XVI. *On the Morphology and the Development of the Perithecium of* Meliola, *a Genus of Tropical Epiphyllous Fungi.*

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[Plates 42–44.]

During the course of recent researches into the nature of parasitic fungi, my attention was arrested for some time by several forms of epiphytal growths which occupy a sort of half-way position between the more pronounced endophyllous parasites, and those fungi which cannot be looked upon as requiring more than a hold-fast or shelter from their hosts. Among these are the *Meliolas,* a group established by Fries in 1825 to receive certain tropical fungi.* In the 'Annales des Sciences Naturelles' for 1851† is a memoir by Bornet on the species constituting the genus *Meliola,* in which the characters of these remarkable epiphytes are enumerated and examined, and a classification of the known forms proposed: this paper is a standing authority on the subject, and I shall have occasion to refer to it at intervals subsequently, partly to confirm some of Bornet's work, partly to add new observations and correct older views as to the nature or significance of various points.

The *Meliolas* are minute epiphyllous fungi, belonging to the *Pyrenomycetes,* the deep-brown or black mycelium of which appears as sooty patches on many and various plants in the tropics, and presents, roughly, a similar appearance to the masses of *Capnodium* or *Fumago* sometimes observed in European woods on the leaves of living plants.

Though, according to Bornet, several species must have been known under different names to the earlier botanists, the name established by Fries, and published in his revised system, was accepted by Montague and Léveillé and has persisted since: Berkeley, in England, has referred to the group in his 'Cryptogamic Botany,' and has described several species from the tropics in various papers.

* 'Systema Orbis Vegetabilium.'

† Ser. iii., Bot., t. xvi., pp. 257, &c.

The habit of these fungi, and the fact that no true *Erysiphe* had been found among the collections of travellers in the tropics, led FRIES* to insist strongly on the known or supposed analogies between the two genera, and, BORNET following FRIES, the *Meliolas* have thus come to be regarded as replacing the *Erysiphes* in tropical countries—as, in fact, "representative species." BORNET added several facts to those already known concerning the coarser anatomy of the group ; but even his excellent and systematic memoir left large gaps in the knowledge of important details, and practically nothing was known of their development or of the formation of their "fruit-bodies." These and other gaps I hope to fill up to at least a large extent in the present essay.

The appearance of this fungus as presented to the unaided eye, is much the same as that offered by *Asterina* and similar forms, and the reader may be referred to a recently published drawing of that fungus for a tolerably accurate idea of it.† The chief difference is that the black maculæ presented by well developed plants of *Meliola* are more decided and thicker than those of *Asterina;* all transitions are found, however, and, as with many other forms of epiphyllous *Pyrenomycetes*, it is impossible to detect exactly what fungus is present by a superficial examination.

The fungus *Meliola* may be conveniently considered as composed of a mycelium, which supports appendages and perithecia, and which arises from spores developed within the asci of the latter. BORNET considered the "receptacle" as an equally important and distinct constituent, but this is perhaps unnecessary since, as will be shown, the so-called "receptacle" can only be looked upon as a more or less accidental development, so to speak, depending and following upon the formation of the perithecium.

The mycelium, forming the chief part of the black patches found on the surface of the affected leaves, petioles &c., spreads in an irregularly stellate manner from a common centre or centres (see Plate 42, fig. 1). It is detached with comparative ease from the epidermis of the leaf, and bristles with fine, simple or branched, pointed appendages, of a black colour, which spring from the main hyphæ, and from around the subglobular perithecia which are irregularly scattered over the surface.

The main hyphæ constituting this vegetative part of the fungus, are irregularly radiating, sinuous or zigzag filaments, closely appressed to the epidermis of the leaf, &c., and composed of cylindrical joints or cells placed end to end, and branching at angles of about 45 degrees (*cf.* Plate 42, fig. 2, and Plate 43, fig. 5). Their stiff and even brittle walls are deeply coloured brown or black, and thus obscure the view of their contents : sections and reagents prove these to be finely grained protoplasm, with or without oily drops in the interior. The diameter of the hypha is equal throughout,

* 'Sumna Vegetabilium,' p. 406 : "Genus in foliis tropicis vulgatissimum ut *Erysiphes* in terris temperatis."

† Quar. Journ. Micr. Sc., October, 1882, plate 27, figs. 1 and 2. See also BORNET's beautiful figures, Ann. des. Sc. Nat., ser. iii., t. xvi., plates 21 and 22.

the apex being, as a rule, evenly rounded: the cross-septa dividing the hyphæ into cells are firmly marked, thick, and dark-coloured like the outer walls.

The main branches of the mycelium all present the same general characters described above. In many cases, however, the blunt apices of the larger hyphæ, instead of being evenly rounded, become curiously deformed by an accumulation of abnormal growths, of the nature of caps (see Plate 43, fig. 7) fitting roughly one over the other: these consist of swollen, more or less cuticularised thickenings of the cell-wall, with or without granular débris between the layers. They are evidently produced by irregularities in the forward growth of the hypha: in the moist intervals the growing apex, more delicate than the older portions of the hypha, creeps along the surface of the leaf in the normal manner; during recurrent dry and hot unfavourable periods, however, sudden hardening and stoppage of growth causes the accumulation of the caps. That unfavourable intervals in outward circumstances may produce such abnormalities is well seen in the *Saprolegniæ*, and I have in these observed the formation of successive shell-like caps of dense cellulose, more or less altered, and enclosing granular matter between the layers: the caps are coloured blue by solution of zinc-chloride and iodine, the granular débris yellow. These phenomena were by no means uncommon with the hyphæ of *Achlya* and *Saprolegnia* grown, in summer, too long in the same water; of course the pathological changes are produced by different causes in the two cases.*

Besides the main branches of the mycelium, certain small pyriform or flask-shaped outgrowths are given off at pretty regular intervals from the cylindrical cells of the larger hyphæ (see Plate 42, fig. 2, and Plate 43, figs. 3 and 4): in some cases each cell or joint gives off such a short branchlet from each side, in others from alternate sides. More rarely they are absent altogether. In all cases examined the short lateral branchlet arises as a simple bulging out of the lateral wall of the cell: as this proceeds, the bud (as it may be considered) swells out, and its cavity finally becomes separated from that of the parent branch by a firm septum. The long axis of the bud-like protuberance is very generally, though not always directed at an angle of nearly 45 degrees with that of the portion of the main hypha lying nearer the growing point (see Plate 42, fig. 2, &c.): its walls are similarly dark coloured and firm, and it contains fine grained protoplasm much as the cells of the main hyphæ. Morphologically considered, the short lateral outgrowths are undoubtedly of the nature of arrested branches.

In one form of *Meliola*, growing on the leaves of a species of Convolvulus, I have observed a second form of the lateral branchlet (see Plate 43, fig. 4), co-existing with the commoner pyriform type. In this case the outgrowth was longer, narrowed into a sort of neck, and presented the general shape of a Florence flask, seated with its bulged out body on the parent branch. In some specimens, each cell of the latter

* There seems reason to believe that further investigation may throw light on this subject in connexion with the apposition of the cell-wall.

supported two opposite flask-shaped branchlets: in others only one, with or without a pyriform body in addition. Sometimes one or the other type occurred singly and irregularly (fig. 4).

The flask-shaped body is sometimes open at the apex, though I have never succeeded in observing anything emitted from the pore. These flask-shaped appendages recall to mind the peculiar bodies figured by WORONIN in another group of the *Pyrenomycetes* (*Sordaria*),* and although no grounds exist for correlating the two phenomena in detail, the fact is at least worth recording that the lateral pyriform bodies in *Meliola* are capable of subserving reproduction, as will be shown hereafter.

When the hyphæ or branchlets of this fungus are looked upon from above, and a strong light passes through from below, one often observes a minute, circular, bright spot, which appears to shine through the upper wall like a very small oil-drop; on reversing the object, so that the lower side of the hypha comes uppermost, this brilliant pore-like spot appears much more evident, and is clearly due to a thinning in the wall of the under side of the hypha, at a spot where no colouring matter is deposited in the cell-walls, and where the contained protoplasm is placed more nearly in connexion with the outside (see Plate 43, fig. 7, and Plate 44, figs. 21, 40).

BORNET apparently refers to these bright spots when he speaks of oily globules in the interior of the hyphæ,† though he may have been speaking of actual oil-drops developed in the dried specimens with which he chiefly worked. If BORNET's remarks refer to the bright spots here described, the facts of their appearing only on the lower wall, and not being altered by alcohol, &c., remain to be explained.

Taking all the facts into account, the view seems to recommend itself that these bright spots are the points of attachment of the hyphæ to the epidermis; if so, they are to be regarded as *haustoria* of a very rudimentary nature. The mycelium certainly is attached to the surface of the leaf, though but feebly, and it appears suggestive that alcohol specimens are more easily detached than fresh ones, possibly because the protoplasm becomes contracted and rendered brittle. No other anchoring bodies have been observed, and one notes that the position of these brilliant spots accords with that of the well-developed *haustoria* in *Asterina*,‡ a genus of fungi at least allied to the *Meliolas*. These bright points are not always present, and in some cases seem to be normally absent. They are very generally formed at once on germination, appearing on the first short tubes put forth by the spore (fig. 40), a condition of things which may again be compared to what occurs in *Asterina*,§ and also in *Erysiphe* and allied forms.|| Still another point reminding us of *Asterina* and the *Erysipheæ* is the function of the pyriform branchlets; in some cases at

* "Beiträge zur Morph. u. Phys. d. Pilze," DE BARY and WORONIN, ser. iii., plate 5.

† *Op. cit.*, p. 260, and plate 21, fig. 3.

‡ See my description in Quar. Journ. Micr. Sc., October, 1882.

§ BORNET, *op. cit.*, plate 28, fig. 5.

|| DE BARY, "Beiträge zur Morph. u. Phys. d. Pilze," 1870, R. iii., plate 12, figs. 1 and 2.

least, they become detached, and act as vegetative reproductive organs or *conidia*, each putting forth bud-like processes which develop into new hyphæ. BORNET remarked the separation of these buds in *Meliola amphitricha*, and hints at their possibly serving as reproductive bodies much as the *Oidium* forms of *Erysipheæ:* since he worked with dried specimens, however, this question could not be decided.

