

SOUTH AFRICAN PERISPORIACEAE.

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(With seven Text-figures).

(Read May 19, 1920.)

VI. THE HAUSTORIA OF THE GENERA MELIOLA AND IRENE.

The genus *Meliola* has received considerable attention from systematists, and is much studied from the taxonomic point of view by collectors and students of tropical and sub-tropical fungi. Comparatively little, however, is known of their method of nutrition or of their relation to the forest trees and shrubs, on whose leaves and shoots they are chiefly found. This is possibly due to the fact that until recent years these fungi were for the most part described by workers in Europe, who only had at their disposal scanty material sent to them by collectors in the Tropics.

The earlier workers, such as Bornet (1) and Gaillard (2), stated that the lesions which one sometimes observes on leaves on which these fungi grow are due to the action of numerous mites, of which one often finds the remains. Gaillard even states that he has satisfied himself by examining numerous sections that the vegetation of the *Meliolas* is entirely superficial, and does not in any way attack the tissues of the plant on which it grows.

In 1908 these statements were challenged by Maire (3) on observations which he had made on four fungi of the genus *Meliola*. The view held by some of the earlier workers that the *Meliolas* are entirely superficial and grow like the *Capnodiums* on the honey-dew produced by insects, he rejects on the grounds that close observation has shown that the development of these fungi is quite independent of the presence of any insects.

A second hypothesis is that the fungus derives its nourishment by osmotic interchanges between their hyphae applied to the cuticle and the epidermal cells. Maire observes that this is improbable, since the hyphae are separated from the cavity of the epidermal cells by a layer of impermeable cutin, of which the thickness is often several times that of the hypha. Moreover, the effect of the *Meliolas* on their host—neglected by most authors—is quite evident in certain cases; for instance, extended purple spots are found on leaves of *Schinus*, radiating from the point covered by the *Meliola* mycelium, and no other cause can be found for the discoloration.

Maire based his observation on four species: *Meliola amphitricha* Fr. on *Schinus molle*, *M. Negeriana* on *Lomatia obliqua*, *M. brasiliensis* var. *sanguineo-maculans* on *Schinus* sp., and one of the two European species, *M. nidulans* on *Vaccinium myrtillus*.

On examining numerous sections he found small haustoria in certain epidermal cells; these appear in the form of a very fine tube with brown walls and very clear lumen, which traverses the cuticle perpendicular to its surface or somewhat obliquely. When the cuticle is not very thick the tube traverses it without any sensible modification, and expands in the cavity of the cell into a more or less spherical vesicle with a thin hyaline wall—e.g. in *Schinus* sp. attacked by *Meliola brasiliensis* var. *sanguineo-maculans* and *M. amphitricha*.

When, on the contrary, the cuticle is thick, the tube completely changes its form and contracts into an extremely fine, filiform tract (about $\frac{1}{2} \mu$ diam.), staining bright blue with lactophenol and cotton blue, in which it is impossible to observe the protoplasmic membrane. This filiform tract expands in the cell cavity in a similar way to the one described above.

Maire experienced some difficulty in finding sections showing the actual connection of the haustoria with the hypha, as the latter frequently fall away in sectioning; but after examining a large number of sections, haustoria were found adhering to the hyphae from which they were produced. He concludes from this evidence that the *Meliolas* are true parasites, deriving their food supply from the epidermal cells of the host by means of haustoria.*

The genera *Meliola* and *Irene* are well represented in many parts of South Africa, and over fifty species have been recorded (4), although there are still many promising localities in which no collections have been made. In view of the prevalence of these fungi on our forest trees, it was suggested to me by Dr. J. W. Bews that they might have an important bearing on plant succession in the forest belts. Seedling trees are especially subject to the attacks of fungi belonging to the genus *Meliola*, and it is not uncommon to find the leaves of seedlings of certain susceptible species so covered with dark mycelium that the normal green colour is only to be seen where young leaves have recently unfolded. It therefore was a matter of considerable interest to discover to what extent the *Meliolas* are parasitic and to confirm and extend the observations made by Maire.

