THE THALLUS OF THE GENUS *PARMELIA*

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(With 6 plates and 12 figures).

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Introduction.

In the ordinary works on Lichenology, the main object of the author is to give such a description of a species as will enable a student to determine a plant by himself, by examination of the thallus with a pocket lens, and of the apothecia and spores by the aid of a microscope. The spermagonia and spermatia may be briefly referred to, but other matters are usually ignored. In this paper no reference will be made to a macroscopic study of the thallus, or to the histology of the apothecium, its paraphyses or spores. For those who require this information any ordinary work on Lichenology will sufficiently meet their requirements.

In such works as Goebel's "Outlines of Classification and Special Morphology," Green's "Manual of Botany," Vine's "Text-Book of Botany," etc., the same illustrations of thalline structures are repeated with wearisome regularity, and with little addition to existing knowledge.

In preparing the material for this paper, serial sections of the following lichens were cut, stained, and mounted for examination:—*Parmelia tiliacea*, Ach., *P. tinctorum*, Despr., *P. perlata*, L., *P. limbata*, Laur., *P. laxa*, M.A., *P. perforata*, Ach., *P. latissima*, Fee, *P. placorhodioides*, Nyl., *P. mundata*, Nyl., *P. olivacea*, L., *P. cetrata v. sorediifera*, Wain., and *P. saxatilis v. signifera*, M.A.

Twelve photo-micrographs illustrating these are submitted with this paper. It may be noted that Dr. Jean Muller of Aargau regarded *P. placorhodioides* and *P. mundata* as varieties of *P. physodes*, and *P. laxa* as a variety of *P. conspersa*, Ach.

Of the material examined, the whole of the specimens are Australian with the exception of *P. cetrata v. sorediifera*, Wain., which was chosen for special study of the development of soredia, and also for comparison with Australian species.

The microscopic examination was made, and will be set down in order under the following heads:—(1) Absorption pores; (2a) Upper Cortex; (2b) Lower Cortex; (3) Hyphæ; (4) Algæ or Gonidia; (5) Rhizinæ; (6) Spermagonia; (7) Alliances with other genera.

For comparison under the last named head, examination was made by means of stained and mounted serial sections, 3-7 μ in thickness of the following species:— *Heterodea mulleri*, Nyl., *Sticta demutabilis*, Krph., *S. pulmonacea*, Ach., *Stictina suborbicularis*, M.A., *S. retigera*, M.A., *Physcia hypoleuca*, Tuck., *Pyxine cocoes*, *Evernia furfuracea*, Mann, and *E. prunastri*, Ach., also of species of *Cladonia*, *Clathrina*, *Collema*, *Synechoblastus*, and *Ramalina*. In all 192 serial slides 3in. x 1½in. were made, each carrying from 30 to 264 serial sections.

1. *Absorption Pores.*

The first plant examined in detail was *Parmelia tiliacea*, Ach., and it was found that the whole thallus was pierced with minute pores with well defined walls, usually presenting a smaller opening on the upper surface of the thallus than on the under side, as a rule slightly oblique to the parallel cortices, but always simple and unbranched. These might well be overlooked, and taken for folds in the minute thalline section, did they not repeat themselves on each serial slice, with such alterations in outline as would be expected from parallel sections of a cylinder. (See Plate II., fig. 1.)

In the walls of these pores the hyphæ usually radiate from the centre upwards and downwards towards the outlets, and form the inner lining of the perforation. The algal cells—Cystococcus—lying just beneath the hyphal sheath in the gonidial zone are larger and more closely beset with hyphæ than in any other portion of the thallus examined.

Under an inch objective (Watson) with No. 5 eyepiece, and a magnification of 120 diameters, the pores could be seen in general parallel lines across the section. Under the ⅙ objective and No. 5 eyepiece, with a magnification of 720 diameters, the pores show as blotches when the rest of the section is in focus, and the objective has to be focussed down to bring the walls of the pore into perfect view, when the cut edges show as black lines and the rest of the lichen section is thrown out of focus. In measurement they are .02-.04 x .007-.018 mm.

Most curious pores exist in *P. placorhodioides*, Nyl. They are very narrow and usually at right angles to the surfaces; when they occur beneath an apothecium they are continued through its hypothecium and hymenium to the surface, and in the hymenium increase in cross diameter, so that in this portion of their course they are conical, while in the thallus itself they are cylindrical, the whole having the form of a funnel with an extra long tube. In other cases they are conical and larger, reaching .07 x .0035 mm. (Plate II., fig. 2.) Pores of similar infundibuliform shape are also characteristic of *P. tinctoria*, L., in which species they abound in all parts of the thallus.

In *P. olivetorum*, Ach. (s. *P. tinctorum*, Despr.), the pores are usually perpendicular to the cortices, but are very narrow, .004-.005 mm., and are readily distinguished by their lining hyphæ crossing the hyphæ of the medulla at right angles. (Plate III., fig. 3.)