BORNET remarks that the mycelium on the upper side of many leaves are sterile, while those below and protected from the direct rays of the sun alone support *perithecia:* this is certainly not true for the species examined by me, and, indeed, I cannot determine any difference between the upper and lower mycelia in this respect. Those on the upper surface seem quite as productive of spores, &c., as those below, and in many cases—*e.g.*, those *Meliolæ* so common on *Memecylon*—the mycelium vegetates almost exclusively on the upper surface, and is quite fertile there.

Besides the short pyriform and flask-shaped branchlets described above, the mycelium bears certain stiff, upright appendages of the nature of *setæ* (see Plate 42, figs. 1, 41, and Plate 43, fig. 8): these *setæ* spring from the cells of the hyphæ at various points in their course, and, from their position and mode of origin, are probably to be regarded, morphologically speaking, as lateral branchlets which become elongated in a direction more or less perpendicular to the plane of the leaf. Such a *seta* grows very rapidly and soon reaches its limit: the cylindrical cells composing it are relatively longer than those of the hyphæ, but resemble them in other respects (the walls being, perhaps, somewhat stiffer and more deeply coloured) and taper above, in the simple types, or become variously branched.

In most *Meliolas* the *setæ* are especially aggregated around the perithecia, forming circles of stiff radii springing from what BORNET terms the "receptacle": they are also developed, however, from various isolated points of the mycelium bearing no direct relation to the fruit-bodies.

The forms of the *setæ* vary from a simple, upright or curved filament, to structures branched like antlers, trifurcate, twisted, &c., at the tip (*cf.* Plate 43, fig. 8 and BORNET'S figures*): BORNET has made use of these details in classifying the formal species, and although it is doubtful whether the more similar types are constant, there can be no objection to their use much in the same manner as the appendages of *Erysipheæ*, &c., are used to distinguish the forms of that group. BORNET regards the origin of the *setæ* at points on the mycelium as marking out places where new *perithecia* are to be developed: I cannot say that this idea is altogether a false one, but investigation of the development of the fruit-bodies seems to show that at least no necessary connexion exists between the two phenomena.

As to the function of the *setæ*, little or nothing can be stated. The earlier suggestions of SPRENGEL and FRIES (as quoted by BORNET) that they may be organs for the exit of the spores cannot be accepted: not only on the ground of the disproportion

* *Loc. cit.*, plates 21 and 22, figs. 6, 15, 16, &c.

between the numbers, but also because the spores are too large to pass through the *setæ,* even supposing the cavity continuous and ending in an ostiolum, which is not in the case. I have often tried to discover *conidia* or other bodies in connexion with the *setæ,* but have been forced to the belief that they have no function whatever connected with spore-production. One is not now impressed with the necessity for assigning any special function to such structures: if the *setæ* are merely free-growing branches of the otherwise appressed, creeping mycelium, there is nothing surprising in the fact that some differences in form and consistency are correlated with their sub-äerial habit. This is at least no more remarkable than that the looser branches of an alga, like *Coleochæte,* should have a facies slightly differing from that of the cell series comprising the lower, creeping, appressed parts of the thallus.

The collection of *setæ* immediately around the "fruit-body" simply results, immediately, from the vigorous development of hyphæ which accompanies the later stages of formation of the perithecium: this mass of setigerous hyphæ, which seems comparable with the formation of *haustoria* and such-like organs in other fungi during the fruit development, was called the "*réceptacle*" by BORNET. As to a possible protective influence of the circles of *setæ,* the question must be left open until we know more of the conditions: in some cases, at any rate, the *setæ* do not arise until the perithecium is completely formed, and the spores nearly ripe.

The perithecium, when completely developed, is a globular or sub-globular body, consisting of a shining black or brown external case, the outer thick walls of which appear regularly embossed, and an internal mass composed of asci and spores, &c. The embossed pattern on the outer walls results from the thick-walled cells, of which it is composed, projecting at their free surfaces: where the cells join each other forming polygonal figures they do not so project.* What may be termed the base of the perithecium is sessile on the mycelium: at the opposite pole, or apex, is frequently a slight papilla, not obviously pierced by any pore. BORNET, noting this fact, imagines that the dehiscence takes place below, the whole upper part of the perithecium becoming broken away by a circular rupture at the base. In some forms, at least, the spores escape through an opening at the apex: how far this is general I do not know (Plate 42, fig. 43), but facts exist to render it probable that a minute and dilatable pore occurs in others.

Vertical sections of the mature perithecium show that within the firm, deep-coloured, external wall is a lining of softer cells, with swollen envelopes and of a more or less flattened form: this inner lining of the perithecium extends two or three cell-series deep, and is slightly yellow or pale-brown in colour (see Plate 44, fig. 33, and Plate 42, fig. 34). In the cavity thus enclosed are the groups of asci in various stages of development: these delicate, clavate sacs contain spores, or have emptied them into the semi-gelatinous, granular matrix around. With these preliminaries, I may pass on to consider and describe the development of the perithecium, as followed

* See BORNET's figures, *loc. cit.*, plates 21 and 22.

step by step on a species of *Meliola* which I have investigated with no slight success:* this will be found to throw light on the morphology of these fungi from the best of sources—development—and aid in a more critical estimation of their proposed systematic position. After describing in detail the origin, mode of development and fate of the fruit and spores, I propose, therefore, to examine the relations of the *Meliolas* to *Erysiphe* and other fungi.

On examining portions of the epiphyllous mycelium bearing the short, pyriform, lateral branchlets so often referred to above, one frequently discovers specimens presenting the appearances depicted at figs. 9, 10, 11, &c. The simple pyriform body, after becoming more swollen, has suffered division into two portions or cells by a septum, usually vertical to the plane of the mycelium and leaf, and passing diagonally across the cavity with a slight curve, so as to abut on the outer walls at right angles, or nearly so. The originally unicellular protuberance becomes in this manner divided into two more or less unequal cells, and it will be shown in the sequel that these two cells have, from the first, each a different destiny in the formation of the fruit. For this reason I have indicated in the drawings, by shading, a difference which does not present itself in the natural object at this stage. The more apical cell, which is smaller and shaded darker in fig. 9 (Plate 42), may be indicated throughout by the letter A: it will be found that this cell produces the central ascogenous tissue of the young perithecium, while the other (which will be referred to as cell B) originates the outer portions of the case or perithecium wall.

Following close upon the preliminary division above described, a septum appears across the larger of the two cells, cutting the first-formed division wall at right angles, or nearly so: this is rapidly followed by another septum (Plate 43, fig. 10), and so the larger cell (B) becomes cut up into three. Following upon these, a number of further divisions in planes at right angles to the preceding are soon established (figs. 11 to 17), and at the same time, though much more slowly, one or two more division walls are formed in the cell A, thus cutting it up into a short series of about three cells (figs. 14, 15).

If the above description has been followed, it becomes clear that the division of the more rapidly growing cell, B, results in the production of a sheet of cells affixed, so to speak, to the few-celled mass resulting from the slow division of A: such being the case, and the sheet extending as new divisions are formed, the cells resulting from A become gradually enveloped more and more in those resulting from B. A comparison of the figs. 9 to 17 will facilitate matters here, and for convenience of description hereafter, and in consideration of its destiny, we may term the mass of cells produced from A the "*ascogenous core*"—or simply the core.

At a stage which may conveniently be considered the next one to fig. 11, the cells resulting from the division of B are observed to be extending as a curved layer over the "core" of cells formed by A. If, at this stage, the young fruit-body is cut off,

* I must take this opportunity of thanking Professor DE BARY for kind suggestions with respect to this work.

and allowed to roll over in fluid under the microscope, the form and arrangement are found to be somewhat as sketched in fig. 12 (Plate 43), where *a* represents the view from below, *b* that from the side, and *c* an end elevation of the structure. The cell A, in fact, is becoming gradually enfolded by the layer of cells derived from B, a process which results, at a later period (Plate 43, fig. 17) in the almost complete tucking in of the "core" as the centre of a subglobular mass of cells.

As this process of "invagination by epiboly" (as it would be termed in the case of an embryo) goes on, the "core" has been more slowly cut up into cells—at first by walls perpendicular to its long axis, and then by septa in other planes at right angles—and the sub-globular body thus produced lies with the open part towards the epidermis.

After this period, two events occur: 1st, the cells of the "core," possessing very thin walls, acquire a different aspect from those of the outer shell; their finely granular protoplasm makes them appear denser and more opaque, shining through the latter until this becomes too thick to be transparent; 2nd, the open part of the growing perithecium becomes closed over, and the internal structures can no longer be made out without the aid of actual sections. At this point my observations have failed to decide which of two possible modes of growth take place: Is the covering in of the "core" completed simply by the extension and closing in of the edges of the outer layer; or are cells, cut off from the "core" below, intercalated, so to speak, into the open gap? One is led to expect by analogy that the former process takes place, but some events lead to the suspicion that such may not be the case.

At the stage corresponding to fig. 19 (Plate 43), the young perithecium appears almost opaque, very little light passing through the dark-coloured and thick outer walls; from below, however, the larger cells composing the "core" can be readily seen in the optical section, shining by means of their dense, fine-grained contents through the shell. In the next stages, the "core" can only be seen dimly through the outer envelope (Plate 44, fig. 20), even after treatment with reagents, or, as in figs. 21 and 22, after cutting or tearing off some of the outer cells.

Nothing but a fortunate vertical section through the young fruit at or near this stage will decide finally whether the lower side is covered in by the meeting of the outer shell edges, or by partial "delamination" from the lower side of the "core," and this I have not succeeded in obtaining. The thick, dark outer walls have now become so opaque, that optical sections fail to determine the course of events; and treatment with reagents does not afford evidence sufficiently satisfactory to decide the questions, since it seems impossible to remove the colouring matter. Potassic hydrate or weak acids do, it is true, render the structures a little more translucent after some time; but even the extreme resort of heating in weak chromic acid has only yielded partial results, and with this slight information on the point I have reluctantly been compelled to content myself for the present. A comparison of figs. 17 to 21 certainly suggests that the process of envelopment is completed by the outer layer of cells

derived from the repeated and rapid division of the cell B, and this view may be recommended on the ground of analogies with the *Erysipheæ*, to be examined hereafter; but, while figs. 19 and 20 by no means decide the point, we shall find that in the perithecium of another species of *Meliola* (or an allied form) the construction almost certainly proceeds by continued cutting up and "delamination" of the results of division of one cell.

Be this as it may, the young perithecium now consists of the following parts:— A central "core" of delicate-walled, colourless or yellowish cells, very rich in finely granular protoplasm, and, surrounding this completely, a single layer of cells with thick, hard, dark-coloured walls (especially those on the exterior surface); the whole mass is attached to the hypha from which it originated by a very short pedicle or joint (see Plates 43, 44, figs. 19–24).

