundles, had grown downwards, and then, extending laterally, ran freely in the intercellular spaces of the mesophyll-cells beneath the elements of the bundle. Haustoria were produced, both by the hyphæ creeping on the surface of the wound, and also by the hyphæ penetrating the intercellular spaces, and occurred in the cells of the mesophyll (in all the layers from the sub-epidermal to the lowest), in the sheath-cells of the bundles, and in the lower epidermal cells, having in the last case entered through the interior walls. The hyphæ growing on the external surface of the cells exposed by the wound produced abundant conidiophores and conidia; the hyphæ, also, enclosed in intercellular spaces, either just below the surface of the wound, or deep down in the internal tissues, had struggled to produce conidiophores. If the intercellular space, where the young conidiophore is produced, was shut off from the open air by only a thin membrane consisting of the walls of collapsed mesophyll-cells, the young conidiophore growing upwards proved sometimes able to force an exit and continue its growth. The details of growth of the hyphæ, of the production of haustoria and of intercellular conidiophores, can best be seen by reference to the figures given at Plate 6.

We will consider first the growth of the fungus sown on wounded Oat-leaves. In this series of experiments the leaves were fixed on the sixth to eighth day, and were subsequently microtomed longitudinally. At all places of the wounded part of the leaf (except where the vascular bundles occurred at the surface of the wound), mycelial hyphæ were to be found entering from the surface and penetrating inwards by means of the intercellular spaces. In fig. 8 (Plate 6) a portion of a leaf is represented, at a place where four rows of living mesophyll-cells remain, as well as the lower epidermis.* Most of the intercellular spaces contained vigorous hyphæ winding in all directions throughout the layers of the mesophyll-cells, even in the spaces between the lowest mesophyll-cells and the interior wall of the lower epidermis. As the hyphæ have a tortuous course, an individual hypha cannot usually be followed, in a single section, for any considerable length. Occasionally sections are obtained which show straight pieces of hyphæ extending for some length, either in the respiratory cavities beneath the stomata of the lower epidermis, or, as in fig. 11, lying along the interior wall of the lower epidermis and under the lowest row of the mesophyll-cells.

When the surface of the wound was covered by the ripe conidiophores,† the hyphæ producing them could be seen either running along the surface of the superficial mesophyll-cells (into which they sent haustoria), or winding in and out of the intercellular spaces between the upper layers of the mesophyll-cells, often filling-up some

* During the time of the experiment, the surface of the wound would be covered in many places with the remains of the dead or dying mesophyll-cells left by the razor. In the process of washing, etc., however, all or most of the *debris*, consisting of fragments of the dead cells, became removed.

† The conidia produced were in every way normal, and proved able to cause vigorous infection when sown on the uninjured epidermis of other leaves of the Oat.

of the intercellular spaces. In the latter case the conidiophores produced pushed their way up to the surface in the spaces lying between the individual mesophyll-cells, and open to the exterior. Often, however, such intercellular spaces are enclosed, and shut off from the open air by a membrane at the surface of the wound as described above. In fig. 3 is represented a part of a leaf, at the edge of the wound, where the tissue consisted of five layers of mesophyll-cells and the lower epidermis.* In the intercellular space between two mesophyll-cells at the surface of the wound, two conidiophores have been formed; one (to the right) has forced its way through the membrane enclosing the intercellular space from the free air; the other (to the left) is still quite young, and has developed only the characteristic bulb-like base.† Both of these conidiophores were formed by hyphæ creeping in the intercellular spaces of the mesophyll-cells, to which they had gained access from the surface of the wound at some point near. In one case observed, the mechanical resistance offered by the membrane had, apparently, been the cause of an asymmetric growth of the conidiophore, occurring just before it broke through.‡ In some cases the sections showed conidiophores beginning to be formed in intercellular spaces of the middle layers of the mesophyll-tissue, where two or more rows of living mesophyll-cells occurred between the conidiophore and the surface of the wound.

In the areas of the leaf where the intercellular spaces are traversed by the hyphæ, haustoria occur commonly in the mesophyll-cells. They are sent by the hyphæ running on the surface of the wound into the superficial mesophyll-cells which remain living, and by the intercellular hyphæ into internal cells of the mesophyll throughout its thickness.