The pores of *P. limbata*, Laur., are .026 x .013-.019 mm. in size.

They are usually wider where they open on the upper surface of the thallus, and diminish to about two-thirds of that diameter at their lower aperture. In some cases they are seen to arise from above the rhizinæ which in this lichen are unusually long and stout, .26 x .09 mm. These rhizoids are hollow and formed of hundreds of parallel hyphæ; the tips, however are not porous. From the fact that the algal cells are more numerous, and penetrate the thallus more deeply in and along the walls of the pores, and that in *P. limbata* the canals are connected with hollow rhizinæ; and since, when viewed in reflected light, the pores show on the upper surface not as perforations, but as shallow closed pits, it seems doubtful that the function of these organs is merely to supply the plant with gaseous food, but that they may also take in water for the use of both symbionts, and inorganic food substances for the supply of the chlorophyll-containing algæ. (See Plate III., fig. 4.)

An examination of the thallus of *Parmelia laxa*, Mull Arg., shows that it possesses oblique capillary tubes, not more than .009 mm. in cross section, and difficult to find, if it were not for the transverse direction of the lining hyphæ, and the fact that those threads, forming the inner surface of each perforation, stain more deeply than the hyphæ forming the medullary layer. (Plate IV., fig. 5.)

An American lichen, *P. cetrata v. sorediifera*, Wain., shows the pores that form such a marked feature of the genus. There are .06 x .02 mm., usually cylindrical and oblique to the thallus, and in several instances were seen, as in *P. limbata*, Laur., to be in communication with the large hollow rhizoids. Occasionally they are conical, and in this case the apex of the cone is always at the upper cortex, while the broad base is in connection with a rhizina. The thallus of this lichen is frequently covered, on the upper side, by colonies of a Sirosiphon, and hyphal threads are seen to project from the cortex into the sheath of the Sirosiphon. (Plate IV., fig. 6.)

The thallus of *P. latissima*, Fee, strongly resembles that of *P. perlata*, Ach., of which species it is by some authors regarded as a variety; but it differs essentially in one respect, it is much more freely supplied with absorption pores. These are .05 x .016 mm. in their cross diameters, and are usually oblique to the surface. As in *P. laxa*, hyphæ lining the inner surface of the canals stain more deeply with Delafield's hæmatoxylin than those of the medulla, and thus aid in revealing the pores. In searching for these canals it is better to use a high than a low power, a $\frac{1}{6}$ for choice, with an eyepiece that will give a magnification of 500-700 diameters. The pores are then out of focus, and appear as blotches when the rest of the thalline section is in good view. The pores seem to be higher developments from the cyphellæ of the genera Heterodea and Sticta, and when an oblique section shows only the lower opening of a pore it can hardly be distinguished from that form known as *Cyphellæ veræ*, which are lined by the hyphæ, and appear under the lens as minute urceolate or thelotremoid depressions. The pores, however, are much more minute, and are not to be confused with the perforations of the thallus of *Parmelia pertusa*, Schaer., which are 1-2 mm. in diameter, or with the perforations in the apothecia of *P. perforata*, Ach., which are also visible to the unaided eye. As several species of Stictaceæ are without cyphellæ, either true cyphellæ or pseudo-cyphellæ, an examination was made of the thalli of *S. pulmonaria*, L., and *S. retigera*, Ach., which belong to the section Ecyphellatæ, and it was found that they also possess the absorption pores of the Parmeliaceæ. It seems clear from this that whatever function is performed for the genera Heterodea and Sticta by the cyphellæ is performed for the lichens of the genus Parmelia, and for the ecyphellate Stictas by the absorption pores. (Plate V., fig. 7.)

The Parmelias grow on rocks, fences and trees, and apply themselves close to the surface to which they are usually attached by rhizoids. The upper surface is usually more heated than the under surface, while the rain water, absorbed by the substratum, is in contact with the lower cortex. The capillary tubes already described, which can give off excess of moisture as vapour from the upper part of their water column, will be replenished from below as long as the supply continues, inorganic salts will be supplied to the alga, and saprophytic matter absorbed by the fungus.

A living specimen of *Parmelia tiliacea*, Ach., whose upper surface was examined in reflected light under a low power (90 diameters), showed the pores as shallow pits, lighter in colour than the other parts of the thallus but *closed*. The plant (symbiotic) structure has therefore the power of closing the pores, but these are always open in thalli killed by chromo-acetic mixtures.

