XX. *On* Mycoidea parasitica, *a new Genus of Parasitic Algæ, and the Part which it plays in the Formation of certain Lichens.* *By* DAVID DOUGLAS CUNNINGHAM, *M.B., F.L.S., Surgeon H.M. Indian Army.*

(Plates XLII. & XLIII.)

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I. *Introductory; Descriptive Characters; and Life-History of Mycoidea.*

NOW that the recent researches of Cohn and others have directed attention to the occurrence of Algal parasites, it may be of interest to record the occurrence in India of a form which not only appears to be the highest yet observed to play a truly parasitic part, but which possesses even greater points of interest in the nature of its characters as compared with those of its nearest allies, and in its relation to epiphyllous Lichens.

At intervals during the past eight years I have met with specimens of the plant in various stages of development; but it was only during the course of the last six months that I have been enabled to work out the subject so as to obtain materials for a consistent narrative of its life-history. The first specimens were obtained on the leaves of a mango-tree in 1869. On these leaves an eruption of bright orange patches or pustules was observed. These patches were at first sight regarded as of a fungal nature, but on close examination presented peculiarities of structure preventing them from being referred to any determined genus of Fungi. Subsequently other specimens were obtained on Rhododendron-leaves in the Nilgiris, on the leaves of species of ferns, Crotons, and various other plants in Calcutta, and on Tea-leaves in the Rumaun hills. The discovery of their presence on the latter host plant attracted renewed attention to their nature; and when they were again encountered in abundance in Calcutta as a destructive blight on plants of *Camellia japonica*, an opportunity was afforded of carefully studying their real nature and modes of development. As to the specific identity of the Algæ occurring on all these various hosts, I am as yet not in a position to form a definite opinion, as, unfortunately, beyond drawings of one form of fructification, I have not preserved the materials necessary for comparison in many instances. With regard to the specific identity of the plant, in many cases there can be no doubt; and I am strongly inclined to believe that this holds good for all specimens yet obtained, however various the nature of the host. If this really prove to be the case, it is, no doubt, remarkable, and in a sense lowers the parasitism of the Alga. One important feature common to most, if not to all, of the leaves affected was the existence of a firm coriaceous texture and a thickened epidermal covering.

Leaving the discussion of any further general questions until a detailed description of the species observed on the *Camellia* has been given, I shall now proceed to describe the structure and life-history of the parasite, and the nature of the lesions which it produces in its host. On examining one of the affected plants, the injuries due to the presence of the parasite are visible at once (Pl. XLII. fig. 1). The leaves in varying number, according to the length of time which the plant has suffered, and dependent on the time of year and the nature of the weather, are seen to be irregularly eaten away at the margins, penetrated by circular patches of decay or of absolute loss of substance throughout their surfaces, or spotted with circular pustules of various sizes and various shades of colour, ranging from pale green to bright orange. On examining the pustules more closely, they are found to be slightly elevated, and of a more or less distinctly marked radiating structure; and on looking at the margins of the holes and other deficiencies in the laminæ of the leaves, they are generally found to be bounded by a distinct rim of like colour and structure. At certain seasons of the year numerous very minute, elevated, green spots and an abundance of barely perceptible orange specks will also be encountered scattered over the surface of the leaves. The pustules and spots are almost invariably confined to the upper surfaces of the leaves; but in some rare instances they may be found on the inferior surfaces also. The latter phenomenon, however, is generally due to the extension of a pustule spreading round the margin from above. The size of the patches naturally varies greatly with the age of the plant causing them. On an average, patches which have not yet begun to die off in the centre do not exceed 5·0 to 6·25 millims. in diameter. The extent to which the leaves are affected varies greatly, but in advanced cases is sufficient very seriously to disfigure the plant. The very young leaves are seldom affected, owing, no doubt, in great part to the slow growth of the parasite. This is a matter of considerable economic importance in connexion with any form of parasitic growth affecting the Tea-plant.

On removing one of the pustules (which is easily done by the aid of a sharp knife), a brown discoloured patch of leaf-tissue is exposed, corresponding closely with the site of the pustule, and of various degrees of depth of colouring from a reddish brown to blackish. These discoloured patches in many cases penetrate the entire thickness of the leaf, and render the distribution of the Alga recognizable on the lower surface. In some instances the pustules are uniform in colour throughout, and end in a smoothly rounded margin; but in others the centre of the patch is pale, surrounded by a ring of deeper colour, or the margins, in place of being even, are more or less distinctly divided into a series of irregular radiating lobes. Even to the naked eye the appearance of the pustules varies much in different instances—in some being smooth and comparatively uniform, in others covered with a crop of erect orange-coloured filaments, or variegated with minute orange points and specks. The structure of the patches always points to a peripheral growth from a central point; but their appearance varies greatly with the season of the year and the nature of the weather.

Commencing with the rains (the season when the vegetative growth of the plant is at a maximum), we find the following to be the anatomical features presented by fully developed specimens. They are then covered with a dense crop of erect filaments of various tints of orange and green. These filaments on close examination may be seen to proceed from beneath the epidermis of the host plant, and to arise from a flattened cushion of radiating filaments situated there. They are erect, rigid, divided into a series of cells by transverse septa, and terminate superiorly either in blunt points or in more or less developed spherical capitella bearing a few large spore-like cells on short curved processes (Pl. XLII. fig. 2). The appearance of a mass of such filaments, with their transparent glassy walls and brilliantly coloured contents, is strikingly beautiful. Besides such filaments, numerous older ones are seen—some prostrate and colourless, others still erect and with coloured contents remaining in their cells and capitella, but with only empty spore-cases adherent to the latter. Some with more or less developed heads are also encountered, which are distinguished by the presence of greenish rounded masses adhering to them laterally, whilst in many the cell-contents, in place of being of an orange colour, are vividly green.

On detaching such a pustule from the leaf, and examining it under higher powers, it is found to consist of a flattened subepidermal disk of radiating filaments, from which numerous ascending twigs arise, which, breaking through the epidermis, are developed into the fructifying filaments just described. Careful vertical sections of the leaves, such as may be obtained by means of paraffin as an embedding medium, show very clearly the arrangement of the various portions of the pustule and its relations to its host (Pl. XLII. fig. 8).