A few remarks concerning the structure of the haustorium of *E. Graminis* may be made here. At the point of penetration a thick collar grows down from the inner wall of the epidermal cell, and surrounds the minute neck of the haustorium. This collar often stains differently from the rest of the cell-wall, and is either produced by modification of the cellulose through the enzymic action of the tip of the penetrating hypha, or consists of some substance added by the protoplasm to the inner surface of the cell-wall in consequence of the injury inflicted in penetration. Under the methods used (described above) the collar is often stained a very deep red, while the surrounding cell-walls are coloured green.§ The main part of the

* Only the three upper rows of mesophyll-cells are shown in the figure.

† See 'Beihefte z. Botan. Centralbl.,' vol. 14, p. 264, taf. XVIII.

‡ In a few cases it appeared that the conidiophore had been unable to break through the limiting membrane of such intercellular spaces, the apex of the conidiophore showing signs of having been arrested in its growth and gradually destroyed.

§ Such deeply-stained collars or plugs may sometimes be found at places where no haustorium occurs in the cell, and probably mark places where only the earliest processes of penetration have taken place. GRANT SMITH ((8), p. 161), who used FLEMMING'S triple stain (safranin, gentian-violet, and orange-G), remarks as follows in connection with the haustorium of *E. communis*:—"The collar from the cell-wall is somewhat different from the wall from which it takes its origin, and usually stains little, while the

haustorium itself consists of an ellipsoid or sub-cylindric body, which contains almost invariably a single large nucleus. Within the nucleus one, or sometimes two nucleoli are found, which stain deep red. At one, or usually at both ends of this body numerous long finger-like processes (which may be forked) are developed. Harper (6) in his account of the haustorium of *Sphærotheca Castagnei* and *Erysiphe communis* states that it invariably contains a single nucleus. GRANT SMITH (8) in describing the haustorium of *E. Graminis* on *Poa pratensis* mentions that though the same is usually the case in this species also, he observed a single example in which a haustorium contained two nuclei. In examples of *E. Graminis* on the Oat I have observed in three cases two nuclei in a haustorium which was lying in a normal epidermal cell. The two nuclei lay close to, or touching, one another towards the middle of the body of the haustorium; each contained one nucleolus. In every other case the haustorium contained a single nucleus. The haustoria formed in the cells of the internal tissues resembled in every way those which occur normally in the epidermal cells.

As can be seen in figs. 7, 9, 10, the collar surrounding the neck often stains deeply, and is sometimes very thick; a single large nucleus, with one, or more rarely two, nucleoli, is present; and from one (figs. 6, 10) or from both ends (figs. 2, 9) of the haustorium long finger-like processes are developed. In some cases where the haustorium is sent into a small mesophyll-cell, the finger-like processes, being unable to extend laterally, coil themselves more or less completely round the body of the haustorium.

Where the hyphæ, penetrating downwards from the surface of the wound, reach the sheath-cells surrounding the bundle, numerous large vigorous haustoria are produced in these cells. The formation of haustoria in the sheath-cells is shown in fig. 2. Here the sheath-cells lie at the surface of the wound, and are attacked by the superficial hyphæ. Three sheath-cells are occupied by haustoria, one apparently having been entered from below. In another case the sheath-cell containing the haustorium was separated from the surface by mesophyll-tissue, and had been attacked by an intercellular hypha. Haustoria had also been formed in sheath-cells on either side, and also in the mesophyll-cells lying above. In the same leaf, at a little distance away, a conidiophore occurred in an intercellular space close to a respiratory cavity beneath the uninjured epidermis (fig. 5). The hyphæ shown in this figure had grown inwards from the edge of the wound. In several other cases hyphæ had penetrated laterally (in a direction parallel to the surface of the leaf) from the edge of the wound, and occurred in the middle of the mesophyll, which consisted of 6–8 layers of cells, and was covered by the uninjured epidermis above and below.

remaining portion stains with safranin intensely." At p. 163, however, the author remarks: "The safranin stain frequently makes evident the beginning of penetration" by causing "a deep staining of the inner surface of the outer wall of the cell immediately under the point where the hypha comes in contact with the epidermis."

In such places both haustoria and young conidiophores were produced. Figs. 9, 10 show haustoria entering mesophyll-cells from intercellular hyphæ.

As mentioned above, the fungus shows vigorous growth when sown on parts of the leaf where the tissue had been reduced by the cut to a single row of living mesophyll-cells together with the lower epidermis, or even where the lower epidermis was the only tissue left. Figs. 6, 7 represent portions of a leaf at such a place. In fig. 6 we see a haustorium sent into one of the mesophyll-cells by a hypha running in the intercellular space between the lowest row of mesophyll-cells and the interior wall of the lower epidermis. In fig. 7 a hypha in a similar position has sent a haustorium into the epidermal cell, entering it through its interior wall.