That these pores, as also the cyphellæ of the Stictaceæ, are not breathing pores only, seems certain from the facts already stated, as also from their position. In higher plants, when the lower surface of the leaf, the part usually provided with stomata, floats on water, the breathing pores are on its upper surface. In Anthoceros so-called stomata are found on the lower surface of the thallus, but their function is to secrete mucilage, and, as Goebel states, they are better named as mucilage pits. In Marchantia the pseudo-stomata are all in the upper cortical layer and not in the cortex that rests on the substratum. That the cyphellæ, and their offspring the absorption pores, should function as breathing pores only, and be placed on the surface closely attached to the bark or rock, is possible, but is unusual in the plant world. It must also be remembered that the pores can be closed above, but are open below, certainly in those species with hollow rhizoids.

To ascertain the true purpose of the cyphellæ of lichens, and of the absorption pores which are believed to be derived from them, the following experiments were made—the plant chosen being *Heterodea mulleri*, Nyl., selected on account of its terrestrial growth. The plants were gathered with a sufficient quantity of the soil of the substratum to prevent injury to the rhizinæ.

(I.) The plants were placed in a desiccator over calcium chloride and left for a space of three months, July to October, 1911. The upper surface and gonidial layer were the most deeply affected, and the drying of these portions caused the curling up of the thallus, so as to hide the upper cortex and show the brown underside. At the end of thirteen weeks, the plants, very dry and crumbly, were placed on absorbent paper, in their natural position, and water was poured from a can in a circle round them. The paper conveyed the water to the plants, it was absorbed by their under surfaces, and in 5-7 minutes from the water reaching them each thallus was green and expanded.

(II.) The plants, now healthy and normal, were divided into two equal portions, and one half was placed on several folds of newspaper; still with a small layer of soil adherent to each thallus, and watered in the same manner as in the first experiment, so that no water was applied to the upper cortex. The water was supplied from an ordinary can, tinned over, but rusted in one or two places, so that the only nourishment came from the tap water, the iron and the soil. These plants were healthy and normal under this treatment in January, 1912.

(III.) The second half of the plants left over from Experiment II. were placed in a japanned dish, and supplied with tap water, sufficient to cover them, which was changed daily. For six weeks they remained healthy and unchanged, but at the beginning of the seventh week they became gummy, as marine algæ do, that are placed in fresh water, and assumed an unhealthy, dark green tint. Taken from the water and placed on soil and paper, and treated as in Experiment II., they recovered, but never quite resumed their normal appearance.

In the first experiment, the loss of food matters, other than gaseous food—carbon dioxide—was felt most severely by the algal symbiont, and the shrinkage in the algal layer caused the curling inwards and upwards of the thallus. The loss of organic food, saprophytic fluids, did not severely affect the hyphæ, as they had the supply of organic food in the gonidia to draw upon.

In the third experiment the supply of gaseous food was cut off, except such quantities as were dissolved in the tap water, and the inorganic food was reduced to a minimum. The algal cells continued beautifully green throughout this experiment, and the thallus kept its normal shape, but the hyphæ became slimy and partly lost their vitality.

In the second case, when supplied with plenty of air, such inorganic foods as can be obtained from the soil, and water absorbed through the lower cortex only, both symbionts were able to develop normally.

As all species of Sticta and Parmelia are provided with upper and lower cortices, this would lead one to infer that the cyphellæ of Stictaceæ, and the absorption pores of Parmeliaceæ are means by which water and dissolved food matters enter the thallus and are carried by the hyphæ to the Cystococcus cells. Under the conditions of the second experiment, the rain water would not only carry inorganic food for the alga, but also organic matter from the humus of the soil, or the decay of cortical matter for the support of the fungus. This last would be additional to that taken from the alga by the haustoria of the fungus.

2. *The Cortex.*

The cortex, where not carrying apothecia, spermagonia or rhizinæ, usually constitutes 30-50 per cent. of the thickness of the thallus. The upper cortex is usually the thicker of the two rinds, and is not seldom twice or thrice the thickness of the lower covering. It takes an artificial stain better, the cells of the lower coat being more deeply tinted with a natural brown or brown-black pigment, resembling the phæophyll or phycophæin of the brown seaweeds. The hyphæ of the medulla have the power possessed by conidiophores of forming chains of cells by abstriction from their extremities. This power is seen in the formation of the cortices, of the haustoria surrounding gonidia, of the walls of the spermagonia, and of the sporiferous hyphæ. This change of hyphal threads into chains of cells can well be studied in the pseudo-cyphellæ of the Stictaceæ, where the ends of the hyphæ protrude loosely in minute necklaces into the cavities of the false cyphellæ, the terminal cells becoming white or yellow. These coloured cells were once regarded as soredia, but are only loosely arranged and partly used up cortical cells.

(A.) In the upper cortex of the Parmelias there are three different methods in which the thickened cells may be arranged. The first is shown in *P. limbata, P. tiliaceæ* and *P. saxatilis*, in which the cells are abstricted to form minute necklaces standing at right angles to the upper surface. The second as exemplified in *P. mundata* and *P. olivacea*, in which the cellular ends of the hyphæ strike the surface of the thallus obliquely, and the third in which the chains of cells are parallel to the surface, as in *P. tinctorum*.