Before proceeding further, however, it may be well briefly to describe the structure of the mature Camellia-leaf. On examining a good vertical section we find the entire thickness of the leaf to measure on an average about 0·3125 millim. Proceeding from above downwards, there is first a very dense layer of epidermal cells. These are colourless, flattened, and on treatment with iodine frequently show a very distinctly stratified structure in their walls. They have sinuous margins laterally and beneath, by means of which they dovetail into one another and into the irregularities of the subjacent stratum. This layer measures about 0·0100 millim. in its thicker and 0·0075 millim. in its thinner portions. The cells of the next stratum are also very thick-walled, and appear on section as a series of cubes. They form a continuous stratum, about 0·02 millim. in thickness, and are distinguished by the small amount of their contents, and by hardly ever showing the presence of any chlorophyll. As a rule, in fact, they appear almost empty, containing only a peripheral layer of protoplasm, or in rare instances a small oil-globule. Beneath this comes a stratum composed of from one to three rows of prismatic elongated cells, measuring about 0·050 millim. in long diameter, and full of chlorophyll granules. The continuity of this stratum is interrupted by the intercalation of a series of very remarkable cells at uncertain intervals. These are the remains of a system of cells which at one stage in the development of the leaf form the greater part of its substance, and are gradually thrust aside and separated by the development of the common cells of the leaf-tissue. They are of great size, in some cases attaining a length of 0·25 millim., and a diameter of 0·035 millim. at their wider basal extremity. They are rendered very conspicuous by the great thickness of their walls, as well as by their colourless finely granular contents. They are usually only found proceeding from the upper towards the lower surface of the leaf, being inserted immediately beneath the subepidermal layer; but occasionally they occupy a reverse position, and are then inserted on the inferior subepidermal layer. They are broad at the extremity of insertion, and frequently expand there into one or two blunt diverging processes, giving them a somewhat funnel-shaped aspect on section. They taper off from the base, and sometimes divide into two or three diverging branches, ending freely among the loose tissue of the interior of the leaf in blunted tips. Their thick walls appear to be channelled by a number of minute canals, leading from the cavity of the cell to its exterior surface; and the cell-contents consist of a colourless fluid full of minute granules. Beneath the stratum of prismatic cells is the loose tissue of the centre of the leaf, containing air-spaces and an abundance of large sphæraphides of oxalate of lime; and this is succeeded by one or two layers of tabular or cubical cells, and finally by a thin layer of flattened epidermal cells. There are no stomata on the upper surface of the leaf; but they occur abundantly below, ranging from 1000 to 1600 per square inch.

On examining a vertical section of a leaf, including young pustules of the parasite, appearances similar to those shown in the drawing are observed (Pl. XLII. fig. 8). The filaments of the disk are seen to lie between the epidermis and the subepidermal layer of cells. According to the degree of development of the patch, the epidermis over it is more or less elevated and separated from the tissue below. In a very young patch, such as that to the left hand of the figure, the displacement is comparatively slight; but where an abundant growth of ascending filaments has taken origin from the disk, it becomes very considerable, and may amount to as much as 0·125 millim. or even more. Simultaneous with and proportionate to the displacement of the epidermis, changes begin to occur in the subjacent cells of the leaf. A certain amount of sclerosis of their walls appears to take place; but the most conspicuous and considerable alteration occurs in the nature of their contents, which become gradually thickened and discoloured, passing through various shades of yellow and brown, and ultimately assuming a dry granular consistence and bright burnt-sienna colour. These changes at first only affect the layer of cells immediately beneath the Alga; but as time goes on they gradually advance deeper and deeper into the substance of the leaf, until they extend throughout its entire thickness, the affected area corresponding closely with the algal disk. As the disease advances the filaments in the centre of the disk become emptied of their contents and die; they then dry up, together with the portion of leaf-substance beneath them; and the dry and withered slough, readily breaking off, leaves a hiatus in the leaf, which, according to its situation, appears either in the form of a hole punched through the surface, or as an irregular space eaten out of the margin. Whilst this destruction of the centre of the patch is taking place, the parasite continues to extend peripherally; so that in many instances a great portion of the leaf is ultimately destroyed. The filaments of the algal disk appear, as a rule, to be confined between the epidermis and the subepidermal layer; occasionally, however, branches are given off which force their way downwards between the cells of the latter and reach the prismatic layer beneath (Pl. XLII. fig. 8).

The disk is originally composed of a single layer of dichotomous filaments, which force their way outwards, between the epidermis and the subepidermal cells. They are thick-walled, and at this time (so long, at all events, as they are in active growth) are filled with a bright green protoplasm. Whilst the disk continues to increase at the margins by means of the dichotomous growth of the filaments, ascending branches are given off by many of the cells of the older central portion; and these, forcing their way upwards, tend still further to elevate the epidermis. From the dense resistant nature of the latter they are generally more or less bent laterally, and in certain instances may even come to follow a course almost parallel to that of those of the disk from which they arise. As they ascend towards the epidermis their contents, in place of retaining their bright-green colour, become first yellowish and then rich golden orange. Some of them become enlarged above, and, again ascending, finally penetrate the epidermis and appear on the surface of the leaf. On examining a patch at this stage it is found to be sprinkled over with erect blunt-pointed filaments, which generally project in small groups through openings in the epidermis (Pl. XLII. fig. 3). This grouping of the aerial filaments is in many cases due to several of them arising at the termination of one of the subepidermal ones, but sometimes appears to be owing to filaments from several different origins making their exit through a common rupture in the epidermis. They continue to increase by apical growth and the gradual separation of cells by transverse partition, and ultimately attain a height of 1·0 millim., with a breadth varying from 0·05 millim. at the base to 0·025 millim. towards the apex. The terminal cell now, in place of remaining pointed, begins to swell out, and to assume a clavate, and ultimately a more or less spherical figure, forming a rounded capitellum about 0·1 millim. in diameter. A great accumulation of orange protoplasm now occurs within it; and a number of smaller clavate processes arise from it, into which much of the contents passes. These processes in course of time become developed into oval spore-like bodies, supported on narrow curved stems; and the process is completed by the accumulation of the greater part of the protoplasm in the former and the formation of septa between them and the partially emptied stems, which remain adherent to the capitellum (Plate XLII. fig. 4).