At a period slightly later than the above, the cells of the outer layer are becoming multiplied by tangential walls, and those of the inner core by radial and horizontal divisions: these processes go on for some time, until the whole perithecium is a complex of many small cells, the outer of which become firmer and darker-coloured, the inner delicate and full of fine-grained protoplasm as described.

No trace of the internal structure is, however, visible now from the outside. On isolating a perithecium at this stage—a matter of no slight difficulty, but practicable with a slender knife used under a low power of the microscope—it presents the forms shown in fig. 25 (Plate 44), on being rolled over. Above, the outer surface curves equally away from the centre, and the slightly projecting walls of the cells give it an appearance of being embossed (fig. 25, *x*.). From below (fig. 25, *y*), the object looks very different; the surface is much flattened and nearly circular, and from many of the cells are processes developing as hyphæ in all directions. These radiating processes creep close along the surface of the leaf, to which the fruit-body is also appressed, and no doubt serve to give a much firmer hold for the fruit; at first their thin walls are only of a pale brown hue, but rapidly acquire the thickness and deep colour of the fruit and mycelium. Seen from the side, the young perithecium presents the appearance sketched at fig. 25, *z*. It is these radiating anchoring hyphæ which form collectively what BORNET terms the "réceptacle," and from them, at a later period, the bristling *setæ* found around the mature fruit are developed.

From the stage just described the development of the fruit-body proceeds rapidly; but, since the objects now become of a more manageable size, I have been able, by actual sections through the perithecium embedded in spermaceti or gum, or, better still, in elder pith, to obtain some insight into the processes going on even in the centre of the mass of cells.

At stages just prior to the one last described, the central core of thin walled cells—which it will be remembered has been derived from continuous divisions of the cell A—is commencing to divide up by septa in several directions (figs. 23, 24), while the outer layers surrounding this—derived primitively from B, and, possibly, in part from

A—are divided more regularly by tangential walls, followed by radial ones at right angles as the area enlarges. As the increasing small and delicate cells of the core become formed more rapidly, a certain tendency at least to a regular arrangement can be recognised in the later stages, as shown in such sections as figs. 28 and 29, (Plate 44), and fig. 27 (Plate 42): this regularity becomes interfered with by the mutual pressure of the cells, and the outer ones, of which the walls are especially soft and swollen, become flattened and pulled in the tangential direction, and only marked by the very granular yellowish protoplasm in their diminishing cavities. In the central lower part of the core, vertical sections at this, and slightly later stages, show that certain cells, with very delicate outlines and finely granular refractive contents, maintain their larger size and upright arrangement, and are by these peculiarities well distinguished as a special group or tuft of cells (see Plate 44, fig. 28 and Plate 42, fig. 31). In oblique (Plate 44, fig. 29) and horizontal (fig. 30) sections passing through the lower third of the developing perithecium, they can also be readily distinguished by their special peculiarities, and no question can be entertained as to their significance in the formation of the essential parts of the fruit-body. This group of cells is the forerunner of the young asci, and may be termed the *Ascogonium.*

As development proceeds continuously, the outermost layers acquiring thicker and more deeply coloured walls, the above named group of upright cells become relatively larger, increasing slowly in number by a few divisions, while the diffluent, compressed cells between them and the outermost layers slowly give up their contents, and become reduced to mere granular streaks embedded in a jelly-like mass of swollen and fused cell-walls (see Plate 42, fig. 31). This process is exactly comparable to what takes place in the developing embryo-sac of certain phanerogams,* or of the pollen mother cells in the anther,† in so far as the larger cells clearly develop at the expense of material derived from those around.

The tuft of successful cells thus nourished is, in fact, the "ascogonium" of this fungus. At a slightly later stage than the one last figured, the space formerly occupied by the deliquescent remains of small cells is filled with an almost transparent semi-fluid mucus, in which a few bright granules are embedded; while the lower part of the perithecium contains a tuft of asci in various stages of development (see Plate 44, fig. 33), and which have evidently proceeded from the large cells of figs. 28 and 31 (Plates 44 and 42), which have devoured all, or nearly all, the smaller soft cells surrounding them.

Sections of perithecia at a stage between those shown in figs. 31 and 33 (Plates 42 and 44) have not been obtained, but enough evidence has been secured to enable me to conclude that the asci are the direct result of the transformation of the elongated upright cells of fig. 31 (Plate 42), which are nourished at the expense of the cells of the inner layers. Partly from the brittle nature of the outer walls, enclosing a space

* *Cf.*, amongst others, STRASBURGER, 'Angiospermer und Gymnospermen.'

† *Cf*, STRASBURGER, 'Bau und Wachsthum der Zell-haute,' 1882.

filled with almost fluid contents, and partly from the extreme delicacy of the young asci, I have been unable to decide whether any distinct branching of the ascogenous cells precedes the formation of the definite asci: probably such is the case. We have now followed the development of the perithecium to the period when it may be considered ripe: a period of some duration, since the asci are continually and successively formed in the tuft for some time.

Fortunate sections of the perithecium wall at this stage have yielded the following information. In the centre of the apical wall, where a slight protuberance sometimes occurs, the cells of the inner wall are found to radiate towards a pale translucent spot or pore (see Plate 42, fig. 36), and although I have not been able to obtain sections exactly through this, and am therefore unable to affirm positively that it is an actual pore, there seems little doubt that this is at least the weak point through which the spores escape from the ripe perithecium, no doubt forced through by the swelling of the materials around. BORNET* believes that the perithecium opens by a circular rupture at the base: I have tried to confirm this, but failed, and am strongly persuaded that the apical spot figured is the point of exit for the spores. That a minute pore should escape observation from without is not remarkable: the reflection of the light from the black shining outer cells might easily obscure it. The general structure of these walls has already been described, and fig. 34, drawn from an extremely fortunate and very thin section, shows the details.

The very young ascus presents no features of importance to distinguish it from that of many other pyrenomycetous fungi. In its earliest state it is recognisable as a single thin-walled, club-shaped cell, tapering to a point at the lower attached end, and filled with finely granular, yellowish protoplasm (see Plate 44, fig. 37, *a.*): sometimes a small pale, refractive nucleus-like point is seen in the protoplasm. As the young ascus grows longer, and its protoplasm increases in quantity, a fine, sharp division line makes its appearance somewhat oblique to the long axis of the whole (fig. 37, *c.*); this is soon followed by a second, similar longitudinal division, in a plane at right angles to the former (fig. 37, *d.*), and four well-defined masses are thus marked out. These, the young spores, do not include the whole of the protoplasm (fig. 37, *d.* and *f.*), but lie in a scanty matrix of granular matter, closely opposed face to face, and following the curve of the enlarging ascus wall on their outer walls.

As the four, almost fusiform young spores increase in size, and acquire more distinct membranous envelopes, they come to lie somewhat more loosely in the cavity of the ascus, and may cross one another in accommodation to the space at disposal. Then appear cross-septa (fig. 37, *e.*, *f.*), dividing the material of the spore into a number of compartments varying from three to five—or, in one case, a single septum only is formed—and vacuoles and granules appear in the hitherto almost homogeneous contents. As the spores ripen, their cross-septa become more firmly marked, their outer walls thicker, and, gradually brown or nearly black in colour, like the hyphæ of the

* *Op. cit.*, p. 261.

developed mycelium ; the side walls of the separate compartments also become bulged out slightly, giving the mature spore the appearance of a long oval body, constricted at intervals (see Plate 42, fig. 39). Very commonly one or two oily-looking drops accumulate in the compartments of the ripe spore.

Such is the typical mode of development of the perithecium, asci and spores. I have found no modifications of importance from a morphological point of view; it should be recorded, however, that the number of spores in the ascus varies from two to eight. Sometimes in the same perithecium one finds asci in which one, two, or three spores develop at the expense of their presumably weaker neighbours (fig. 38), in other cases the number two appears constant, only one complete division occurs in the ascus (fig. 38), while in one case to be referred to later, the asci normally produce eight two-chambered spores (Plate 42, fig. 43).

On germination, which may take place soon after their emission from the ripe perithecium, the spores seem to behave generally in the same manner; one or several simple protuberances emerge from any of the partitioned chambers (see Plate 42, fig. 40), and proceed to develop into a typical mycelium, often with a preliminary formation of the rudimentary haustoria referred to in an earlier part of this paper. This mycelium grows rapidly in moist weather, forming branches, *setæ* and fruit-bodies as before. In some seasons the leaves of various plants may be seen covered with hundreds of these young mycelia, which dry up when the atmosphere does, only to renew their growth with the rains.

Before passing on to the consideration of the pathological influence of these fungi, and of their systematic position, I will record a few details concerning a form of *Meliola* which varies somewhat from the typical cases hitherto considered; at any rate, it seems to differ more from the six or eight forms to which the above description refers, than they do among themselves.

The species to be examined has only been found on the leaves of *Pavetta indica*, and its mycelium forms more spreading and less defined patches on the leaves of that plant, than the easily recognisable sooty patches of the other *Meliolas*. The main features of its mycelium, &c., are shown in fig. 41, and differ chiefly in the delicate straggling hyphæ, with a paler brown colour and no trace of haustoria. The branching is very irregular, and somewhat like that of the form figured at fig. 3, but the short, lateral branchlets are not always ovoid, but often have sinuous, almost angular outlines, reminding one of the similar structures in *Asterina*, except that the latter bear distinct haustoria. The *setæ* are here quite simple, short, and not so hard and brittle as usual; they are also produced in smaller numbers than in the more typical species.

The greatest peculiarities, however, are offered by the fruit-bodies, or perithecia. Each of these arises as before by the successive dividing up of a short, lateral branchlet (Plate 44, fig. 42), with this difference, that the rapidly following septa permit no recognition of primitive cells destined to form the outer walls, ascogonium, &c., as before.

After a few radial, vertical, and horizontal walls have been formed, tangential septa (fig. 42, *d.*) make their appearance cutting out series of cells which are to form the outer walls, and which become firmer and more deeply coloured, from an inner cell mass which gives rise to the ascogonium much as before. Only a few asci are formed, in each of which arise eight small oval uniseptate spores, which acquire a pale brown colour as they ripen (fig. 42, *f.*, and Plate 42, fig. 43).