The first series, with cells at right angles to the surface, has a cortex made up of larger units than those of the two following series. It is usually a mass of oval-oblong cells, .005-.006 mm. long, with a small lumen, not more than .0015 mm. in transverse diameter, and with very thick walls. The structure of the cortex in such lichens as *P. limbata* and *P. saxatilis* reminds one of the formation of similar tissues in the brown algæ Hormosira and Fucus, but in these the lumen of each cell is larger in proportion to the wall.

Although not belonging to Parmeliaceæ, this type of cortex can best be studied in *Thamnolia vermicularis*, Sw., in which the hyphæ of the medulla are loose, parallel and horizontal, on each side of the central cavity, but in the algal layer they turn outwards at right angles, surrounding the gonidia, and are continued beyond them to form the cortex. The same arrangement holds good for Parmelias of the *P. limbata* type, but the hyphæ are not as discrete and easy to follow as in Thamnolia, nor are they as wholly parallel and longitudinal in the centre. In *P. limbata* the upper rind is 5-6 cells in thickness.

The second series, typically shown in *P. mundata* and *P. olivacea*, has still smaller cells, but with thinner walls, these have 3-5 cells to the chain in each hyphal termination, and average .004 mm. in length. The obliquity of each thread is affected by curves and depressions of the surface, but, as a rule, the oblique threads are raised at their outward terminals towards the apex of the thallus.

The third type is best studied in *P. tinctorum*. In this lichen the hyphæ ramify in and around the small segregated masses of gonidia, and above and outside these run parallel to the surface. In dividing into necklaces of cells there is no enlargement by means of thickened walls as in the two preceding species. This form gives the most delicate cortex to be found in the family.

(B.) The lower cortex is continued into and supplies the lining hyphæ for the rhizinæ. These rhizinal threads are usually undivided into cellules, except those forming the outer layer in solid rhizinæ, and the outer and inner layers in hollow rhizinæ. Like the hyphal threads of the medulla which adjoin them, the cells of the lower cortex are arranged parallel to the surface, except in the neighbourhood of a rhizina, where they turn parallel to its walls.

The cellules of the lower cortex are equal in size to those of the upper layer in lichens of the first and second divisions, but in the third type, exemplified in *P. tinctorum* and *P. laxa*, the cells of the lower layer are larger, and possess thicker walls than those of the upper rind.

Where the cell-wall is thinner than usual, and less provided with the dense brown colour, as in the lower cortex of *P. tiliacea*, the cellules are seen to be uninucleate or binucleate.

In *P. perlata* the two cortices are of equal thickness, but the cellules of the upper layer are oblique to the surface, while those of the lower layer are parallel to the substratum. *Parmelia perforata* differs from all others of its genus in having the cellules of both the lower and upper cortices set at right angles to the horizontal surface. The long axis of the cell lumen is the guide in determining the direction of the cellules.

3. *The Hyphæ.*

These are best studied in *Parmelia placorhodioides* (Plate V., fig 8), in which they are the largest of the genus, reaching .002 in transverse diameter. As a rule they lie in the thallus longitudinally, but, as before stated, they turn at right angles to the medulla in the algal or gonidial layer, and reach the upper surface in various ways as described in the last subdivision. Each hypha is multinucleate, and, by long staining in Delafield's hæmatoxylin, the nuclei may be made visible in many species. The medullary hyphæ of *P. placorhodioides* and *P. mundata* are also remarkable for presenting an apparently cellular appearance. This is due to their containing oval masses of protoplasm, revealed through the gelatinised walls. Sometimes these oval masses are larger than usual, and bulge out the hyphal wall. These larger masses are single or occasionally in pairs and recall in their position and relative size the heterocysts of Nostoc and its allies. It was probably through being misled by these appearances that Minks and his school combated the theory of the dual nature of lichens, and strove to prove that the gonidia were produced from the hyphal threads. This appearance is figured by Willey in his "Introduction to the Study of Lichens," p. 60, Plate II., as micro-gonidia.

In the algal (gonidial) layer the hyphæ put out fine branches which adhere to the coat of the alga, joining it like the stalk joins a cherry, and from this stalk branches of much less diameter than the medullary hyphæ surround each algal cell. These branches have the same necklace appearance, from a division into cellules, as has the cortical weft. When, in sectioning, a gonidium has been displaced, a cavity lined with these smaller hyphæ is disclosed.

In illustrations of thalline structures, small gonidia are often shown scattered through the gonidial layer. These supposed gonidia are usually the cut ends of hyphæ, which, by an optical illusion, are made to appear, when viewed end on, as if they were of greater diameter than the hyphæ of which they are transverse sections.