The growth of a filament may cease permanently here; but in many cases, after the formation of the capitellum, the cell immediately beneath it begins anew to grow, shooting upwards at one side of the capitellum and forcing it aside. In the course of development this displacement advances so far that the new portion of the filament comes to lie more or less in the axis of the older one, and appears as a direct continuation of it; whilst the old capitellum, bearing the remains of the spore-cases, and containing more or less orange or green protoplasm, appears as a lateral swelling, attached to the filament in its course (Pl. XLII. fig. 2). This further development, however, is by no means universal; and in no instance has it been seen to proceed beyond the formation of a second head. It occurs most frequently during the height of the rains, when the leaves are almost constantly wet and all the vegetative processes of the parasite at a maximum.

Although the growth of the filaments appears to be apical only, there are in many instances evidences of what may perhaps be a tendency to intercalary growth; for, on examining the cells under high powers, processes may frequently be seen projecting from the walls into the cell-cavity, and in some cases proceeding so far as to give rise to marked constriction of the protoplasmic contents (Pl. XLII. fig. 7). When under what may be regarded as normal conditions, the contents of the filaments and spores are of a brilliant orange colour and granular consistence, and at once strike a deep blue or black with solutions of iodine. When, however, the specimens are submerged, or when, during a continuance of wet weather, they are constantly saturated with moisture, the orange-colour is gradually replaced by a bright green, and the contents eventually come to resemble exactly those of the subepidermal disk-cells.

The mature spores, if they may be so termed, vary somewhat in size; one of medium size, which was measured, was $0{\cdot}0379 \times 0{\cdot}027$ millim. Their contents appear at first as a uniform granular mass; but as time goes on a process of segmentation occurs in this, ultimately dividing it into from twelve to twenty-four, or even more, oval bodies; and whilst this process is being completed a rounded orifice forms in the thick wall of the spore (Pl. XLII. figs. 4, 5). This orifice is generally situated laterally, but occasionally occurs towards one or the other end of the spore. When such ripe spores are wetted by the addition of water, by dew, or by rain, active swarming rapidly commences among the included oval bodies; and after this motion has continued for a short time, they separate from one another, and emerge in rapid succession through the orifice in their mother cell as active zoospores. These are at first pear-shaped, measuring about $0{\cdot}00825 \times 0{\cdot}0052$ millim., and are provided with a couple of long slender flagella, arising from the anterior pointed extremity (Pl. XLII. fig. 6). This extremity is almost colourless; but the rest of the body is of a reddish-orange colour by transmitted, and greenish by reflected light. They swim about actively for a short time, and then gradually become spherical and cease to move. The minute anatomy and subsequent history of these zoogonidia is identical with that of those developed in the sexual fructification, and will be further referred to in describing them. In some cases all the zoospores do not escape, one or two remaining behind in the mother cell and there undergoing various changes (Pl. XLII. fig. 5). Among the commonest of these is one in the course of which they gradually become circular green cells. The process of the formation of zoospores is at any time liable to be arrested by the addition of excessive moisture, which, as in the case of the filaments, causes the contents of the mother cells to become green, even after the process of division has advanced so far as to have caused the formation of distinct masses. Such green cellules do not usually appear to be capable of movement, but become gradually invested by distinct cell-walls, and remain within their mother cell until freed by accidental violence or by a process of gradual decay. They are met with in great abundance during the height of the rains; but the subsequent events in their history have not been observed.

After the escape of the zoospores from their mother cells, the latter remain as empty colourless appendages adherent to the capitellum. The filament, if it does not undergo further development, remains for some time erect, and then, falling over, lies prostrate on the surface of the pustule. The number of zoospores produced in this way is very great during the continuance of moist weather, and amply suffices for the propagation of the parasite at such times. Towards the close of the rainy season, however, the formation of filaments gradually diminishes, and, as the cold and dry season advances, ultimately ceases altogether. The patches of the parasite are now entirely subepidermal, and hardly extend at all peripherally. They are of a bright orange colour; and many of them dry up entirely and die off. Were there no special arrangement securing the preservation of the parasite under these circumstances, the amount of it surviving from one season to another would be comparatively small.

Such an arrangement is, however, provided in the sexual fructification. During the height of the rains, and whilst vegetative growth is actively progressing, only the asexual fructification is produced; but subsequently the sexual form begins to appear, and, gradually increasing in abundance, eventually more or less completely replaces it. The sexual organs, in place of taking origin from the aerial filaments, are developed on those of the subepidermal disk. These filaments, in place of containing an abundance of brilliant green protoplasm, as at first, begin to assume a yellowish tint, and ultimately come to contain only masses of globules and granules of as vivid an orange colour as that of the contents of the aerial branches (Plate XLII. figs. 9, 10). Whilst this change of colour is taking place, the contents also become greatly condensed and contracted, so as in many cases to be reduced to one or two isolated masses, or to a mere band along the centre of the cell. Their coarsely granular consistence also disappears; and a number of separate globules of large size and oily aspect are ultimately formed.

Whilst these changes are advancing, the organs destined for sexual fructification begin to appear. Certain of the filaments, in place of, as before, continuing to grow by a process of dichotomous division, resulting in the formation of two nearly similar branches, give origin to only one filament at the site of division, whilst the other member of the dichotomy, in place of elongating, swells up into an obovate dilatation (Pl. XLII. fig. 11). This is sometimes sessile, but is generally situated on a short process of the mother cell. A septum now forms at the base of the dilatation; and the latter rapidly increases in size, and becomes filled with a great accumulation of orange protoplasm. The new cell now appears as a large thick-walled sac inserted between the neighbouring filaments of the disk, which are displaced laterally by its growth, and, curving along its margins, come again into contact at its distal extremity. The thickness of the cell-wall is very considerable, amounting in many cases to as much as 0·004 millim., and frequently shows distinct evidences of stratification. The cells, when mature, vary considerably in size; but average specimens may measure about $0·0625 \times 0·0415$ millim. Due to the dense nature of the disk, to its subepidermal site, and to the fact that, when detached from the leaf, only retrograde changes, tending to a recurrence to pure vegetative growth, occur in the developing fructification, I have been unable continuously to follow out the further steps in the development of these cells, or oogonia as they now are. In so far, however, as very numerous examinations of separate specimens are capable of throwing light on the matter, the following appears to be the order of events. The contents of the oogonia, which were at first in close relation to the walls of the cell, become gradually removed from them as the cell enlarges, and form an oospheric mass, separated from its case by a distinct interval, save towards the basal extremity, immediately over the septum dividing the oogonium from its mother cell. Whilst these changes have been occurring in the oogonia, numerous slender-branched filaments have arisen from the neighbouring cells of the disk. Some of these become dilated at the extremity; and the large terminal cell becomes applied and closely adherent to an oogonium (Pl. XLII. fig. 12). These filaments appear, as a rule, to arise from the under surface of the disk;