The mature perithecium is shaped like a pear or top, the broad end attached to the hypha by a short pedicel, the narrow free end, or apex, becoming thin and diffluent in order to allow of the escape of the spores (fig. 43). Very few or no *setæ* are formed around the perithecium, and these of the same simple type as those scattered on the mycelium (Plate 42, fig. 41). The whole structure of the fruit-body is, therefore, much simpler than that of the above described forms, and, from the semi-translucent characters of the thinner cell-walls, allows the main details to be made out by optical sections only. In some of the dark-coloured cells of freshly prepared specimens, a bluish tint is often observable; I have not seen this in any other similar form.

In no case have I succeeded in tracing a distinct alterative or destructive action of the *Meliolas* on the cells of leaves to which they are attached. In many instances, as, for example, thick leathery leaves like those of *Memecylon capitellatum*, &c., the haustoria seem to have no function beyond that of holdfasts; in others, such as *Pavetta*, *Triumfetta*, &c., attacked leaves certainly suffer from the presence of the fungus. Nevertheless, I cannot trace this to any direct action of the mycelium; the contents of the cells show no effects which can be regarded as due to the fungus mycelium directly. We must conclude, therefore, that where the life of the leaf is interfered with at all, it is indirectly; the dense crust of a well-developed *Meliola* no doubt obstructs the play of physiological functions in an obvious manner, by obscuring it from light, blocking up stomata, &c.

It is now possible to consider the question of the systematic position of these remarkable and interesting fungi. BORNET,* following FRIES and LÉVEILLÉ, places *Meliola* near the old group of *Sphaerias*, with especial reference to *Erysiphe*. I have already quoted the view of FRIES that the *Meliolas* may be considered tropical representatives of our *Erysipheæ*, and BERKELEY† takes the same position. These opinions appear to have been based simply on the resemblance in habit and the more obvious anatomical characters, and on the fact that no *Erysiphe* is known in the tropics.

The detail of structure, and especially of the development of the fruit-bodies above described, enable us to criticise these views from a somewhat firmer standpoint.

Apart from minor points of resemblance between *Meliola* and the typical *Erysipheæ*, such as the haustoria (not well developed in *Meliola*), the asci, &c., there can be no question as to certain points of agreement in the structure and development of the perithecia; nevertheless, the origin of the fruit-body in the two groups is not obviously similar, and at first sight the differences may seem greater than they really are.

* *Op. cit.*, p. 266. † Introd. to 'Crypt. Bot.,' p. 275.

In the typical simpler *Erysipheæ*, such as *Podosphaera*, as is well known from DE BARY's classical researches,* the "*carpogonium*" and "*antheridium*" arise each as a short lateral branch from separate hyphæ, at the point where two hyphæ cross: each becomes cut off by a septum, which is formed close to the parent hypha in the case of the pyriform "*carpogonium*," and about half way up the curved "*antheridium*" branch. The free end of the latter becomes closely applied to the top of the *carpogonium*, and fertilisation—possibly not complete in a physiological sense, however—is said to be complete. After this process numerous branchlets arise from the base of the *antheridium* filament (and also from the base of the *carpogonium*), grow rapidly and with numerous segments, and invest the *carpogonium*, which meanwhile begins to be (more slowly) cut up into cells.

In *Eurotium*† we have an essentially similar process, except in minute details, and the *antheridium* is a branch springing from the same hypha which bears the *carpogonium*, and arises just beneath the latter. Here, as before, the perithecium envelope is formed chiefly by the rapid overgrowth of cells derived from the *antheridium* branch. It is quite conceivable that a form allied to *Erysiphe* and *Eurotium*, &c., might have the unicellular *carpogonium* and *antheridium* arising quite in contact at their bases from the same branch.

If we now compare the above with the succession of events in the development of *Meliola*, the following points of analogy seem to me sound. The original pyriform branchlet—containing in itself, so to speak, the elements of the fruit-body—after the first division (Plate 42, fig. 9), may be considered as establishing morphologically an "*archecarpium*"‡ and an *antheridial branch*—or the latter may be considered as containing in itself the *antheridium*, *plus* the elements of the perithecium wall.

If the cells A and B (fig. 9) became further developed, and diverged at their apices, we should have no difficulty in seeing these points of homology.

Thus much cannot but be allowed. The cell A resembles a true *archecarpium* in so far that it slowly produces the ascogonium and asci; the homology will not be weakened, but the contrary, if further research shows that part of the perithecium wall results from cells derived from A. The cell B so far acts as an *antheridium* branch in that it is closely applied to A, divides up more rapidly, and thus produces most—*perhaps all*—of the perithecium wall.

The above may possibly suggest some difficulties to those who have not followed the recent progress in our knowledge of sexual organs and their homologies in the lower fungi. It has of late been shown to be not improbable, but on the contrary very likely, that we should view the *Erysipheæ* as a group connecting the higher *Ascomy-*

* "Beitr. z. Morph. u. Phys. d. Pilze," R. iii., 1870.

† *Cf.* DE BARY, *loc. cit.*

‡ DE BARY, Beiträge IV., proposes to use this word as denoting that part of the body which becomes the ascus and pedicel in *Podosphaera*.

cetes, on the one hand, and the *Phycomycetes** (*Mucor, Peronosporeæ* and *Saprolegniæ*) on the other: the evolution of the latter group seems undoubtedly attended by a fusion of parts before separated—a withdrawal of the sexual organs, so to speak, into one another,—and DE BARY has followed this out with marvellous skill and success in a number of forms passing from *Pythium,* through the *Peronosporeæ,* to certain *Saprolegniæ,* in which the male sexual organ ("*antheridium,*" "*pollinodium,*") is normally suppressed. Whether or not we suppose, with DE BARY, that the *Erysipheæ* took origin from some *Peronospora*-like form, it seems reasonable to look upon *Meliola* and its immediate allies as a branch group derived from the *Erysiphe* stem, either from the ancestor of *Erysiphe* itself or from ancestors which gave rise to *Eurotium* and *Erysiphe,* and that this group has become developed in tropical lands along lines more or less parallel to those along which the European forms have proceeded in temperate climates, being, in fact—though not in the strictest sense perhaps—"representative species." Be this view entertained or rejected, I am strongly impressed with the necessity for further and closer investigation of the very remarkable group of fungi centering around or near the *Meliolæ,* since they will probably fill up yet more completely the gap—partially bridged over, it is true—between the lower and higher *Ascomycetes.*

DESCRIPTION OF PLATES.

Fig. 1. *Meliola* sp. with portion of epidermis of *Memecylon.* On the mycelium are *setæ,* branchlets, and fruit-bodies in various stages of development.—ZEISS D.

Fig. 2. Mycelium of another species of the same, found on the leaves of *Schutereia* (*Conv.*), with portion more highly magnified.—GUNDL. $\frac{1}{3}$ and ZEISS D.

Fig. 3. Portion of mycelium of a species of *Meliola* on *Triumfetta* (*Tiliaceæ*).—ZEISS D.

Fig. 4. Portions of more advanced mycelium of fig. 2 more highly magnified, and showing various forms of lateral branchlets.—ZEISS J.

Fig. 5. Portions of mycelium on *Memecylon* showing mode of branching and young fruit-bodies.—GUNDL. $\frac{1}{3}$ and ZEISS D.

Fig. 6. Vertical section through portion of mycelium where fruit-body is being formed. The section is not median.—ZEISS J.

Fig. 7. End of hypha with three cap-like thickenings and pore-like spot (*haustorium*?) seen from below.—ZEISS J.

Fig. 8. Various forms of *setæ* in plan and elevation.—ZEISS D and J.

* *Vide* DE BARY, "Beitr. z. Morph. u. Phys. de Pilze," R. IV., 1881.

Fig. 9. End of hypha (with one cap-like thickening) bearing lateral pyriform branchlet which is to become a Perithecium. The first oblique septum has already appeared, the smaller cell (A) represents the ascogonium, &c., and is shaded darker; the larger one (B) will divide up more rapidly, and enclose the cell A and its progeny.

Figs. 10 and 11. Further stages in the development of the young Perithecium. The cell B is becoming divided.—ZEISS J.

Fig. 12. Young Perithecium seen from below (*a.*), from the side (*b.*), and from one end (*c*). In all, the dark cell is the one marked (A) in fig. 9; the remainder have resulted from the growth and division of the cell (B.)—ZEISS J.

Figs. 13 and 14. Slightly later stages seen from below. The cell (A) has become divided by a cross septum.—ZEISS J.

Figs. 15 and 16. Similar preparations seen from above and below.—ZEISS J.

Fig. 17. Somewhat more advanced Perithecium seen from the side. The cells resulting from the division of A ("ascogenous core") are seen through those formed by B, which are growing over them.—ZEISS J.

Fig. 18. Somewhat more advanced stage.—ZEISS J.

Fig. 19. Slightly later stage. The upper figure is seen from above, the lower from below: the latter shows the "ascogenous core."—ZEISS J.

Fig. 20. Similar preparations seen from above (lower figure) and below (upper figure.) —ZEISS J.

Figs. 21 and 22. Slightly advanced Perithecia cut by the razor. The "ascogenousc ore" is exposed at the cut parts.—ZEISS E.

Figs. 23 and 24. Similar preparations treated with chromic acid. The "ascogenous core" is seen enveloped by the cells forming the Perithecium-wall: all much swollen, and fig. 23 slightly crushed.—ZEISS J.

Fig. 25.—More advanced Perithecium seen from outside and above (*x.*), below (*y.*), and from the side (*z.*). The radiating hyphæ (réceptacle) spring from the external walls below.—ZEISS E.

Fig. 26. Portion of mycelium with young Perithecium seen from above and below.—ZEISS E.

Fig. 27. Somewhat older Perithecium. The razor has cut off one side obliquely. —ZEISS J. (camera).

Fig. 28. Vertical section through young Perithecium about this stage. The ascogenous cells in the middle are distinguished by their larger size and arrangement. —ZEISS J.

Fig. 29. Oblique (nearly horizontal and median) section through the same.—ZEISS J.

Fig. 30. Horizontal section above the base of same.—ZEISS J.

Fig. 31. Somewhat older stage in vertical section. The ascogenous cells in the centre are enlarging at the expense of those around.—ZEISS J.

Fig. 32. Portion of outer wall with disorganised cells lining it.—ZEISS J.

Fig. 33. Vertical section through nearly ripe Perithecium, showing asci and spores embedded in the gelatinous mass produced by the disorganisation of the unemployed cells.—ZEISS D.

Fig. 34. Portion of outer wall of latter in vertical section.—ZEISS J.