Although, as shown above, the hyphæ branch repeatedly in surrounding the Cystococcus cells, they divide very sparingly in the central or medullary layer. The branches in any given lichen usually fork at about the same angle, varying from 45 deg.-60 deg. in *P. placorhodioides* to 75 deg.-90 deg. in *P. mundata*. The hyphæ of the former branch in the central portion of the thallus very sparingly, in the latter rather more freely.

4. *The Algæ or Gonidia.*

With an exception to be given later, the algal layer in Parmeliæ is confined to the stratum immediately beneath or within the upper cortex. It has already been stated that the medullary hyphæ turn from their parallel longitudinal course in the centre of the thallus, and pass at right angles to their former direction to penetrate between the gonidia, and form a close cellular weft around them. This weft is then continued to the surface to form the upper cortex. The algæ lie loosely among these cortical threads at their inner extremity, or are ordinarily gathered into small groups probably derived from a common ancestral cell.

In some species, as *P. placorhodioides*, the algal cells below the apothecia are few and colourless, or nearly so, and look as if they were exhausted or dying; but in these situations a second algal layer is produced near the lower cortex, of vigorous cells well supplied with protoplasm. They are .008 mm. in diameter in *P. placorhodioides* and .006 in *P. limbata*. (Plate VII., fig. 12). In *P. latissima* the Cystococcus (Pleurococcus) cells are thickly packed between the necklace-like rows of cells of the superior cortex, and are not more than .004-.005 mm. in diameter. They are difficult to study, as they seldom show below the cortical threads, which surround and hide them.

However carefully the tissue may be treated before sectioning, many of the algal cells become plasmolysed. The best killing mixture is chromo-acetic, Schaffner's formula, and the species that permits the best study of its gonidia is *P. tiliacea*. These are scattered singly through the thallus, are promptly killed by the solution, and show no relative shrinking of the protoplasm, although there is a shrinkage as a whole, since they no longer fill the hyphal cavity. In the Cystococcus cells of this lichen the nucleus and single chloroplast can be studied. The nucleus usually occupies a central position in the alga, and occasionally bands of protoplasm radiate from it towards the circumference, in which are set rather large chromatophores, presenting an arrangement, more apparent than real, as if they were in circles round the nucleus.

Algal cells in the act of dividing are not frequently observed, but they may be found by careful searching, and by the fact that two of these cells, or more rarely four, enclosed in the same plexus, have flat surfaces where they face one another. (Plate VI., fig. 9.)

The best stain for algal cells, as also for lichen spores, is methylene blue.

5. *Rhizinæ.*

Of the ten species of Parmelia examined, all are provided with rhizinæ except *P. placorhodioides* and *P. mundata*, which belong to the section classified by Nylander, Synopsis, p. 400, as "Stirps Parmeliæ physodis, Thallus subtus glaber."

The rhizinæ in Parmelias differ markedly from those of their allies the Stictas. In the latter they are composed of comparatively few hyphæ, which separate readily, and disclose their ultimate structure of cylindrical cellules, bounded by rather thin walls. These cellules contain the curious protoplasmic pyrenoids, which Willey, Minks, and Jean Muller classed as micro-gonidia.

In Parmelia the rhizinæ are formed of dense multitudes of hyphæ lying parallel to the long axis of the rootlet, derived from the hyphæ of the medulla, and encased by a continuation of the cortical threads, which coat them externally, and when they are hollow as in *P. limbata* and *P. cetrata,* also form an inner layer to the tubular rootlet. The walls of the rhizinal hyphæ are dense, and the threads are by no means discrete as in the genus Sticta. The outer threads have the thick walls and necklace-like structure of the cortical hyphæ, the lumen of each cell being small in contrast to its diameter.

In the central threads which show no division into cellules, the so-called "micro-gonidia" can be clearly distinguished.

Parmelia perforata differs from its allies in having rhizinæ wholly composed of hyphæ made up of tubular cellules whose course in the rootlet is less parallel than those of kindred species.

The Parmelias inhabit stones, rocks, fences, and trees, in situations where there are, in Australia, strong contrasts of temperature and rainfall. The Stictas inhabit scrubs and brushes, where shade and rain are plentiful. With the steady drip of rain and dew on the tree trunks and branches, moisture is always available to a Sticta, and its rhizinal system is simple and delicate. The Parmelia has to face more difficult circumstances; its rhizinæ are thicker, the threads have stronger walls to prevent desiccation, the hyphæ are more numerous to take advantage of every particle of water, and to cling to every crevice, and the cortical system of each rhizina keeps the unseptate threads from loss of imbibed water by evaporation, and from interference with their functions.