Dried material from the National Herbarium was employed, and although recent collections were chosen where possible, satisfactory preparations were obtained even from old material. Small areas covered with the mycelium of the fungus were cut out and boiled in 10 per cent. formalin

* A number of valuable papers by G. Arnaud, containing references to the haustoria of the *Microthyriaceae* and allied families, only came to my notice when this paper was in the press, and have not been taken into consideration.

until most of the air was expelled from the tissues, and the portions of leaf sank to the bottom of the tube. When the formalin was cold, sections were cut with the freezing microtome and transferred direct from the 10 per cent. formalin to the stain.

The stain employed was Guéguen's triple stain (5), which was recommended by Maire as giving beautiful preparations. This is a solution of Sudan III and "bleu coton" (Bleu C₄B Poirrier) in lactic acid, but "bleu coton" not being obtainable methyl blue was used and proved to be a very satisfactory substitute. The sections were left in the stain for fifteen to thirty minutes, and were then mounted and examined in lactic acid. Successful preparations showed the cuticle stained a beautiful clear red, while the haustoria and the contents of the external fungus hyphae were stained bright blue.

Some of the species of *Meliola* are very readily detached from the host, and a considerable search had to be made before sections were found showing the haustoria attached to the hyphae from which they were derived; others adhere more closely and no difficulty was experienced in demonstrating the attachment of the haustoria.

A fairly large number of species was examined, and these will be considered separately.

Meliola amphitricha Fr. has been recorded from this country on a number of hosts chiefly belonging to the Rubiaceae. The first specimen examined was on *Sapindus oblongifolius*. This plant has an ordinary mesophytic type of leaf with a fairly thick cuticle on the upper side, the cells of the lower epidermis are smaller than those of the upper, and the cuticle on the under surface is much thinner. Haustoria were present in great numbers in the epidermal cells, and the fungus being amphigenous they were observed on both the upper and the lower surface. In every case they consisted of a very fine filiform tract—which may be termed the penetrating filament—traversing the cuticle and expanding just within the epidermal cell into a small spherical thin-walled vesicle. The whole haustorium stains bright blue by the method used, and the vesicle has a single central nucleus which stains more deeply. This type of haustorium is very similar to that described by Harper (6) for many of the Erysiphaceae. On *Grumilea caffra*, which has a very thin cuticle, *Meliola amphitricha* has exactly the same type of haustorium as on *Sapindus oblongifolius*; a fungus on *Jasminum streptopus*, which is placed under *M. amphitricha*, was also examined and found to have the same type of haustorium.

The leaf of *Olea laurifolia* has a thick cuticle on the upper surface and edges, the distance from the leaf surface to the lumen of the epidermal cells being 12 to 13 μ ; on the lower surface the cuticle is thinner, the distance being only 4.5 to 5 μ . There are sclerenchyma fibres scattered through the mesophyll, and occasionally occurring between the epidermis and the

palisade cells. A *Meliola* species on this host closely resembles *M. amphitricha*, and was assigned to this species, as I was in doubt as to whether the morphological differences justified describing it as distinct from *M. amphitricha*. This fungus occurs on both sides of the leaf.

No difficulty was experienced in demonstrating the haustoria of this fungus, and in observing their connection with the hyphae on the leaf surface. The penetrating filament is $6-75\ \mu$ thick, and stains bright blue. It passes through the cuticle, but instead of expanding into a spherical vesicle in the epidermal cell, it traverses the epidermis and penetrates into a palisade cell, or the first cell of the mesophyll encountered, according to whether the fungus is growing on the upper or under surface of the leaf. If a sclerenchyma fibre is encountered it pierces through it and so reaches a chlorophyll-bearing cell, where it expands into a thin-walled, spherical, uninucleate vesicle. The fungus, therefore, is obviously a distinct species from *M. amphitricha*. It was suggested that the character of the leaf might in some way be responsible for the form of the haustoria. Two other species of *Meliola* occur on *Olea laurifolia*, and these were examined in order to discover whether they produced the same form of haustorium.