and those which are developed into pollinodia are usually attached to the oogonia towards their bases. The contents of the terminal adherent cell appear next to be emptied into the oogonium, and to blend with the oosphere. Owing to the reasons previously mentioned, this process has never been actually observed to occur; but the contents of the pollinodial cells in many cases almost entirely disappear, and many examples of oogonia have been met with containing a mass of protoplasm independent of, or only partially blended with, the oosphere.

The oosphere now begins to show a distinct cell-wall, and is soon converted into a large spherical or oval oospore, which lies free in the cavity of the oogonium (Pl. XLIII. fig. 2). The cell-wall is at first thick and soft, but gradually becomes very thin and delicate. Another series of changes has been occurring in the oogonium itself. Its position, which, like that of the filaments of the disk, was originally horizontal, has been gradually exchanged, in the process of growth, for a more or less vertical one, the base of the organ being depressed beneath the plane of the disk, whilst its apex ascends and approaches the epidermis of the leaf. Its shape also exhibits alterations, frequently becoming more or less acuminate at the apex, and losing its original smooth obovate outline. Changes also begin to occur in the walls. At one point or other towards the apex a thinning of the wall begins to occur; and this process, confined to a limited area, gradually advances until the entire thickness is perforated, and a circular opening of considerable size and sharply-defined outline (by means of which the interior of the oogonium communicates freely with the subepidermal space) is formed (Pl. XLIII. fig. 2, & Pl. XLII. fig. 14).

With this the development of the oogonium itself ceases. In many instances they remain in this condition; but in others the mature organs are more or less completely invested, save around the ostiolum, by a loose coating of fine filaments, similar in appearance and origin to those bearing the pollinodial cells. In any case the original filaments of the disk now die off, and the oogonia, with their contained oospores, are left persistent among the dried-up débris of the disk beneath the thick epidermis of the leaf. How long such oospores may retain their vitality in this condition has not been definitely determined; but that they do retain it for a considerable time is certain, as they have frequently been obtained in a lively condition from the under surface of dried-up flakes of epidermis on the site of old patches of the parasite—where hardly any other evidences of its previous presence persisted, and where the leaf-tissues among which they were encountered were thoroughly dried up and destroyed (Pl. XLIII. fig. 1).

The mature oospores are spherical, and on an average measure about 0·035 to 0·031 millim. in diameter. Sooner or later, when exposed to favourable circumstances, the last events in the course of their development occur. The dried-up epidermis eventually cracks, and in doing so leaves channels of communication open between the external surface of the leaf and the interior of the oogonia, as the open mouths of the latter communicate, as before mentioned, with the subepidermal space, and in many cases, after the rupture of the epidermis has occurred, even project free on the surface (Pl. XLII. fig. 15). On the addition of moisture the mass of the oosporic contents now breaks up into a multitude of oval bodies like those developed in the aerial spores; and, the amount of fluid being sufficient, these soon commence to swarm actively, rupture the thin wall of the oospore, and, escaping in succession through the ostiolum of the oogonium, swim off freely into the subepidermal space and over the surface of the leaf. In size, colour, and general appearance, these zoospores are precisely similar to those developed in the asexual fructification. Like them, they are provided with two elongated flagella, one of which, so long as the body retains its original oval form and active motion, is usually trailed behind, whilst the other is employed in progression. Occasionally they become adherent to one another, or to other solid bodies, by their trailing filaments. Sometimes a pair of them may be seen to become adherent to one another by the extremities of these filaments, and, continuing their rapid rotating movement, to twist them so tightly up as to bring their bodies into close contact with one another. Under such circumstances, an actual fusion or conjugation appears in some cases to occur, resulting in the formation of one large biflagellate zoospore. Such a phenomenon, however, is very rare, and seemingly accidental.

The zoospores, when first emitted, are of an oval or pear-shaped form, and average about 0·00825 × 0·0052 millim. in size. As they become less active and begin to change their form, they frequently increase in size considerably. Eventually they cease to move and become spherical, the flagella continuing to vibrate for some time, and, after becoming motionless, persisting for a considerable period as two delicate hair-like filaments, attached to a portion of the cell, which, by its comparative freedom from colouring matters, indicates the site of the original hyaline extremity. When examined under a high power at this time, the cells sometimes appear to be invested by a delicate halo of gelatinous matter (Pl. XLII. fig. 16, *a*). They are provided with a very delicate membranous wall, and contain a fluid with numerous reddish granules, and a mass of greenish colour investing from ten to twenty, or even more, oval particles of considerable size. When confined beneath a cover-glass, the greater number of the cells next undergo the following changes:—A swarming movement begins among the reddish granules of the cell-fluid; this attains a great intensity, the cell-wall bursts, an escape of granules occurs, and the green mass or globule is partially protruded from the cell. The body now presents an appearance similar to that shown in the figure (Pl. XLII. fig. 16, *b*). After remaining for some time in this condition, the oval particles within the green mass begin in their turn to swarm, and, ultimately escaping from it one by one, swim off and are dispersed in the fluid, leaving the green mass adherent to the fragments of the original cell. At the time of exit the oval particles measure about 0·001 × 0·0005 millim.