In the series of experiments in which Barley leaves were used, the latter were fixed on the seventh day after inoculation. Most of the leaves were microtomed transversely. In these wounded Barley leaves, just as in the Oat leaves, the same vigorous growth resulted at the wounded place, and intercellular hyphæ penetrated the spaces between the cells of all the layers of the mesophyll, and sent haustoria into the cells. The production of young conidiophores, also, occurred in the intercellular spaces at all depths in the mesophyll-tissue.

Fig. 1 shows part of a vascular bundle and the surrounding tissue that had not been cut away. Most of the numerous large intercellular spaces between the cells are occupied by vigorous hyphæ, which in many cases are beginning to form conidiophores. Two young conidiophores are shown in the figure; one formed just below the membrane at the surface of the wound, the other in a respiratory cavity above the lower epidermis.* Fig. 12 shows a group of vigorous hyphæ producing conidiophores in a respiratory cavity above the lower epidermis. The young conidiophores, in growing upwards, have forced apart the membrane originally extending across the intercellular space at the surface of the wound. In other instances similar groups of young conidiophores occur in such places under an unbroken membrane. Several cases were observed where a single conidiophore had broken through the membrane at the surface of the wound and produced its chain of conidia.† Vigorous young conidiophores produced in intercellular spaces deeper down in the mesophyll were found pressing against the lower walls, or between the lateral walls, of the overlying mesophyll-cells. In one case a hypha was observed which was creeping in an intercellular space beneath the membrane on the surface of the wound, and which had produced a young conidiophore; the direction of growth of this conidiophore was towards the interior of the leaf.

* The mesophyll-cells situated near the apex of the lower conidiophore showed signs of degeneration, both as regards their walls and cell-contents. This degeneration is not to be attributed to the action of the fungus, as the same was met with in places where no hyphæ were present; it was very possibly caused by the action of bacteria, which in some cases occurred in the dying leaf-tissue.

† In one case the upper part of a young conidiophore appeared to have become disorganised in consequence of its upward growth having been stopped by the membrane, which it had been unable to break through.

A few remarks may be made here concerning the direction of growth taken by the young intercellular conidiophores. In many places where the leaf-tissue has been cut away so as to leave only one or two rows of mesophyll-cells, and the lower epidermis, the intercellular spaces of the mesophyll and the respiratory cavities are found to be full of vigorous hyphæ. These hyphæ send haustoria into the cells of the mesophyll and epidermis, and produce freely young conidiophores.* In fig. 4, two young conidiophores are shown in a respiratory cavity; a haustorium has been sent into the epidermal cell. Most of these conidiophores grow vertically, with the apex directed towards the cut surface of the leaf. Sometimes, however, when the parent hypha lies at right angles to the surface of the leaf along the vertical wall of a mesophyll-cell, the young conidiophore grows in a direction parallel to the surface of the leaf. Also, in places where the cut leaf consists of several layers of mesophyll-cells, young conidiophores are not infrequently found growing in a direction parallel to the surface of the leaf. In such cases as these, it appears that the conidiophore is produced at right angles from the free surface of the parent hypha, and grows into any available space.

As in the case of the Oat leaves, there was an abundant formation of haustoria in the cells of the internal tissues. Vigorous haustoria, with long spreading finger-like processes, occurred in all the layers of the mesophyll, in the sheath-cells of the bundles, and in the cells of the lower epidermis. In one section, at a place where three layers of mesophyll-cells and the lower epidermis remained, haustoria had been sent by the hyphæ creeping on the surface of the wound into three superficial and contiguous mesophyll-cells; a haustorium had also been sent into one of the underlying mesophyll-cells by a hypha in an intercellular space. As was noticeable in the case of the Oat leaves also, the sheath-cells of the bundles were much invaded by very vigorous haustoria, the finger-like processes of which often extended the whole length of the cell. In one case, three haustoria had been formed in a single sheath-cell.†

Reviewing the results of the above investigations, one of the most interesting points is the proof obtained that *E. Graminis* is not—as perhaps might have been expected—so highly specialised as an ectoparasite as to be restricted for its food-supply to cells of the epidermis, but is able to thrive vigorously and attain its normal development when allowed to grow on the mesophyll-tissue of the leaf. Although in nature a strict ectoparasite, *E. Graminis* shows itself capable of immediate adaptation—an adaptation complete as regards the mycelium and haustoria—to conditions closely resembling those obtaining in endophytism.

* A group of two or three conidiophores in one space frequently occurs.