Meliola petiolaris Doidge occurs chiefly on the petioles and on the under sides of the leaves, but often spreads somewhat from the lower side over the upper margin. On the lower surface the fungus has haustoria similar to those of *M. amphitricha*, consisting of a fine filament penetrating the cuticle and a small, spherical vesicle, about $3\ \mu$ diam., in the epidermal cell. Near the edge on the upper surface, where the cuticle is much thicker, the haustoria are similar in character, but the penetrating filament is stouter and brown-walled. This change in the character of the penetrating filament appears to be correlated with the thickness of the cuticle, and is very unusual; in every other case the form of the haustorium has been found constant for any given species. Of all the specimens examined this was the only species, with a vesicle in the epidermal cell, in which the penetrating filament retained the brown colouring of the wall of the parent hypha. Maire mentions two species, *Meliola brasiliensis* var. *sanguineo maculans*, and *M. amphitricha* on *Schinus* sp., which have this peculiarity, and considers that in hosts with a thin cuticle the tube traverses the cuticle unchanged, but when the cuticle is thick the tube becomes a very fine, filiform tract with hyaline walls. In the majority of cases I have found that there is no relation between the thickness of the cuticle and the nature of the wall of the penetrating filament, which appears to be a specific character. In the case of *M. petiolaris* the tendency is for the filament to be brown-walled and stouter where it penetrates the thicker cuticle.

It will be noticed that Maire found a brown penetrating filament in leaves of *Schinus* attacked by *M. amphitricha*, whereas on other hosts in South Africa this fungus has a fine, hyaline penetrating filament, which stains blue with

Gueguen's triple stain. I think it is probable that the species *M. amphitricha* as at present constituted consists of a number of species which are morphologically similar, and that the form of the haustoria should be taken into consideration by taxonomists.

The third species parasitic on *Olea laurifolia* is *Irene ditricha* (K. & Cke.), Doidge, which occurs on the upper surface. The penetrating filament is thin walled, staining blue; it traverses the cuticle and the epidermal cell and expands into a globular vesicle just inside one of the palisade cells. It thus differs from the first of the fungi described on this host only in the broader penetrating filament, which in this case is about $1.5\ \mu$ thick.

Irene ditricha also occurs on *Celastrus* sp.; the form on *Olea laurifolia* differs in one or two minor points, and should perhaps be considered a variety. The leaf of this plant becomes discoloured over a considerable area, the centre of which is the *Meliola* mycelium; the discoloured parts become yellowish brown. This fact makes the leaf rather an unfavourable one for study as the contents of the epidermal and hypodermal cells are badly disorganised and stain deep blue. The haustoria appear to be similar to those of *I. ditricha* on *Olea laurifolia*.

Meliola carissae Doidge occurs on *Carissa arduina*, which has a leaf with a very thick cuticle. The penetrating filament is fine, staining blue, but its walls are often brown or brownish for a short distance where it enters the cuticle. The vesicle is in the epidermal cell, and is of the usual type, thin-walled, globular, hyaline and uninucleate.

Meliola leptidea Syd. on *Cussonia umbellifera* has also what may be termed the ordinary type of haustoria, with a fine penetrating filament and a globular vesicle in the epidermal cell. These are very small and inconspicuous, but the contents of the epidermal cells are obviously disorganised and filled with a granular deposit.

This type of haustorium was also produced by *Meliola ganglifer* K. & Cke. on *Curtisea faginea* and *M. capensis* (K. & Cke.) Th. on *Hippobromus alatus*.