Under normal circumstances and favourable conditions, however, many of the zoospores proceed to give origin to new plants of the parasite. The various stages in development may be traced by means of specimens which may be obtained in abundance from the surface of the leaves, near patches of the parasite containing mature oospores, and which have been exposed to sufficient moisture. On examining such portions of the leaves under a low power, or even, in some cases, with the naked eye, they may be seen to be sprinkled with minute yellowish or orange specks. These are readily detached from the surface, and consist of the spores and young plants derived from them. The spores, on ceasing to move, become spherical and increase slightly in size. The contents melt into a homogeneous mass of an orange or sometimes of a green colour, and a certain amount of thickening of the cell-wall occurs. The cell-wall and coloured contents now become separated by a distinct interval. The coloured mass next begins to assume a lobed or more or less distinctly cruciate outline, due to the development of marginal projections; and these continuing to grow, and becoming divided dichotomously, a flattened disk or rosette is gradually formed (Pl. XLII. fig. 17). Whilst this division of the coloured contents is advancing, processes are developed from the cell-wall, which, shooting inwards, and giving off branches as the division of the contents progresses, ultimately coalesce with one another, and divide the disk into a series of cells arranged in a radiant fashion. The formation of new cells now continues by the repetition of the process described above; and as the original cell-wall of the spore does not rupture, for some time at all events, but appears to stretch with the development of its contents, a series of coherent, flattened, cellular disks are gradually formed. Although the septa marking out the constituent cells are at first common to their adjacent cavities, they ultimately divide into two layers, so as to transform the originally continuous disk first into a series of segments, and ultimately more or less completely into radiating filaments, which, although remaining closely in contact, may be separated from one another, and in some cases even broken up into their constituent cells. These disks vary in size from mere points to 0·4 millim. in diameter, or even more in some cases, and adhere closely to the surface of the leaves (Pl. XLIII. figs. 3, 6).

These disks differ from those of the mature plant both in their position, which is superficial to, not beneath, the epidermis of the host, and in their much denser structure (Pl. XLIII. fig. 4). In order conveniently to distinguish the two sets of disks from one another, those formed directly from the germinating zoospores may be termed germinal or primary disks. We have next to follow the steps by means of which the primary disks come to be replaced by the subepidermal disks of the mature plant. Many of them never are so replaced, but, after persisting for some time, dry up and disappear from the surface of the leaves, or are utilized by parasitic fungal elements in a fashion which will be subsequently described. Were it not for these limits to the spread of the disease, the destruction of leaf-tissue would be incalculably greater than it is; for the number of primary disks originally formed is often excessive, not unfrequently being generally diffused over the entire surface of the leaf. It is a matter of some difficulty to follow the progress of development in those specimens which pass beyond this epiphytic condition; but a series of horizontal and vertical sections shows the process to be of the following nature. Some of the cells of the primary disk, in place of merely growing outwards by the formation and separation of peripheral lobes, give origin to buds from their under surface, which gradually penetrate the thickened epidermis, and ultimately reach the subepidermal space, or, more correctly, the line of separation between the epidermis and the subepidermal layer of cells (Pl. XLIII. fig. 7). Having done so, they take on an active growth, and, forcing their way along beneath the epidermis, and dividing dichotomously as they advance, soon form a mass of radiating filaments. Owing to their mode of origin, these filaments never occur in such regular and coherent disks as the primary disks; but, as they continue to spread and to become crowded upon one another, they form dense masses of radiating structure, such as are found in the mature plant. Under favourable circumstances, large numbers of such secondary disks are formed, and appear as elevated green patches and spots on the surface of the affected leaves. The primary disks cease to grow, and, after remaining for some time recognizable as small brownish patches on the surface of the epidermis of the new plant, gradually dry up and disappear. The relation of the primary and secondary disks to one another, and to the epidermis of the leaf, may sometimes be very clearly determined in transverse sections (Pl. XLIII. fig. 5). When the weather is dry the young plants, which are originally bright green, soon assume an orange colour; and they then remain dormant and protected by the epidermis until favourable conditions of temperature and moisture rouse them to go on to increased growth and the ultimate development of the various forms of fructification.

The various processes described in the previous pages seem to constitute the most important features in the life-history of this plant; and it now remains to consider some more general questions regarding it. As to its truly parasitic nature there can be little doubt. The situation of the mature plant, within the tissues of its host, and protected by a thick and highly cuticularized epidermis, would, even at first sight, lead to the conclusion that it was dependent on these tissues for its nourishment; and this conclusion is confirmed by the destructive effects which it produces. Whilst its essential parasitism is thus rendered clear, it remains an open question, how far the Alga makes use of the organized materials of the tissues for its nutrition, and to what extent it produces its prejudicial effects by merely appropriating inorganic elements of nutrition normally destined for the tissues of its host. That it acts, mainly at all events, in the latter way is rendered probable by the very various nature of the host plants on which specimens are found to occur; and much of the destructive effect which it produces may be ascribed to the large amount of water which it draws off whilst in active growth.

In regard to the precise nature and alliances of this Alga, there are several points calling for consideration. So far as the vegetative growth is concerned, it agrees very closely with the genus *Coleochæte*, the primary disks resembling the disks of *C. scutata*, whilst the secondary ones approach in characters those of some of the more loosely branched species. There is, however, an entire absence of the bristles characteristic of *Coleochæte*. When we come to consider the reproductive organs, the resemblance ceases, and very striking differences make their appearance. The asexual zoospores, in place of being produced indifferently in any cells of the disk, are here developed only on highly specialized filaments; and the sexual fructification, in place of being a well-developed carpospore, the result of fertilization by motile antherozoids, is rather an oospore than a carpospore, and is the result of fertilization by means of antheridial filaments. There is never a formation of true carpospores, although in many cases a tendency to such formation is indicated by the investment of the fertilized oogonium by a mass of cellular filaments. So in regard to the ultimate development of the sexual process, in place of the formation of a cellular mass, the individual cells of which give origin to zoospores, there is here an immediate resolution of the contents of the oospore into zoospores, and the subsequent development of each of these into a compound cellular body—the so-called primary disk.