It has been shown that, in two species at least, *P. limbata* and *P. cetrata,* the hollow rhizinæ are in connection with absorption pores, and this gives an additional reason for believing the pores to be used for taking in liquid food.

6. *The Spermagonia.*

These are small conceptacles, sunk in the thallus, and varying from circular to ovate or obovate in transverse section, ranging from .3-.7 mm. in diameter. They arise as small coils of hyphæ in the medullary part of the thallus, without pores or connection with the upper or lower cortex. At first occupying a central position, growth develops more rapidly on the side towards the upper cortex. The hyphæ forming the wall of the spermagonium are brown and recall in appearance those of the rhizinæ. At an early stage the original coil is lost sight of under the outer layer of numerous brown threads, but a section which cuts these away renders the now enlarged coil visible. (Plate VI., fig. 10.)

As soon as the wall of the spermagonium has grown into touch with the upper cortex, the portion of the spermagonial wall in contact becomes raised into a papilla, which breaks through the cortex (Plate VII., fig. 11), and then opens to form a pore for the discharge of the spermatia. The lip of the ostiole is the thickest portion of the wall. In a few instances the upper cortex was observed to increase in thickness by downward growth towards the spermagonium, the two dark-brown mass s of hyphæ interwove, and a pore developed by separation of the hyphæ in the cortical filaments that now form part of the spermagonium. The centre of the ostiole is depressed, with raised circular lips. The opening may appear on the surface of the thallus as a black or brown speck, or may be concolorous with the upper cortex.

The jointed sterigmata, the stalks that bear the spermatia, the supposed male germ-cells, radiate from all parts of the inner wall towards the centre. In Parmelias they are .02-.04 x .002-.0008 mm. in cross diameters, and usually composed of 5-7 jointed cylindrical cellules. By some authors these jointed sterigmata are called arthrosterigmata, but by others this term is restricted to those spermatial supports that have cellules broader than they are long.

The study of the sterigmata is difficult from the fact that they are bound together by a gelatinous substance; which, in sections of spermagonia parallel to the sterigmata, cause the section to appear as if homogeneous. This appearance is further aided by the colourless or faintly yellow colour of the threads.

The spermatia of Parmelias are of two types, the first series possess acicular spermatia with slightly fusiform apices, as in *P. perlata*, *P. perforata*, and their allies. This form of spermatium is also characteristic of the genera Sticta and Stictina. The second section have acicular-cylindrical spermatia, as in *P. laceratula*, *P. polytropa*, *P. placorhodioides* and other Australian species. In this respect they resemble the genus Physcia.

The spermatia in the genus Parmelia are .005-.008 x .006-.001 mm. in diameter, and are colourless and do not stain readily. They are found either *in situ* on the sterigmata, or loose and embedded in the gelatinous substance, or ejected from the spermagonium in myriads, and still immersed in the same gelatinous substance.

7. *Alliances with other Genera.*

The great lichenologist, Nylander, made his classification depend mainly on the thallus, the apothecia and the spermagonia. On p. 57 of the Synopsis, he says, "Toutes les parties des Lichens, le thalle, les apothécies et les spermagonies, peuvent offrir des caractères servant à la distinction des espèces, et tantôt c'est l'une, tantôt l'autre de ces parties qui decide le diagnostic dans des cas ambigus. Mais lorsqu'il s'agit des lichens inferieurs, il faut avoir recours au microscope pour chercher dans la texture des tissus et la conformation des éléments, soit du thalle, soit du fruit ou des spermagonies, les signes qui caractérisent les espèces. Ou ne doit cependant pas oublier que les caractères microscopiques, dans certain espèces, sont aussi sujets à varier que les autres. Ainsi le nombre des spores dans les theques, le nombre des cloisons dans les spores, la couleur de ces dernières, leur grandeur, varient souvent dans les espèces polymorphes, tandis que les mêmes caractères offrent une grande fixité dans d'autres. Les spermaties et leurs stérigmates serviront aussi quelquefois à la distinction des formes douteuses ou des échantillons manquant de fruits."

Of these tests for specific and generic differences that of the spermatia and sterigmata has, since Nylander's time, fallen out of use. In the last great work on Lichenology—"A Monograph of the British Lichens, Part II., by Annie L. Smith," published by the authorities of the British Museum, although the characters of the spermatia are given for the orders, and generally for the genera, there is seldom a reference to these organs in the specific descriptions, even when, as in the characteristics of the genus Lecidea, p. 10, the spermatia are described as "acicular, straight, rarely arcuate or shortly cylindrical."

In the Monograph referred to above the classification does not lean greatly on the symbiosis of alga and fungus, for though the gonidia are spoken of throughout as "algal cells," yet such statements are common as p. 206, "algal cells, Trentepohlia or Palmellaceæ," p. 275, "algal cells, Pleurococcus or Palmella," etc.