Meliola bifida Cke. on *Osyridicarpus natalensis* occurs on the stems, and no satisfactory preparations could be obtained of this species, as the stem was too hard to cut with the freezing microtome, and the fungus very readily became detached from the host.

Meliola Evansii Doidge is found on *Scolopia* sp. Here the haustorium penetrates to the hypodermal cell (Fig. 1). The penetrating filament is hyaline and stains blue, but is fairly stout, and the expanded vesicle is formed in the chlorophyll-containing cell of the mesophyll which is encountered.

Exceptionally clear preparations were obtained of *Meliola arcuata* Doidge on *Viscum anceps* (Fig. 2). The stem—it is a leafless species of *Viscum*—has a very thick cuticle which is traversed by a fine penetrating filament, and swells into a globular uninucleate vesicle just inside the epidermal cell.

Irene natalensis Doidge is found on several species of *Doryalis*. The specimen selected was on the upper surface of the leaves of *D. tristis*, which have a thin cuticle. The penetrating filament has brown walls like those of

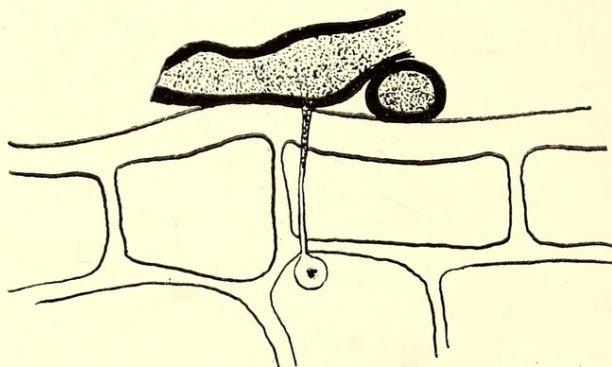


FIG. 1.—Haustorium of *Meliola Evansii* penetrating into leaf of *Scolopia*, sp. (comp. oc. No. 8). All the figures were drawn with the aid of the camera lucida and a Zeiss $\frac{1}{12}$ -in. oil-imm. obj.

the mycelial hyphae, but very much thinner, and it passes through the epidermis into the first layer of palisade cells, the expanded vesicle being just within the latter. These haustoria differ from those of *M. Evansii* in

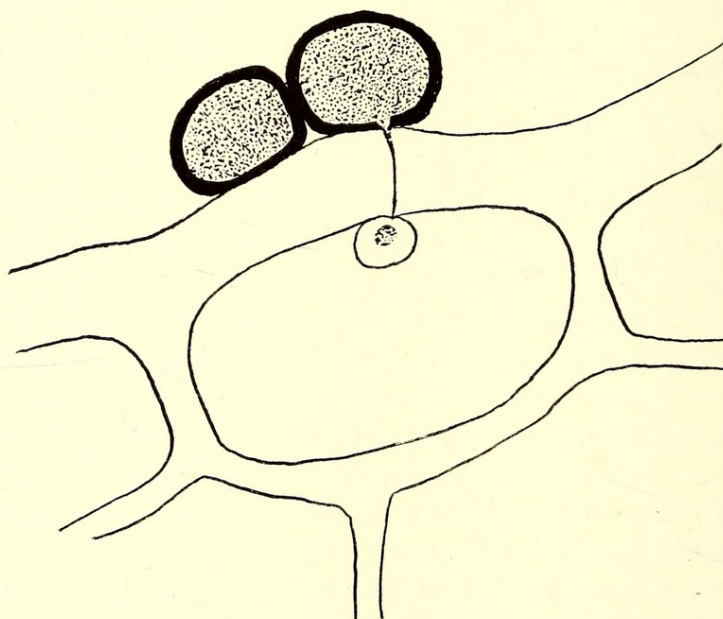


FIG. 2.—Haustorium of *M. arcuata* in epidermal cell of *Viscum anceps* (comp. oc. No. 4).

the brown coloration of the walls of the penetrating filament. The latter may be at right angles to the leaf surface, but is very often oblique and sometimes its course is quite crooked or even tortuous.