In certain respects it appears to be more closely allied to the genus *Phycopeltis* than to any other. The development of the zoospore into the primary disk is of the same nature as that by which the disks of *Phycopeltis* are formed; there is the same absence of setæ, the same colouring of the cell-contents, and the habitat (on the leaves of living plants) is similar. It is, however, distinctly marked off from that genus by the development of the secondary subepidermal disk, and by the peculiar arrangement of the cells which produce the asexual fructification.

In spite of the peculiarities which it presents, the close relation of this Alga to *Coleochæte* and the allied genera is unmistakable; and all the departures from the ordinary type which it presents are explicable as the result of modifications adapting it to its parasitic habit and peculiar locality. The production of zoospores by the common cells of the disk would be useless, where such zoospores would be imprisoned beneath the epidermis of the host, and unable to find a fit site for their further development. So in regard to the sexual fructification; a process of fertilization by motile antherozoids is replaced by one effected by means of pollinodia, where the sexual organs, in place of lying free in a fluid, are buried in the tissues of a host plant.

MYCOIDEA, nov. gen.

Thallus entophyticus, disciformis, e filis articulatis formatus et filis erectis, aeriis, sporiferis præditus.
Cytioplasma aureum aut viride.
Propagatio zoogonidiis et oosporis fit.
Zoogonidia in cellulis matricalibus, quæ extremis filorum aeriorum superimpositæ sunt, formata.

MYCOIDEA PARASITICA, Cunningham.

Generis quæ differentia eædem speciei.
Zoogonidiis numerosis, diametro 0·00825 × 0·0052 m. m.
Oosporis globosis.
Habitat, Indiæ Orientalis, in fruticum et arborum foliis.

II. *Its relations when attacked by Parasitic Lichens and Fungi.*

The first part of this paper has been occupied with the description of the characters and life-history of this Alga *per se*; it now remains to give some account of its relations as a gonidia-former when in its turn subjected to the attack of parasites in the guise of fungal filaments. As far as my observations have yet gone, it may enter into the formation of various species of lichens, according to the stage of development in which it is attacked; but at present attention will be confined to one species, the development of which has been comparatively fully worked out, and which occurs on the leaves of *Camellia japonica*, of *Nephelium*, and of various other plants, all of which are subject to the attacks of the Alga.

It has been already mentioned that only a relatively small number of the primary disks give origin to subepidermal filaments, and that many of them dry up and disappear after having attained a more or less considerable size. A still larger number, however, are utilized by fungal filaments, and in association with these go to the development of patches of a heteromerous lichen. The leaves on which this occurs begin, shortly after the onset of the dry weather of the winter months, to show conspicuous dry superficial patches of a grey colour, and which, on close inspection, are seen to be composed of colonies of minute whitish circular disks (Pl. XLIII. fig. 8). In some cases almost the entire surface of the leaf is covered; but in general the groups are more or less isolated, circular, and mingled with distinct patches of the Alga in various stages of growth. On moistening such lichenoid patches the grey colour disappears in great part; and the separate disks now appear as circular green spots shining through a semitransparent veil, which invests them and unites them to one another. The patches come in course of time to be besprinkled with minute elevated black specks, and ultimately show a greater or less number of flattened circular apothecia, with black raised margins and brownish contents (Pl. XLIII. fig. 9).

On removing such a patch (a process which is readily accomplished, as it adheres but slightly to the surface of the leaf), it is found to be composed of a basis of delicate colourless membrane, passing continuously over the grey disks and the intervening spaces, and in many instances readily separable from the disks save towards their centres. On examining such a detached flake of membrane and its attached disks, the former is found to consist of a dense web of empty interwoven hyphæ, whilst the latter are readily recognizable as primary disks of the Alga, which have undergone greater or less modifications (Pl. XLIII. fig. 10). The cells of the disk are in great part empty and colourless; but beneath the colourless framework or skeleton is a great mass of circular cells. These are quite distinct from one another; and many of them become detached from their places in the process of preparing the specimen, and may be found floating free in the surrounding fluid (Pl. XLIII. fig. 18). The larger number of them, however, remain *in situ*, and appear to be embedded in a granular matrix. Entangled in the flake, in some cases, other primary disks may be encountered, which are as yet completely unaltered, or exhibit various stages of transition to those just described. The black specks in the patch are now resolved into spermogonia full of minute spermatia, and the apothecia present all the characters of those of gymnocarpous lichens (Pl. XLIII. figs. 9 & 10).

The following account of the details of structure and the history of development of these lichenous patches is founded on very numerous careful examinations of specimens in every stage of formation. Before any of these lichenous patches had appeared, and whilst the study of the development of the primary disks of the Alga occupied attention, it was frequently observed that fungal filaments had become attached to the latter (Pl. XLIII. fig. 12). These filaments were colourless, ramified over the surface of the leaf, and, where they came into contact with the disks, were frequently bent at right angles to their previous course, becoming closely applied to the margins of the disks, adhering firmly to them, and sending numerous branches over their surfaces. On following out the subject more closely in connexion with the lichenous patches, the subsequent history of these adherent filaments was ascertained to be as follows:—After becoming adherent to the disks the hyphæ proceed to ramify abundantly, and eventually form the densely interwoven film of empty filaments (corresponding with the cortical layer of other lichens) which covers the disks and the intervals between them (Pl. XLIII. fig. 19). Whilst this film is forming, changes occur in the disk beneath. The cells multiply greatly by the formation of tangential septa dividing the rays into rows of short spaces; and their contents pass from orange into bright green. Each of the cells now buds out below, and forms a rounded prominence on the inferior surface of the disk; and these buds, gradually absorbing all the contents of their parent cells, are ultimately detached as independent bright green circular cells, and form accumulations beneath the now empty framework of the disks (Pl. XLIII. fig. 16). The process begins from the centre of the disks, and gradually extends peripherally until the disks are left as empty cellular shields covering a mass of detached circular cells. The hyphæ of the cortical layer, after ramifying over the upper surface of the disks, finally force their way downwards between the constituent cells of the latter towards the central point from which the rays diverge. At the point of entrance a dense cellular mass of fungal cells is developed, causing an appearance, very frequently to be observed in the disks of the mature lichen, of a central colourless space in the groups of gonidial cells (Pl. XLIII. fig. 14). Having gained an entrance, the hyphæ then ramify among the projecting buds on the under surface of the disk, and, becoming adherent to them, retain them in position when freed from their parent cells. The green gonidial cells continue to multiply by the division of their contents, and frequently form several strata, beneath which a colourless layer of hyphæ is more or less distinctly developed. Owing to the ease with which the lichenous patches are detached from their position on the surface of the leaf, it is a matter of some difficulty to obtain good demonstrations of their structure; but the accompanying illustrations show the appearances present in successful vertical sections, as well as in cases in which masses of gonidia and hyphæ have been teased out from beneath their investing disks (Pl. XLIII. figs. 11, 17).