Fig. 35. Vertical—not median—section through ripe Perithecium (and portion of epidermis of host-plant), showing crowds of spores.

Fig. 36. Thin slice from top of similar Perithecium. A pore-like spot is seen in the centre of the radical marking.

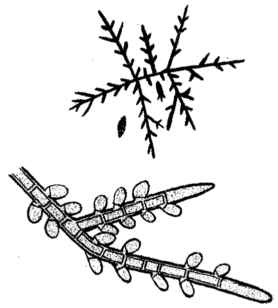
Figs. 37, 38 and 39. Various stages in the development of the asci and spores.—ZEISS J.

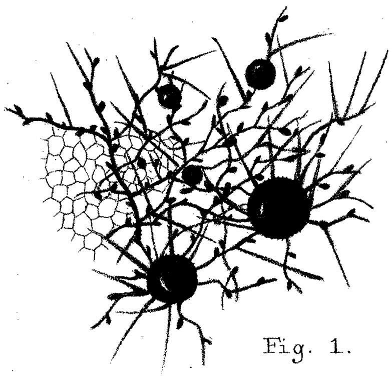
Fig. 40. Germinating spores.—ZEISS D. and E.

Fig. 41. Portion of mycelium of a species of *Meliola* found on *Pavetta,* showing mycelium, *setæ,* and young Perithecia.—ZEISS J. and D.

Figs. 42 and 43. Development of Perithecia and extrusion of spores.

Fig. 2.





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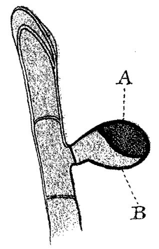

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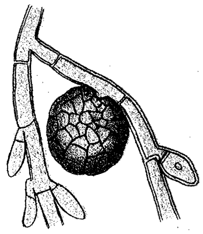

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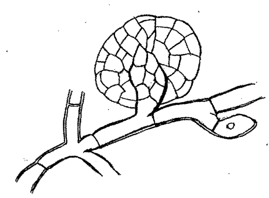

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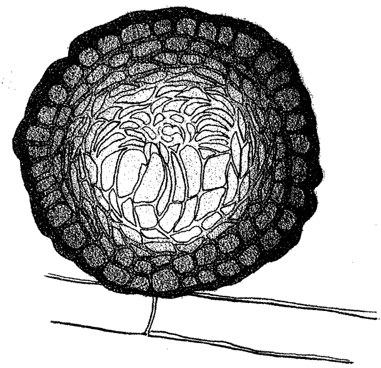

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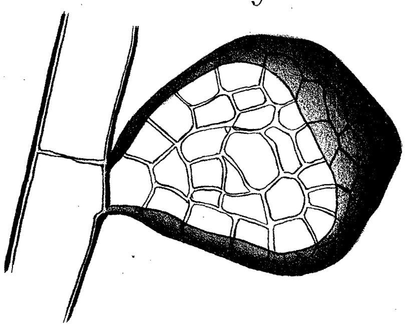

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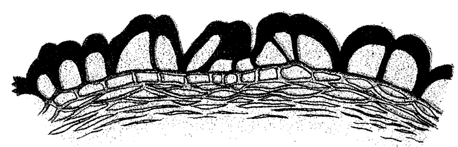

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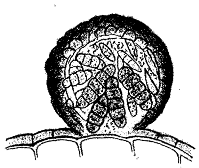

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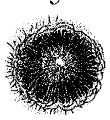

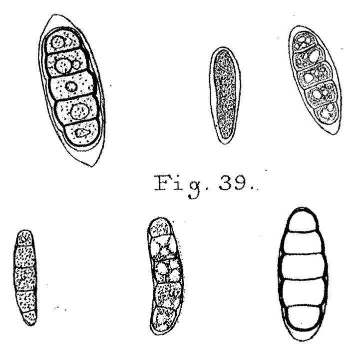

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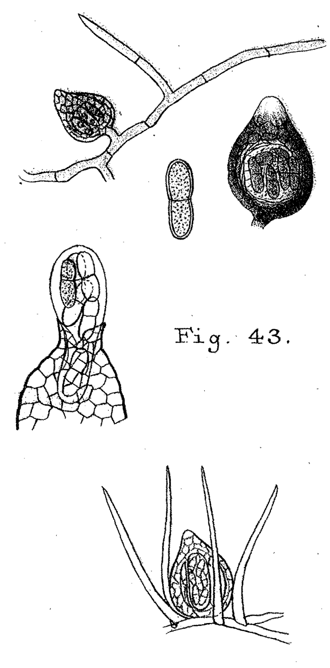
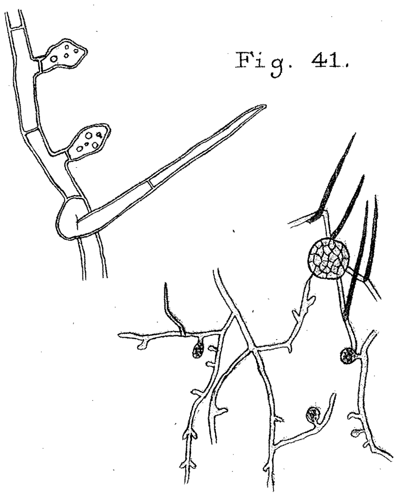


Fig. 43.

Fig. 41.



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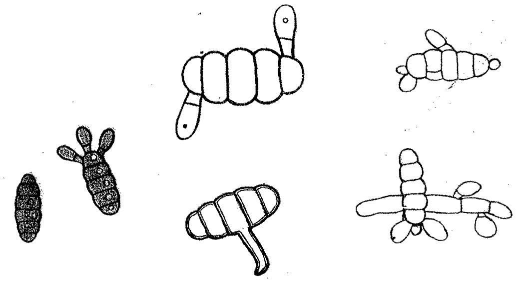

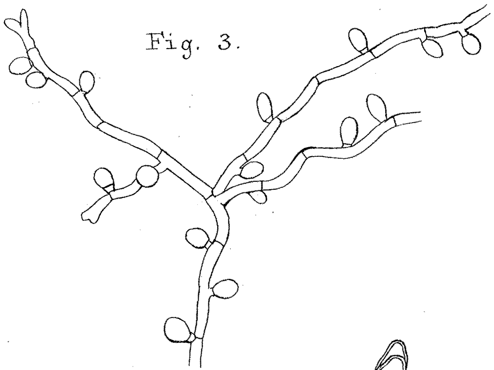

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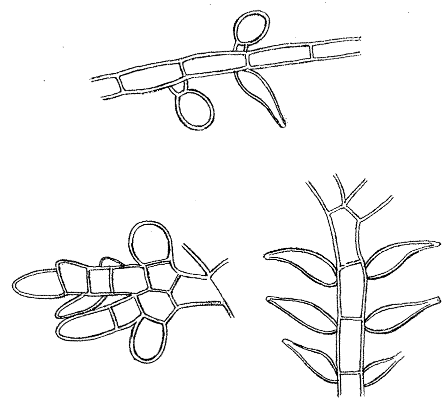

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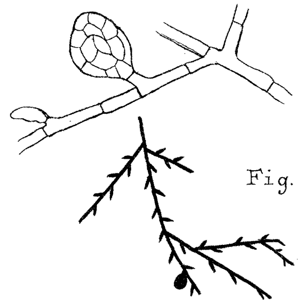

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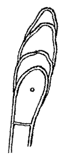
Fig. 6.



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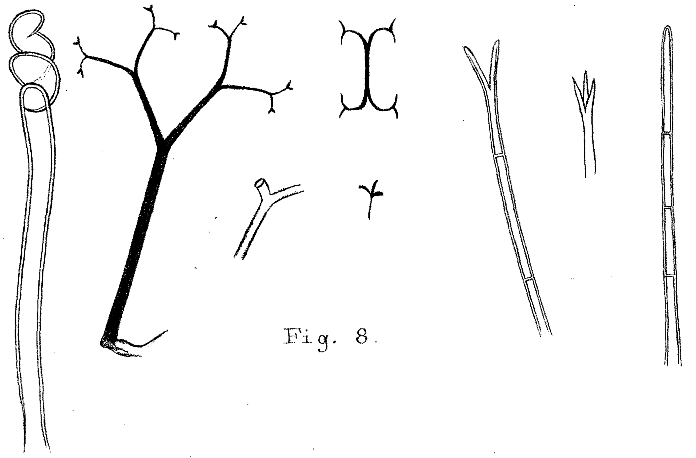

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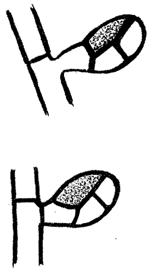
Fig. 10.



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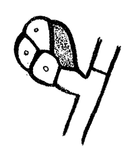

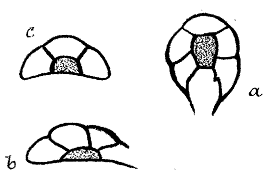

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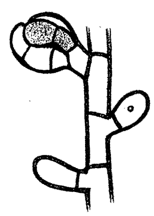

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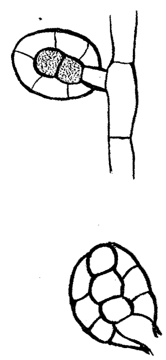

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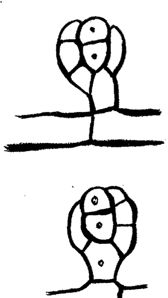
Fig. 15.



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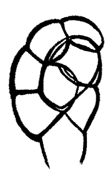

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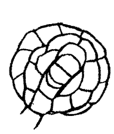

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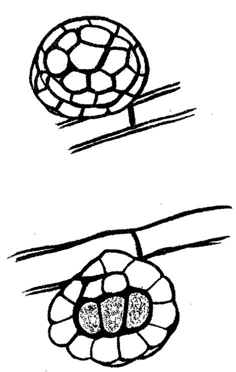

Fig. 19.

West, Newman & C^o. lith.

Fig. 21.