Irene puiggarii Speg., which occurs on a number of rosaceous hosts, is

morphologically similar to *I. natalensis*, differing only in minor points in the form of the hyphopodia and spores. It is interesting to find, therefore, that the haustoria are of a different type. Those of *I. puiggarii* have a fine, blue-staining penetrating filament, and a small uninucleate vesicle about $6\ \mu$ diam. in the epidermal cell. The specimen examined was on *Cliffortia strobilifera*, which has not a very thick cuticle, but it is wavy in outline. The difference in the haustoria cannot be accounted for by the character of the host plant, for both species occur on plants with quite a mesophytic type of leaf.

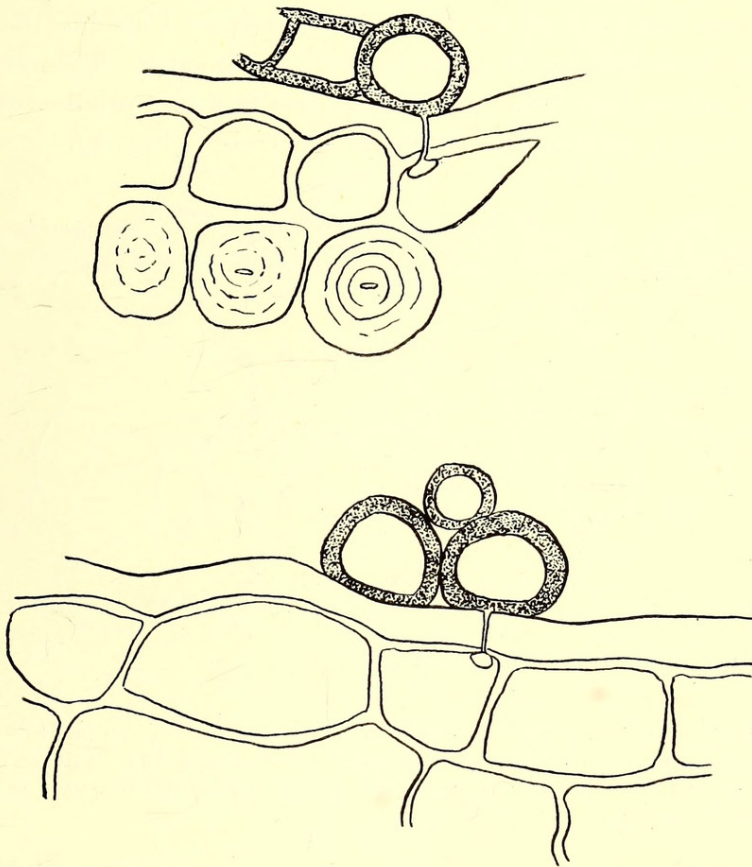


FIG. 3.—*M. Podocarpus* on leaf of *Podocarpus falcata* (comp. oc. No. 8).

Some of the most interesting results were obtained in connection with two fungi parasitic on *Podocarpus* spp., which further emphasise the fact that the form of the haustorium is a specific character, and is not dependent to any great extent on the structure of the host.

Irene podocarpus Doidge is found on *Podocarpus Thunbergii*, *P. falcata* and *P. elongata*, and specimens on the two last-named hosts were examined. This fungus has the most usual form of haustorium, consisting of a thin-walled penetrating filament with a small vesicle in the epidermal cell (Fig. 3). It occurs mostly on the under side of the leaf where the cuticle is not very thick.

Meliola peltata Doidge occurs on *P. Thunbergii* and *P. falcata*; these two species have a very similar leaf structure, while that of *P. elongata* differs considerably, being quite of the ordinary mesophytic type.

The leaves of the first two species have a thick cuticle, especially on the upper side, and just under the epidermis there are one, two or three rows of sclerenchyma fibres. These form a continuous band on the upper surface, but on the lower surface they are interrupted in the neighbourhood of the stomata.