At various points of the patch the filaments, sometimes those of the film, and more rarely those apparently of the intergonidial hyphæ, give origin to an inferior layer of loose tissue. This rapidly multiplies and forms dense whorls of tangled filaments, from which the spermogonia and apothecia are gradually developed; and it is only around these structures that any loose tissue corresponding to a medullary layer can be encountered (Pl. XLIII. fig. 20).

The spermogonia, as previously mentioned, are developed anteriorly to the apothecia. They ultimately appear as slightly elevated circular spots of a greenish-brown hue, measuring 0·175 millim. in diameter, and discharge their contents on the surface of the patch through minute rounded ostiola. The spermatia are colourless, slightly curved, and measure 0·004 by 0·001 millim. (Pl. XLIII. fig. 13). The apothecia measure about 0·7 millim. in diameter by 0·2 millim. in height, and appear to the naked eye as minute blackish cups on the surface of the patch. They are invested by a distinct rim, derived from the cortical layer, and show the usual features presented by the apothecia of gymnocarpous lichens—being anatomically separable into excipulum, subhymenial layer, hymenium, and nucleus, consisting of the remains of the whorls from which they are developed (Pl. XLIII. fig. 15). The asci contain eight curved uniseptate spores, and are surrounded by an abundance of slender somewhat capitate paraphyses (Pl. XLIII. fig. 21). I am uncertain whether any of the spores yet obtained were mature; but those showing most indications of being so were colourless or very pale yellow, somewhat constricted at the septum, and measuring 0·0227 × 0·0075. Numerous experiments were made as to the reaction of the asci with solution of iodine. In no instance was there any distinct indication of blue staining as encountered in most lichens observed. The walls of the asci, on the contrary, appeared to be unaffected; but the presence of a large quantity of the material styled epiplasma by De Bary was demonstrated around the spores, which, under such circumstances, appeared as pale yellow bodies embedded in a deep-red-brown basis.

The history of the development of this species of epiphyllous lichen appears in itself to afford a complete demonstration of the composite nature of such structures. There can be no doubt here as to the source of the gonidial cell, and that that source is an Alga capable of independent existence and of producing perfect forms of fructification. On the other hand, it is only in association with these algal elements that the fungal filaments form a tissue capable of giving origin to spermogonia and apothecia.

Various other points might be touched upon; but in the mean time I would merely suggest that the anomalous subepidermal site and so-called cephaluroid conditions of the various species of *Strigula* are probably explicable as owing to their gonidial elements belonging to Algæ identical with or similar to the species here described. The subepidermal site is at once explicable by the supposition of the entrance of hyphæ along with the filaments of the Alga going to the formation of the secondary disks; whilst the cephaluroid condition may, so far as can be judged from figures at all events, be referred to cases in which the algal element has partially retained or regained the ascendancy, and has given origin to a crop of the asexual fructification normally belonging to it.

In conclusion, it may be well to call attention to the fact that the existence of structures closely resembling the primary disks of the Alga forming the subject of the present paper has been already indicated by various authors. The organisms described by Mettenius as occurring on the leaves of ferns, and referred by Millardet to the genus *Phycopeltis* *, may with as much propriety be ascribed to the present genus. Even the relation of the disks to fungal elements would seem to have been noticed. For example, the Rev. Mr. Berkeley, in a paper on "The Thread Blight of Tea," mentions the occurrence on tea-leaves of "minute shield-like bodies, consisting of cells radiating from a central aperture containing spores," and gives a figure which might well pass for that of one of the primary disks †. Mr. Archer also, in exhibiting some of Dr. Bornet's preparations, commented on one showing a minute lichen with its hyphæ investing a form of *Phyllactidium* or *Coleochæte*, and pointed out the singular habitat of the Alga, "on the leaves of living trees in the tropics" ‡.

* "De la Germination des Zygospores dans les genres *Closterium* et *Staurastrum* et sur un genre nouveau d'algues Chlorosporées," par M. A. Millardet, Mémoires de la Société des Sciences Naturelles de Strasbourg, 1870.

† Quarterly Journal of Microscopical Science, 1875, p. 132. ‡ Ibid. p. 334.

DESCRIPTION OF THE PLATES.

Plate XLII.

Fig. 1. Leaf of *Camellia japonica* affected by *Mycoidea parasitica*.

Fig. 2. Aerial filaments bearing the asexual fructification : × 92.

Fig. 3. Group of young aerial filaments emerging from beneath the epidermis : × 180.

Fig. 4. Upper extremity of an aerial filament, with stipitate spores arising from it : × 480.

Fig. 5. A spore from which the zoospores have escaped, showing the rounded opening of exit and four zoospores yet remaining in the cell-cavity : × 960.

Fig. 6. A free zoospore in its original condition : × 840.

Fig. 7. A portion of one of the aerial filaments, showing projections on the inner surface of the cell-wall : × 960.

Fig. 8. A vertical section through a portion of a *Camellia*-leaf affected by two patches of *Mycoidea parasitica* : × 180.

Fig. 9. Filaments from the subepidermal disk in their original condition : × 180.

Fig. 10. Similar filaments from a plant with sexual fructification : × 180.

Fig. 11. A young oogonium : × 180. Fig. 12. An oogonium with attached pollinodium : × 980.

Fig. 13. Mature oogonium with escaping zoospores : × 960.

Fig. 14. Portion of an oogonium showing development of ostiolum : × 980.

Fig. 15. Portion from the surface of a leaf, showing the ruptured epidermis and protruding ostiolum of the oogonium : × 1960.