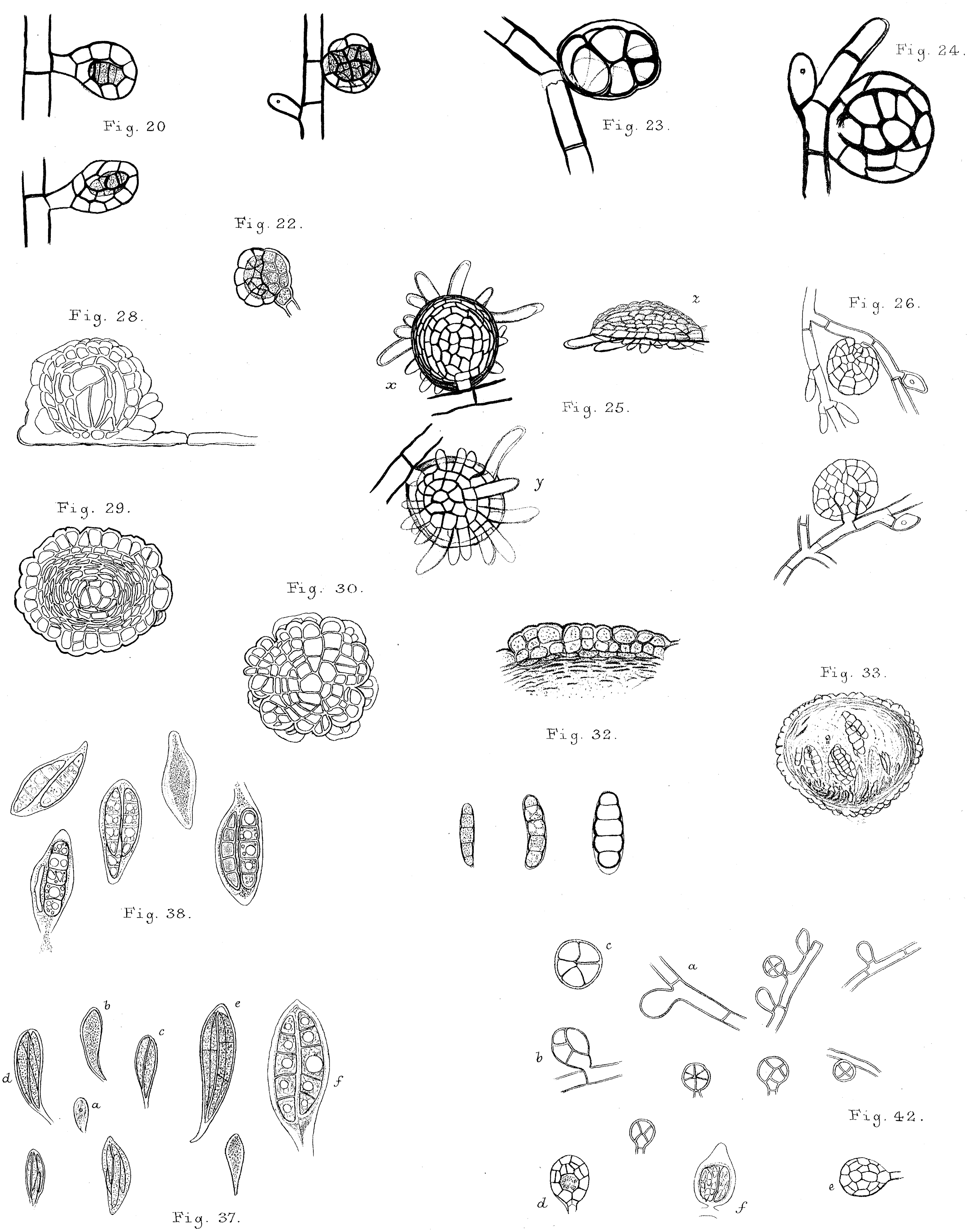

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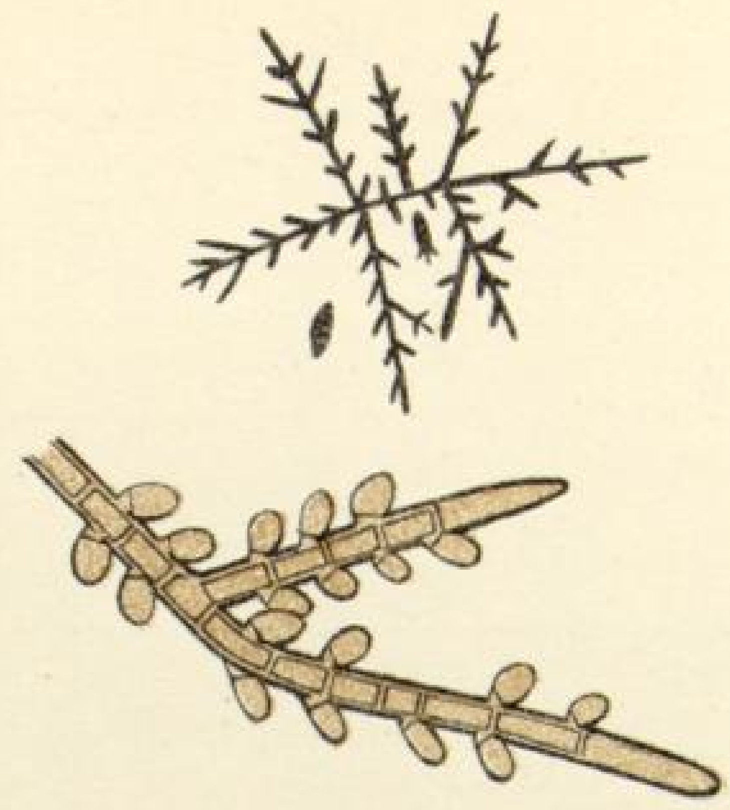
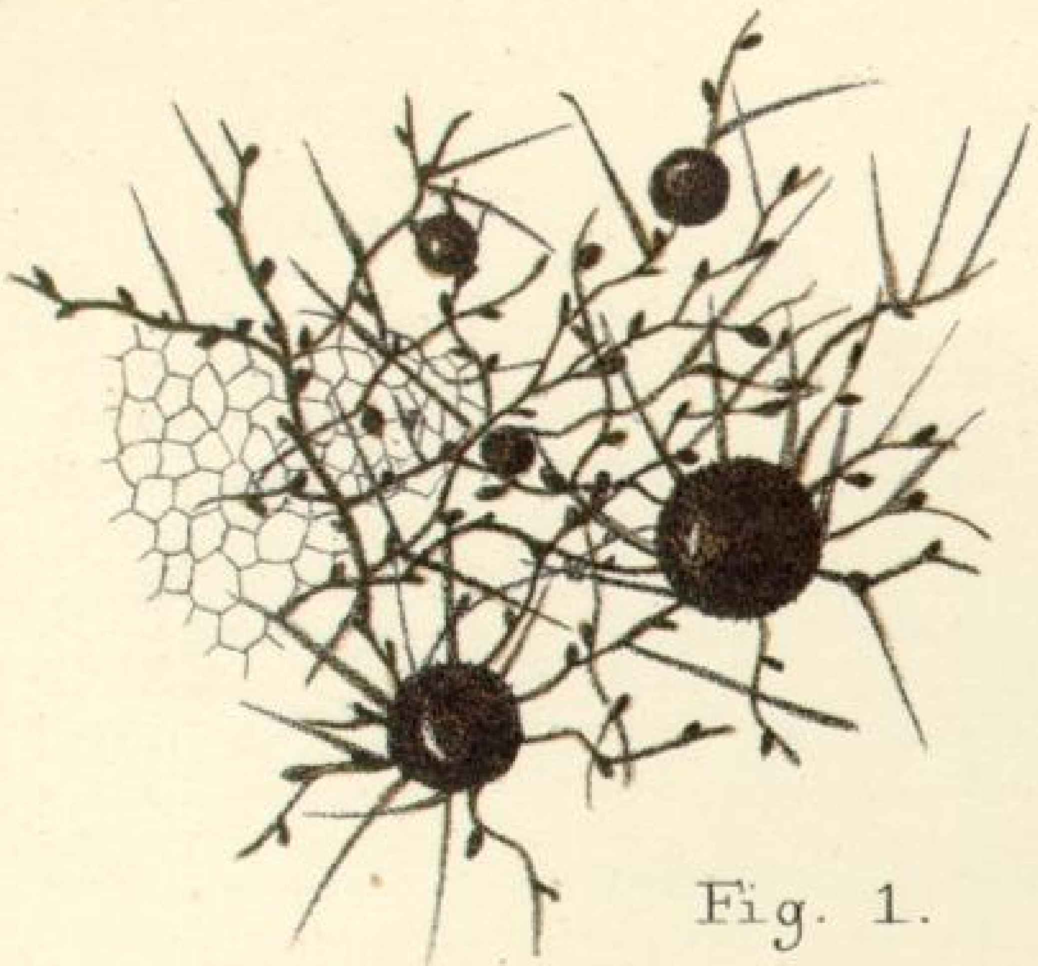
Fig. 2.





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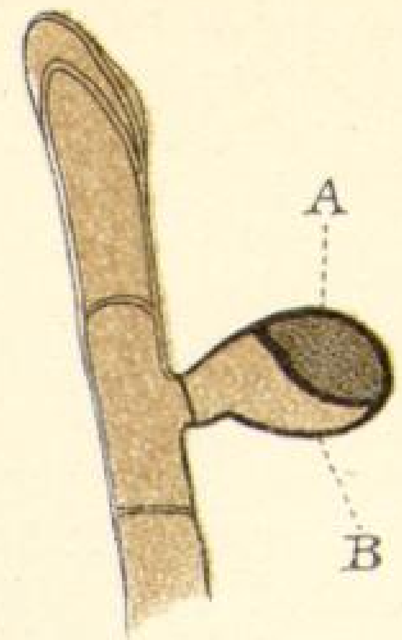

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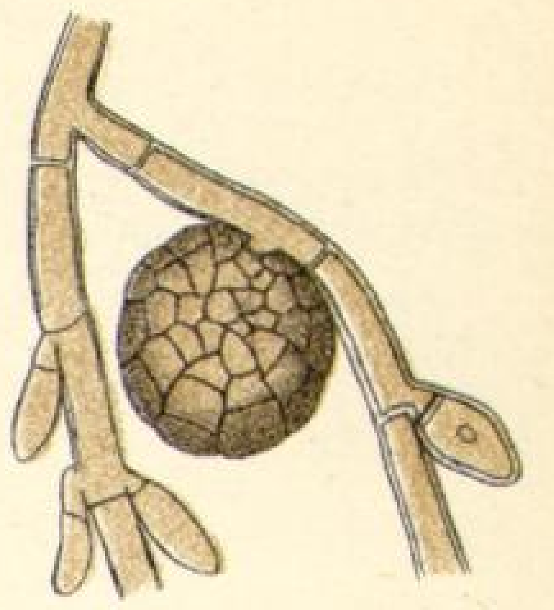