† GRANT SMITH ((8), p. 178), in his investigations on *Phyllactinia*, observes that "the majority of the intercellular hyphæ in several of the hosts studied take a more or less direct course to the regions near the bundles. The development by the fungus of the absorbing organs in regions abundantly supplied with available food, such as the parenchyma sheath of the bundles, indicates a selective chemotropism in the fungus."

In the present investigations the early death of the leaf used precluded the possibility of observing whether the fungus was capable of gradually adapting itself, as regards the mode of growth of its conidiophores, to the endophytic conditions. If in the course of time such an adaptation could be accomplished as the sending of the conidiophores through the stomata (as in the *Peronosporaceæ*), or the massing together of the conidiophores when young, and the production of an erumpent sorus (as in the *Uredineæ*), the endoparasitism would be complete.

The present investigations show, I think, that *E. Graminis* is a facultative endoparasite as regards its vegetative existence. The readiness with which *E. Graminis* under suitable conditions grows with vigorous intercellular mycelium leads us to wonder whether under some circumstances the mycelium of this and other species of the *Erysipheæ* may not invade the internal tissues of their host-plants exposed at wounds caused *in nature* by the attacks of animals or physical agency.* It must be remembered, however, that in the case of actively growing leaves the healing processes shown by many plants and the drying up of the superficial layer of cells of the wound would tend to prevent the entry of the mycelial hyphæ.

I offer my sincere thanks to Professor H. MARSHALL WARD, F.R.S., for permission to carry out the work at the Cambridge University Botanical Laboratory, and for the facilities afforded me.

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* Herein lies a possible explanation of the occurrence of the sub-epidermal haustorium of *E. communis* observed by GRANT SMITH (see above, p. 88, footnote).

Explanation of Plate 6.

Figs. 1, 4, 12 represent sections of Barley-leaves (in 1 and 12 cut transversely, in 4 cut longitudinally). Figs. 2, 3, 5–11 represent sections of Oat-leaves (cut longitudinally). All the figures are magnified 400 times.

Fig. 1.—Part of a leaf, with remains of a vascular bundle (xylem elements seen to left), mesophyll-tissue, and the lower epidermis. Most of the intercellular spaces are occupied by hyphæ. Two young conidiophores have been formed, one in the respiratory cavity, the other just below the membrane at the surface of the wound.

Fig. 2.—Part of a leaf where the sheath-cells of a vascular bundle are exposed at the surface of the wound. Haustoria have been sent into three of the sheath-cells. Hyphæ are seen in the intercellular spaces, and in the respiratory cavity beneath a stoma of the lower epidermis.

Fig. 3.—Part of a leaf towards the edge of the wound, where the leaf-tissue consisted of five rows of mesophyll-cells and the lower epidermis. Only the three upper rows of the mesophyll are shown here. In an intercellular space between two mesophyll-cells of the superficial row, two conidiophores have been formed; one (to the right) has forced its way through the membrane at the surface of the wound, the other (to the left) is quite young, and shows only the bulb-like base.

Fig. 4.—Two young conidiophores formed in a respiratory cavity; a haustorium has been sent into a cell of the epidermis.

Fig. 5.—Part of a leaf, at a little distance from the edge of the wound. The hyphæ occurring, beneath the uninjured upper epidermis, in the intercellular spaces and forming there a young conidiophore, had gained access by growing inwards, from the edge of the wound, in a direction parallel to the surface of the leaf.

Fig. 6.—Part of a leaf at a place where only a single row of living mesophyll-cells and the lower epidermis remain. A haustorium has been sent into one of the mesophyll-cells by a hypha running in an intercellular space. The haustorium has developed the finger-like processes at one end only. The nucleus of the mesophyll-cell lies by the side of the body of the haustorium. Two fragments of hyphæ creeping on the surface of the wound are shown.

Fig. 7.—Part of a similarly wounded leaf. A haustorium has been sent into a cell of the lower epidermis, entering it through its interior wall. The collar of the haustorium is very thick and deeply stained.