The fungus examined was on the lower surface of *P. Thunbergii*; it closely follows the contour of the leaf, completely blocking the depression above the stomata and pressing on to the guard-cells. This circumstance, which has not been mentioned before, was noticed in a number of the species examined and is apparently of constant occurrence (Fig. 4).

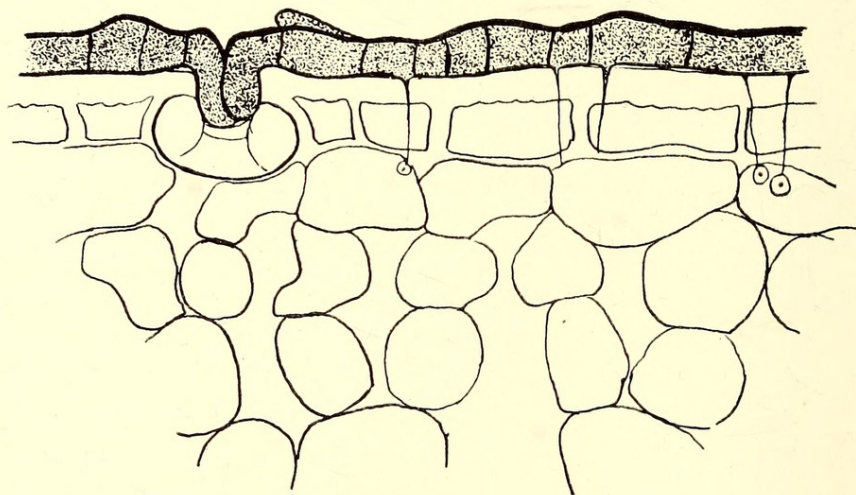


FIG. 4.—Hyphae of *M. peltata* on leaf of *Podocarpus Thunbergii* (low magnification, comp. oc. No. 1), showing five haustoria, and the hyphae following the contour of the leaf into the depression above the stoma, and completely blocking the stoma.

No haustoria were seen penetrating the guard-cells, but numerous thick-walled filaments penetrate the thick cuticle, traverse the epidermal cells, and the sclerenchyma fibres if these are encountered (Fig. 5), and enter the first layer of chlorophyll-containing mesophyll cells. The latter are considerably disorganised and stain deeply with the methyl blue.

Where it begins to penetrate the cuticle the haustorium is slightly bulbous or funnel-shaped, and measures $4.6-5\ \mu$ in diameter (Fig. 6). This diameter immediately below decreases to about $1.5\ \mu$, often continuing to taper slightly till it reaches the mesophyll cell, where it expands into a globular or ovoid vesicle, $4.5-5\ \mu$ diam. The penetrating filament is brown throughout, but becomes paler as it grows away from the external hypha; the vesicle is delicate, hyaline, stains a clear blue, and has a single, central,

deeply staining nucleus. The shortest penetrating filaments, found where the chlorophyll-containing cells were immediately under the epidermis, were $17-20\ \mu$ long; the average length where two sclerenchyma fibres were traversed was $40\ \mu$ (Fig. 6), and in exceptional cases where there were three layers of fibres under the epidermis they were up to $60\ \mu$ long. Cases were observed where the haustorium pierced through the lateral wall of the epidermal cell (Fig. 7).

The haustoria could be readily picked out with the low power of the microscope; fairly thick sections were better than extremely thin ones, as the latter did not show the entire course of the penetrating filament. The filaments were for the most part straight and perpendicular to the leaf surface or somewhat oblique, but a few were curved or even tortuous.