Fig. 16. (*a*) A zoospore in the circular condition : × 1960. (*b*) A zoospore after rupture of the cell-wall. (*c*) Oval particles contained in the interior of the zoospores.

Fig. 17. Zoospores which have become circular and are beginning to germinate : × 1960.

Plate XLIII.

Fig. 1. Group of mature oospores with filaments ramifying around the oogonia : × 180.

Fig. 2. Mature oogonium with its ostiolum and oospore : × 960.

Fig. 3. Young primary disk, resulting from the germination of a zoospore : × 700.

Fig. 4. Vertical section showing the relation of the primary disk to the epidermis : × 180.

Fig. 5. Portion of epidermis, with a primary disk and the mass of subepidermal filaments arising from it : × 180.

Fig. 6. Primary disk as seen from the surface : × 37.

Fig. 7. Vertical section, showing germinating cells of the primary disk, and penetration of the epidermis by the buds arising from them : × 960.

Fig. 8. Lichenous patch on the surface of a *Nephelium*-leaf : of natural size.

Fig. 9. Portion of a patch with spermogonia and apothecia, viewed laterally : × 23.

Fig. 10. Detached portion of a patch, showing the film of connecting hyphæ, the spermogonia, apothecia, and circular groups of gonidia : × 23.

Fig. 11. Section through a portion of a gonidial patch, showing the filamnets of the cortical layer, the remains of the algal disk, the green gonidial cells, and the intergonidial hyphæ : × 960.

Fig. 12. Portion of a primary disk, seen from below, with fungal filaments attached to it : × 960.

Fig. 13. Spermatia : × 960.

Fig. 14. Portion of dense cellular tissue from the point where the fungal filaments penetrate the disk : × 960.

Fig. 15. Apothecium in vertical section : × 44.

Fig. 16. Portion of the skeleton of a primary disk detached from a group of gonidia, with one or two gonidial buds still connected with the cells : × 960.

Fig. 17. Detached mass of hyphæ and gonidia from one of the groups : × 960.

Fig. 18. Free gonidia ; two of them showing division of their contents : × 960.

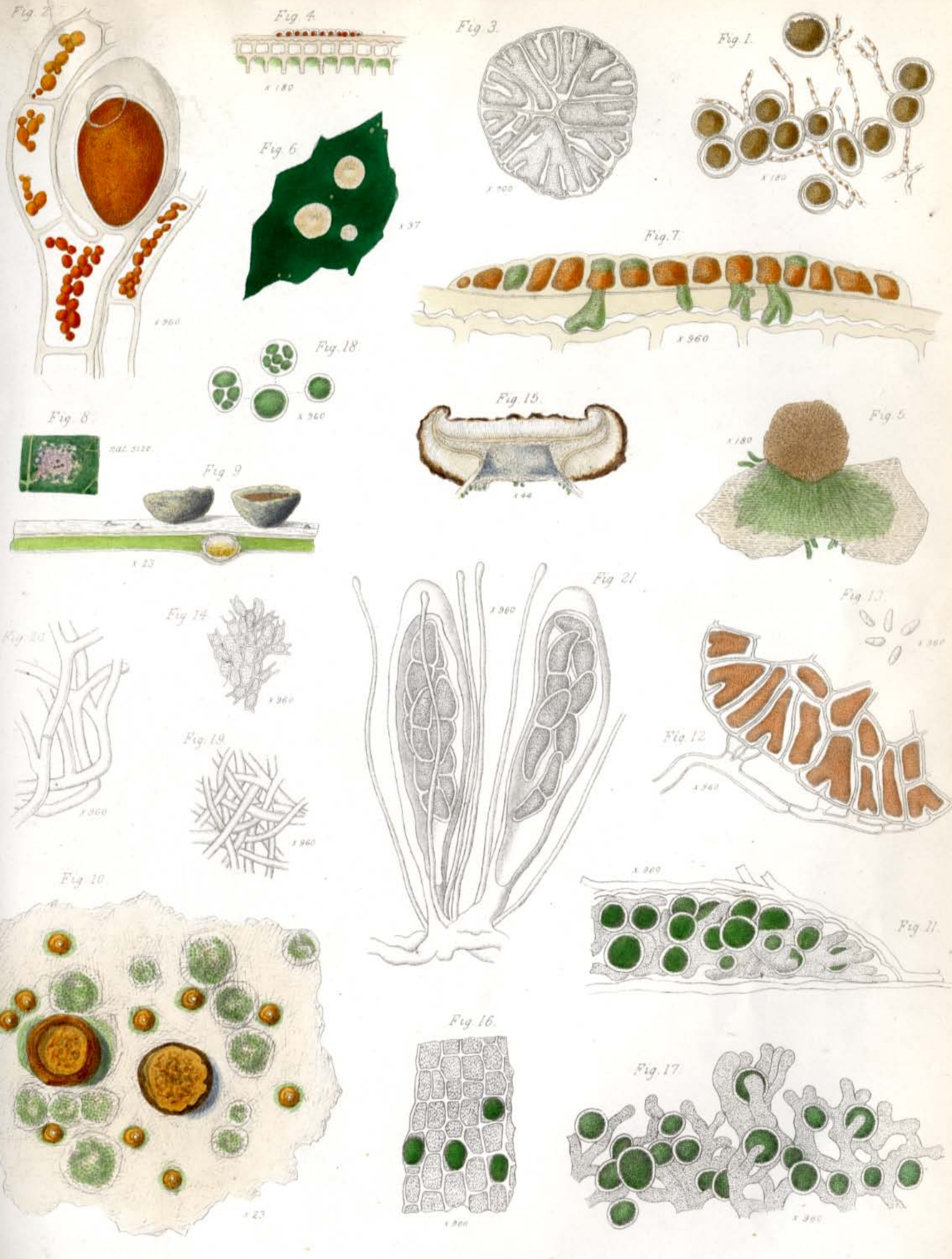
Fig. 19. Hyphæ of the cortical layer : × 960.

Fig. 20. Medullary fibres : × 960. Fig. 21. Asci and paraphyses : × 960.

D.D. Cunningham del.

MYCOIDEA PARASITICA.

D. Blair lith. Fitch imp.



D.D. Cunningham del.

MYCOIDEA PARASITICA.

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