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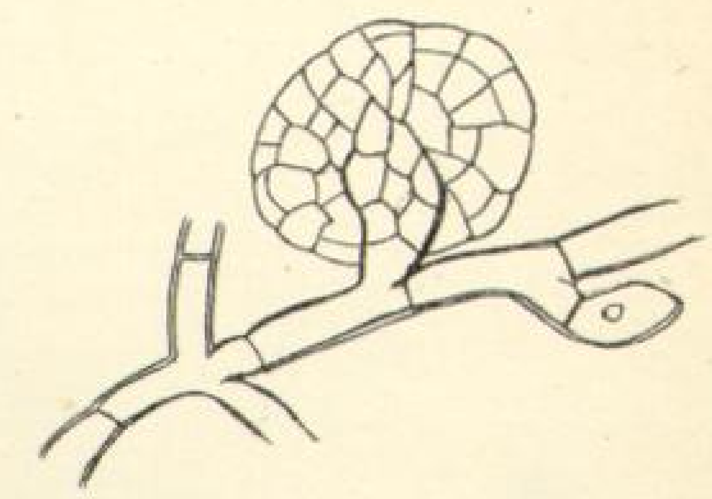

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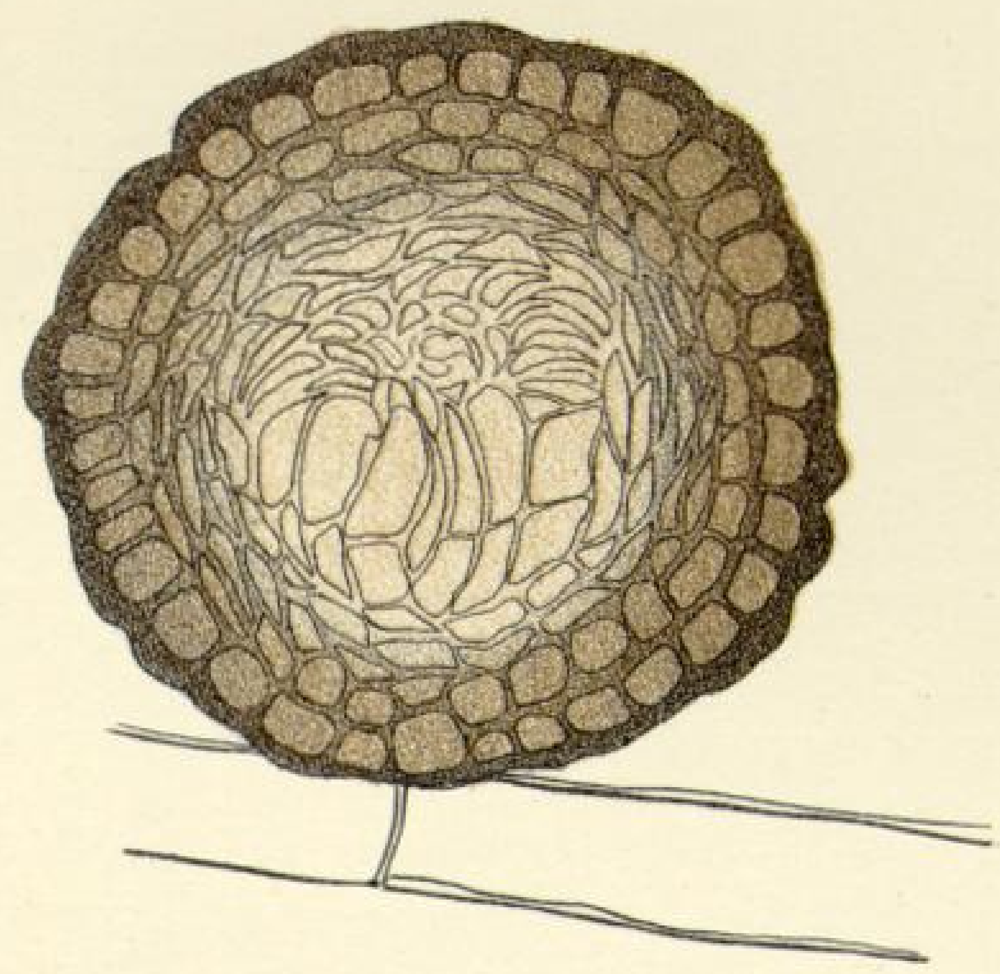

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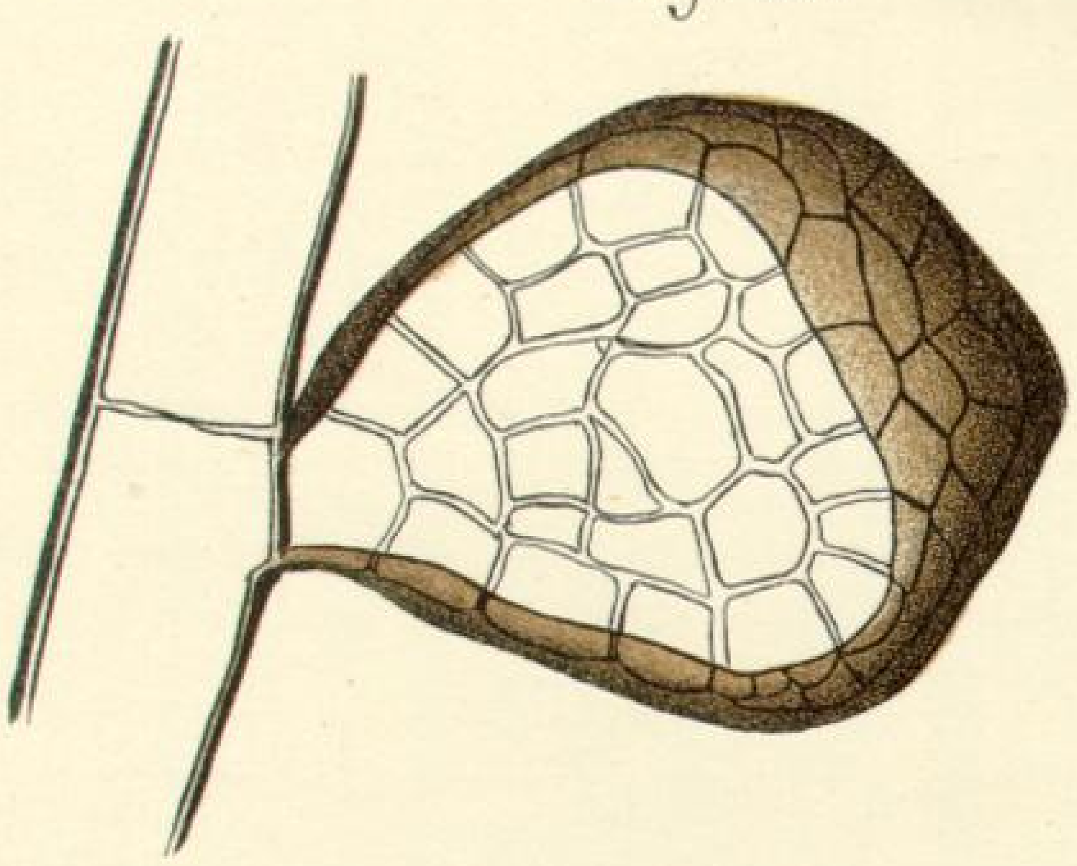

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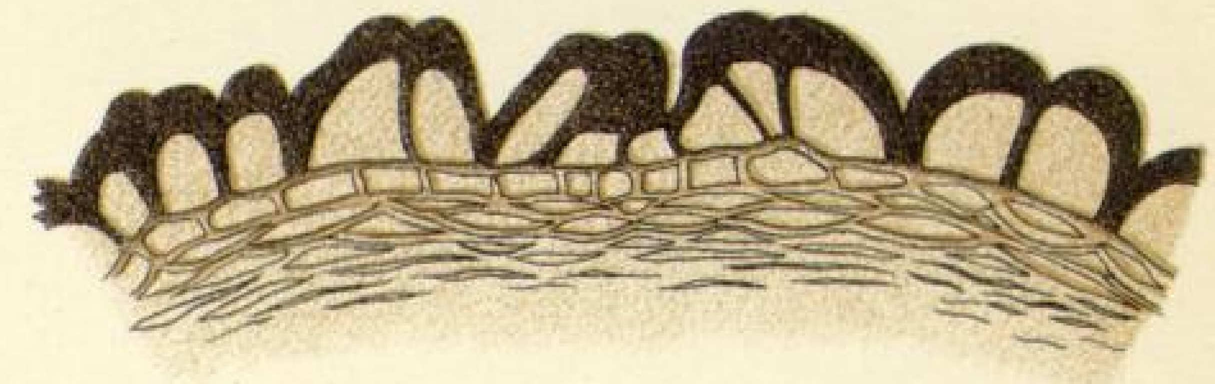


Fig. 35.

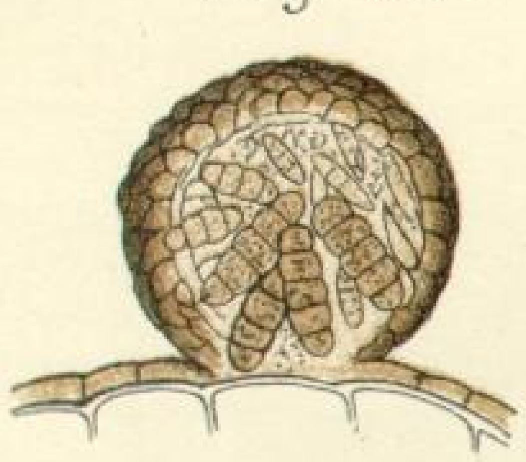
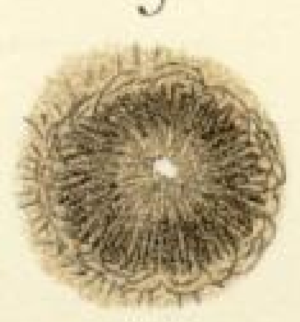


Fig. 36.