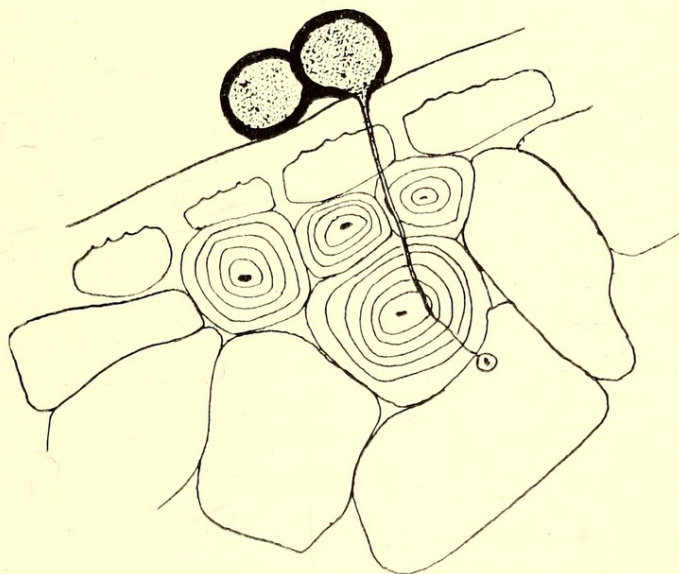


FIG. 5.—Shows the haustorium of *M. pellata* penetrating through two sclerenchyma fibres (comp. oc. No. 2).

The penetrating power of the haustorium is best realised in examining a transverse section, in which the thickness of the walls of the sclerenchyma fibres is most evident (Fig. 5). On the upper surface of the leaf on which the fungus is able to flourish, the distance from the leaf surface to the first chlorophyll-containing cells is often as much as $130\ \mu$.

The other genera of the *Perisporiaceae* are poorly represented in South African species in the National Herbarium. Two of these fungi, *Zukalia transvaalensis* and *Phaeodimeriella capensis*, on careful study proved to be parasitic on *Asterina* spp., the hyphopodiate mycelium described for these two species being that of the host, and the mycelium actually belonging to them forming a weft of pale fine hyphae investing the *Asterina* mycelium. *Zukalia transvaalensis* should therefore be placed in the genus *Perisporium*.

Dimeriella annulata Syd. has a large part of its mycelium internal to the leaf, lying between the cuticle and the epidermis, and therefore does not belong to the genus *Dimeriella* as at present defined.

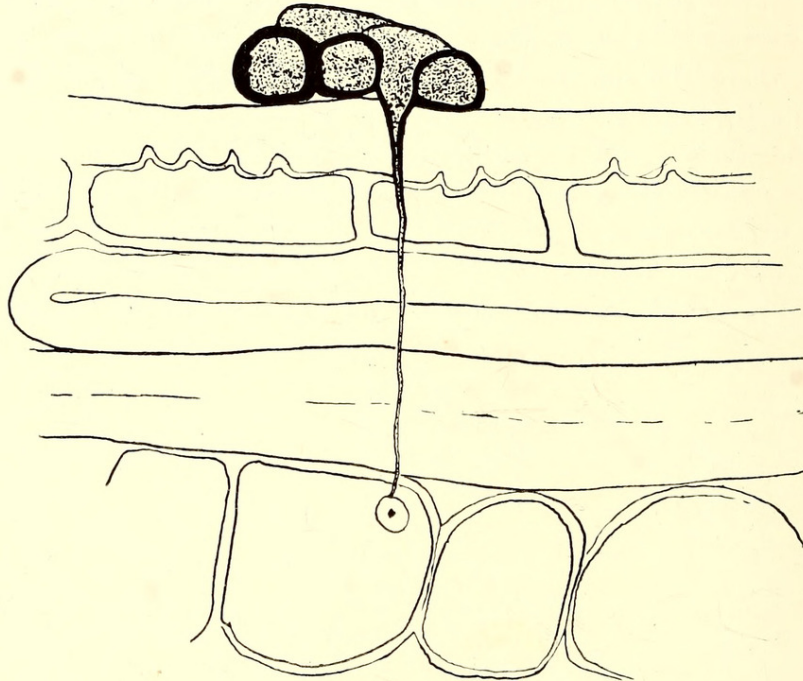


FIG. 6.—Shows sclerenchyma fibres in longitudinal section penetrated by the haustorium of *M. peltata* (comp. oc. No. 6).