In this extremely important work the classification depends almost wholly on the microscopic structure of the fruit. As Miss Smith states in her Introduction, "More importance is assigned to the microscopic structure of the fruit than was allowed by Nylander and Crombie in their scheme of classification. The systematic value of the form, colour and septation of the spores had, however, been recognised by Massolongo and other continental Lichenologists, and by Mudd in our own country."

The system adopted is, in fact, that devised by my correspondent of many years, the late Dr. Jean Muller of Geneva, and perfected by Dr. Zahlbrückner in Engler and Prantl's Pflanzen-familien. To show the want of concordance under this system, let us look at the place assigned to Parmelia by a few of the great modern lichenologists: —

(1) A. M. Hue, Nouvelles Archives du Museum d'hist. Nat. 3e series. T. II., unites Evernia, Everniopsis, and Anzia with Parmelia under Parmeliei, but separates from these Sticta and Stictina.

(2) Jatta, in "Lichenum Italiæ Meridionalis," places under Parmelias—Cetraria, Peltigera, Nephroma, Solorina, Sticta, Imbricaria, Parmelia, and Physcia.

(3) Dr. Jean Muller, "Lichenes Ernstiani," Hedwigia, Band XXXIV., 1895, etc., etc., unites under Parmeliæ—Sticta, Stictina, Parmelia, Anzia, Pseudo-physcia (or Anaptychia), and Physcia.

(4) Fink, in the "Lichens of Minnesota," pp. 190-210, groups under Parmeliaceæ—Parmelia, Cetraria, Evernia, Ramalina, Alectoria, and Usnea.

It is evident that dependence on the microscopic structure of the apothecium may separate species but will not give the major feature of classification.

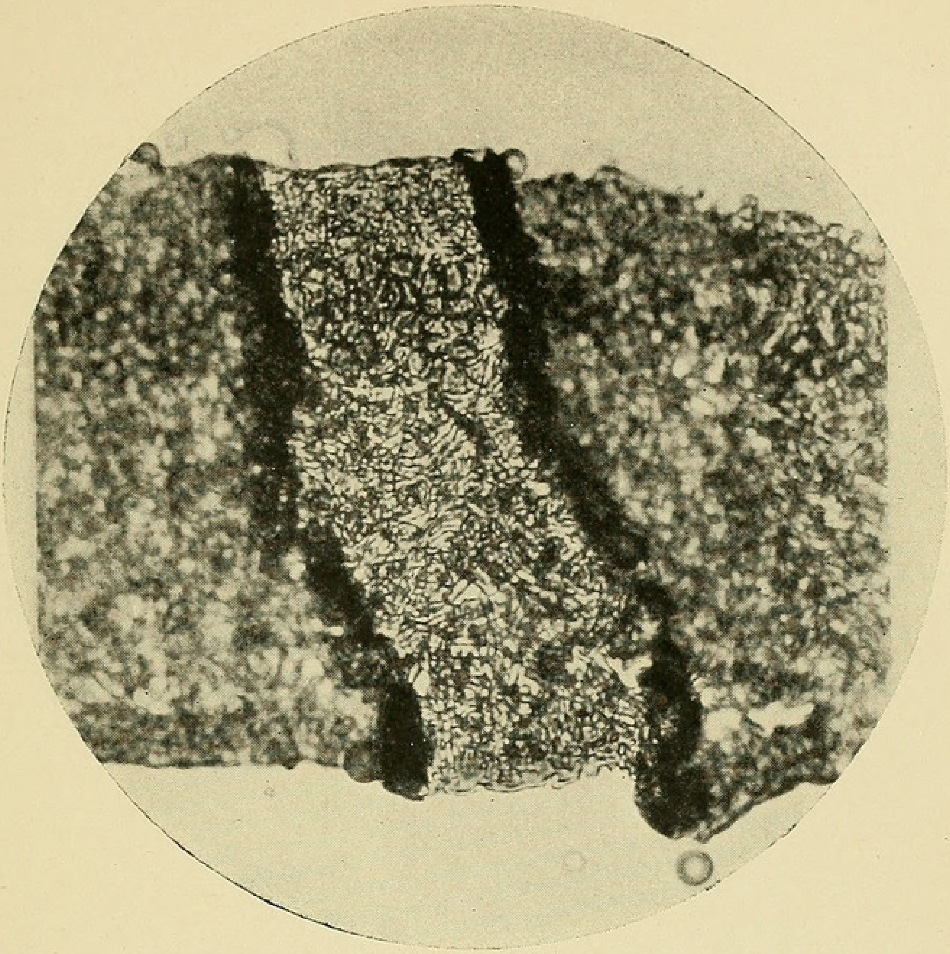
To divide the genera into orders a microscopic examination of the thallus is also necessary. In Sticta, Stictina, and Parmelia both an upper and a lower cortex are present; and the thalli are provided with cyphellæ or absorption pores. In Sticta and Stictina there are, besides the cyphellæ, openings in the upper cortex. These are not joined to the cyphellæ by tubes, but by air passages of irregular shape ramifying through the thallus, and best studied in *S. suborbicularis*.