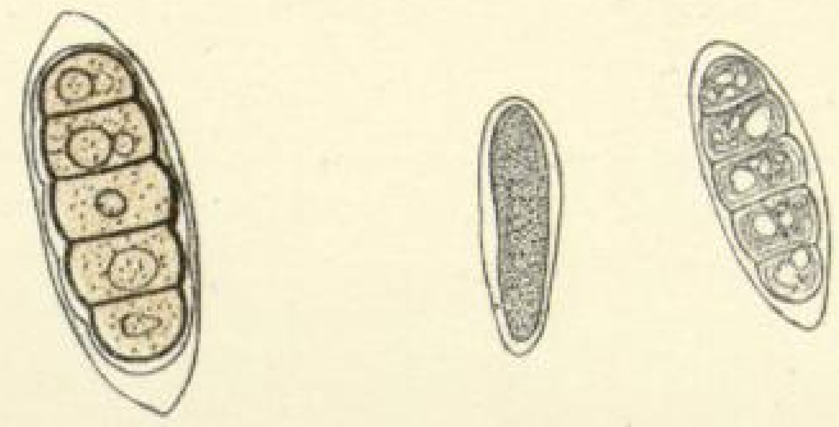
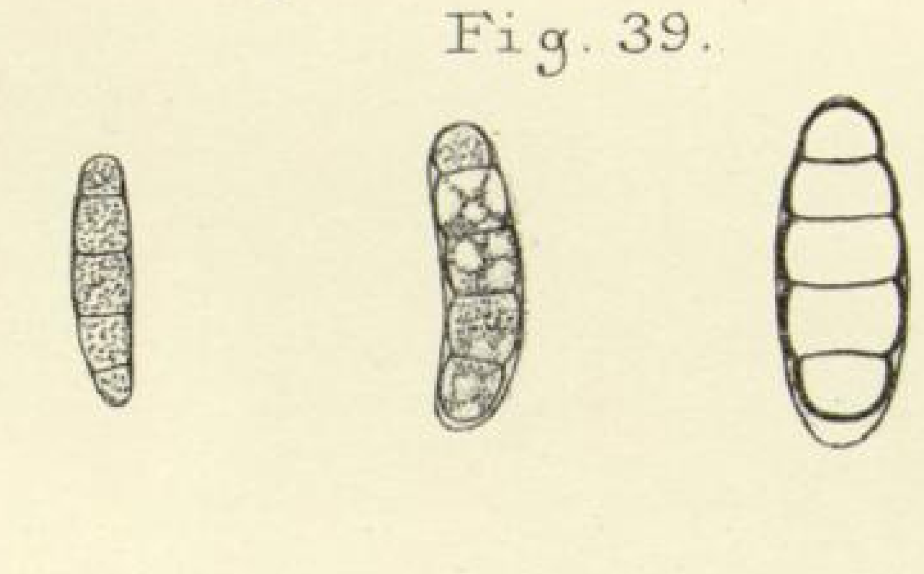


Fig. 39.



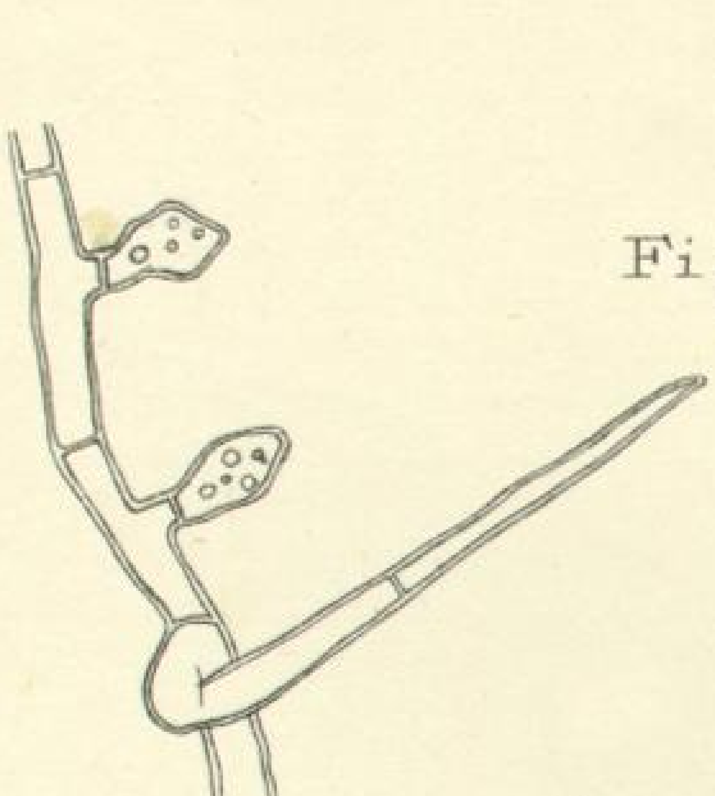


Fig. 41.

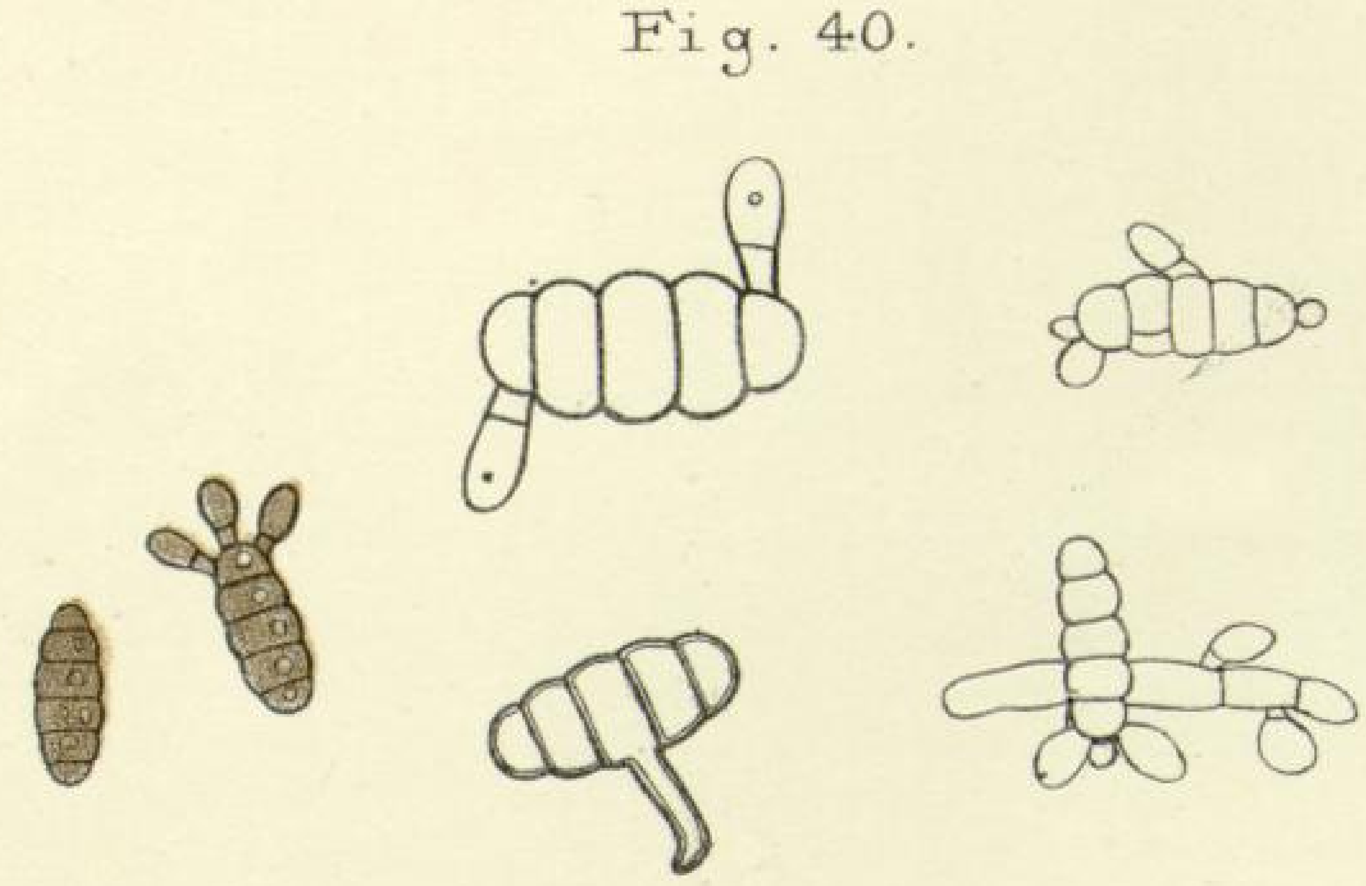
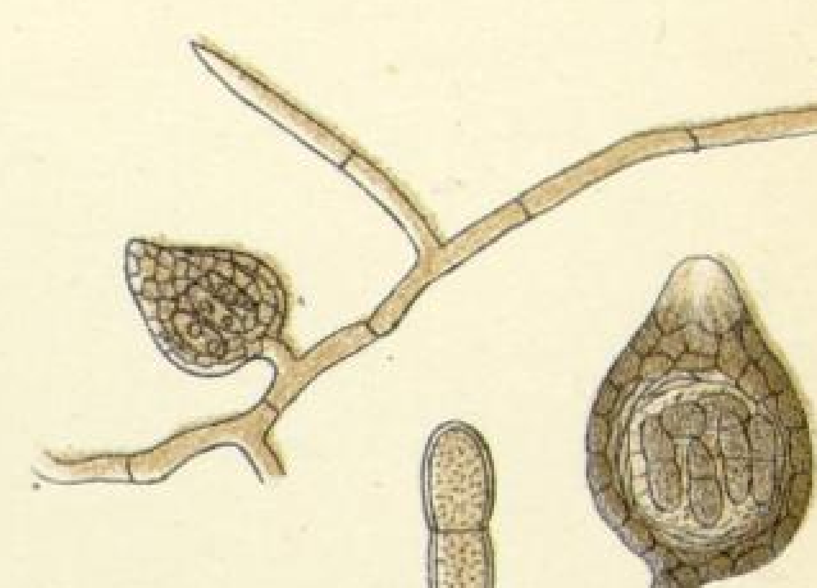


Fig. 40.



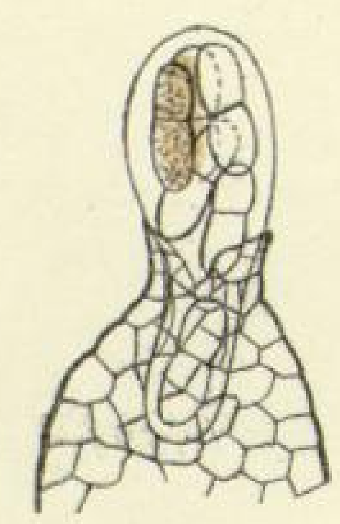


Fig. 43.