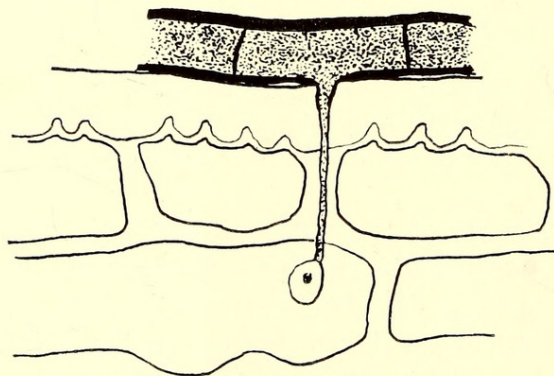


FIG. 7.—Haustorium of *M. peltata* piercing its way through in wall of epidermal cell (comp. oc. No. 8).

Balladyna velutina (B. & C.) v. Höhn on *Kraussia floribunda* and *Dimerium psilostomatis* (Thuem) Sacc. on *Plectronia ciliata* have the same type of haustoria as many species of *Meliola*. The penetrating filament is thin-walled, staining blue, and there is a hyaline, globular, thin-walled uninucleate vesicle in the epidermal cell.

SUMMARY.

The fungi belonging to the genus *Meliola* are true parasites, sending haustoria into the cells of the host.

The most common type is that which has a fine filament penetrating the cuticle and a small, globular, thin-walled, uninucleate vesicle in the epidermal cell.

The nature of the filament, whether hyaline or brown, thick or thin, appears to be a character specific to the fungus concerned, and is not generally, as suggested by Maire, correlated with the thickness of the cuticle to be traversed.

Certain species penetrate through the epidermis, through sclerenchyma cells, if these are present, into the first chlorophyll-containing cells of the mesophyll; but the form of all the haustoria examined was in general the same, consisting of a penetrating filament and a delicate uninucleate vesicle. The differences in different species consist in the length and character of the penetrating filament.

The character of the penetrating filament is of diagnostic value; and may, in some cases, be employed as a determining factor when there is any question of the identity of two species.

The haustoria cause a considerable disorganisation of the cells into which they penetrate, and the mycelium completely blocks many of the stomata. The fungi of the genus *Meliola* must therefore have a prejudicial effect on plants which are heavily infected, especially on the young seedling trees which seem to be generally susceptible.

LITERATURE CITED.

1. BORNET.—“Organisation des *Meliola*,” ‘Ann. Sc. Nat. Bot.,’ xvi, 1891.
2. GAILLARD.—‘Monographie du genre *Meliola*,’ Paris, 1892.
3. MAIRE.—“Les Sucoirs des *Meliola* et des *Asterina*,” ‘Ann. Myc.,’ 6 (1908), pp. 124–128.
4. DOIDGE.—“South African Perisporiales,” ‘Trans. Roy. Soc. South Africa,’ v, Part 6, 1917.
5. GUÉGUEN.—“Emploi du Sudan III comme colorant mycologique, seul, ou combiné au bleu coton et à l’iode,” ‘Bull. Soc. Myc. France,’ xxii, p. 224 (1906).
6. HARPER.—“Ueber das Verhalten der Kerne bei der Fruchtentwicklung einiger Ascomyceten,” ‘Pringsh. Jahrb. für wiss. Bot.,’ xxix, pp. 655–685, 1896.



Doidge, Ethel M. 1921. "SOUTH AFRICAN PERISPORIACEAE." *Transactions of the Royal Society of South Africa* 9, 117–127.

<https://doi.org/10.1080/00359192109520200>.

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