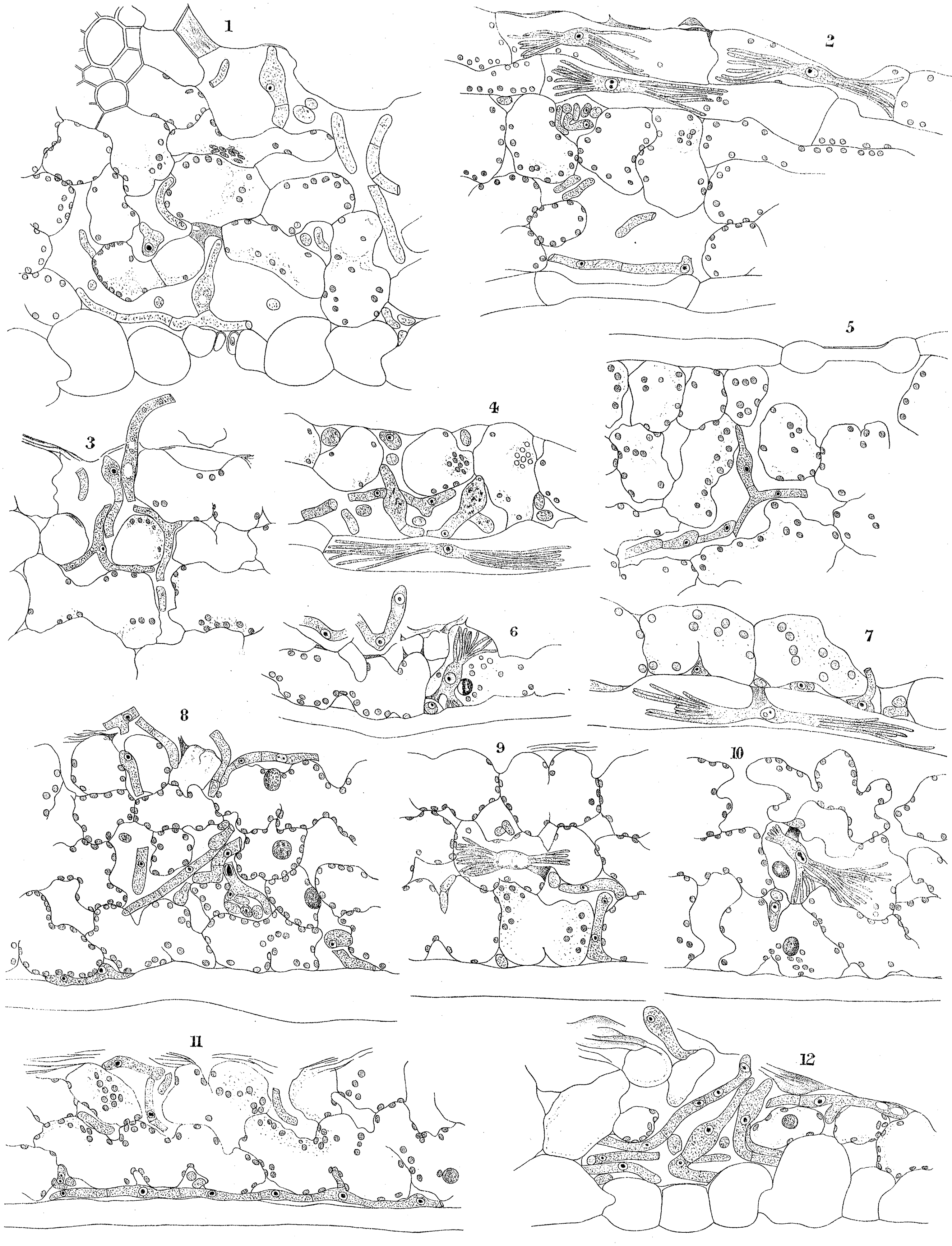
Fig. 8.—Part of leaf at wound where four rows of living mesophyll-cells and the lower epidermis remain; the intercellular spaces contain numerous tortuous mycelial hyphæ.

Fig. 9.—Part of leaf at place where three rows of mesophyll-cells and the lower epidermis remain. A haustorium has been formed in a mesophyll-cell. The haustorium has a thick deeply-stained collar, and has developed finger-like processes at both ends.

Fig. 10.—Part of a similarly wounded leaf. A haustorium has been sent by an intercellular hypha into a mesophyll-cell of the middle layer. The neck of the haustorium is very thick and darkly stained. Apparently through lack of room, the finger-like processes have developed at only one end of the haustorium.

Fig. 11.—Two rows of mesophyll-cells and the lower epidermis remain (fragments of collapsed mesophyll-cells still occur, in places, on the surface of the wound). A hypha is seen running straight for some distance in the space between the interior wall of the epidermis and the lowest row of the mesophyll-cells. In one place (to the right) the hypha has sent a minute branch into one of the spaces due to the lobed outline of the mesophyll-cell.

Fig. 12.—A group of hyphæ and conidiophores, formed in a respiratory cavity; by their upward growth the membrane at the surface of the wound had been split.



E. S. Salmon, del.
M. P. Parker lith.

Parker & West imp.