Physcia and Solorina have an upper cellular cortex, but in *Physcia hypoleuca* and *Solorina bispora* there is a lower pseudo-cortex of hyphæ passing into rhizinæ. The former is also provided with absorption pores, the latter has curious slender tufts of contorted paraphyses scattered through the hymenium, that probably serve the same purpose. In *S. bispora*, where an apothecium rises from the upper cortex, the pseudo-cortex of hyphæ of the lower surface is replaced by a true cellular cortex.

Heterodea has the thallus of Parmelia and the apothecium of Cladonia. It is of considerable phylogenetic importance as it forms a link between the two families.

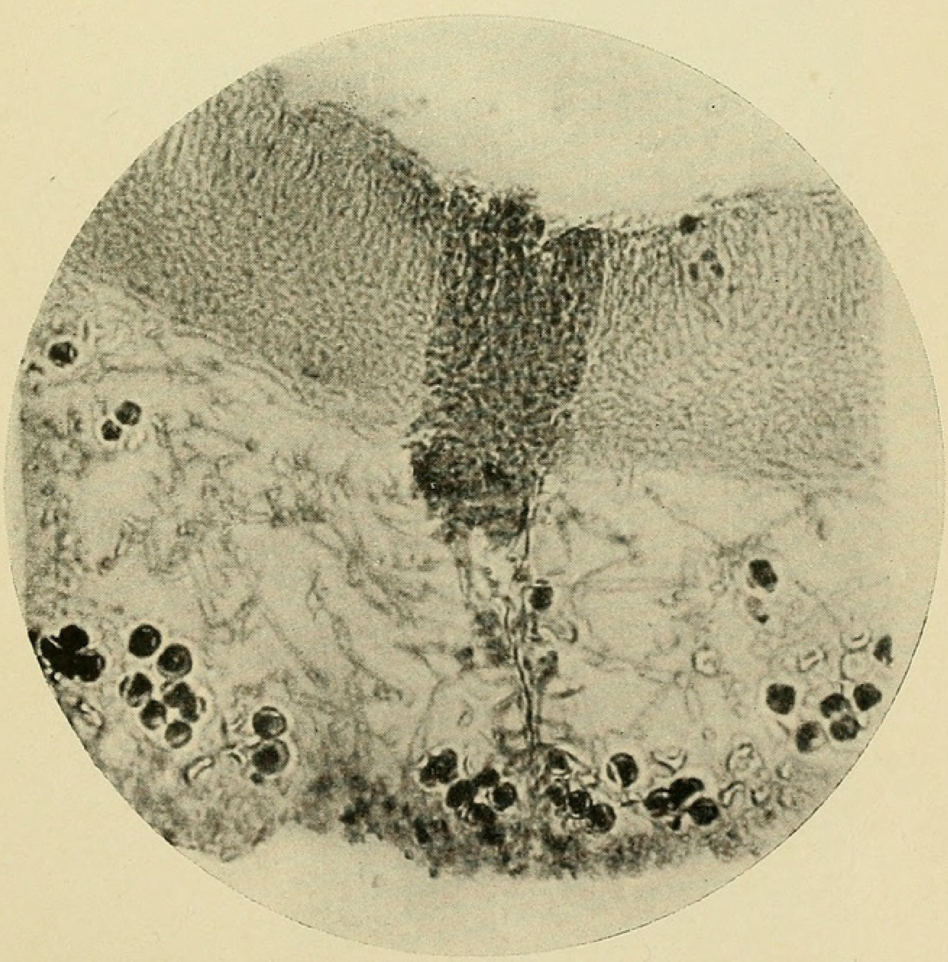
Taking all the histological factors into consideration, Evernia is best placed with Alectoria, Ramalina, and other fruticose species under Usnaceæ, as in Zahlbrückner's classification; and with these I would also range Cetraria on account of the frequently subpodicellate apothecia, and because of the close relationship of the fruticose species to Usnea. Peltigeraceæ should be restricted to Peltigera, Nephroma and Solorina, in which the algal symbiont is provided by the Cyanophyceæ-Polycoccus or Dactylococcus; while Parmeliaceæ should include Sticta (comprising also Lobaria and Ricasolia), Stictina, Parmelia, Physcia, Pseudo-physcia or Anaptychia, and Anzia. This last order, Parmeliaceæ, should be divided into two sections, the first made up of genera with both upper and lower cortex—Sticta, Stictina and Parmelia, the second formed of the remaining genera with upper cortex and lower pseudo-cortex.

Figure 1.



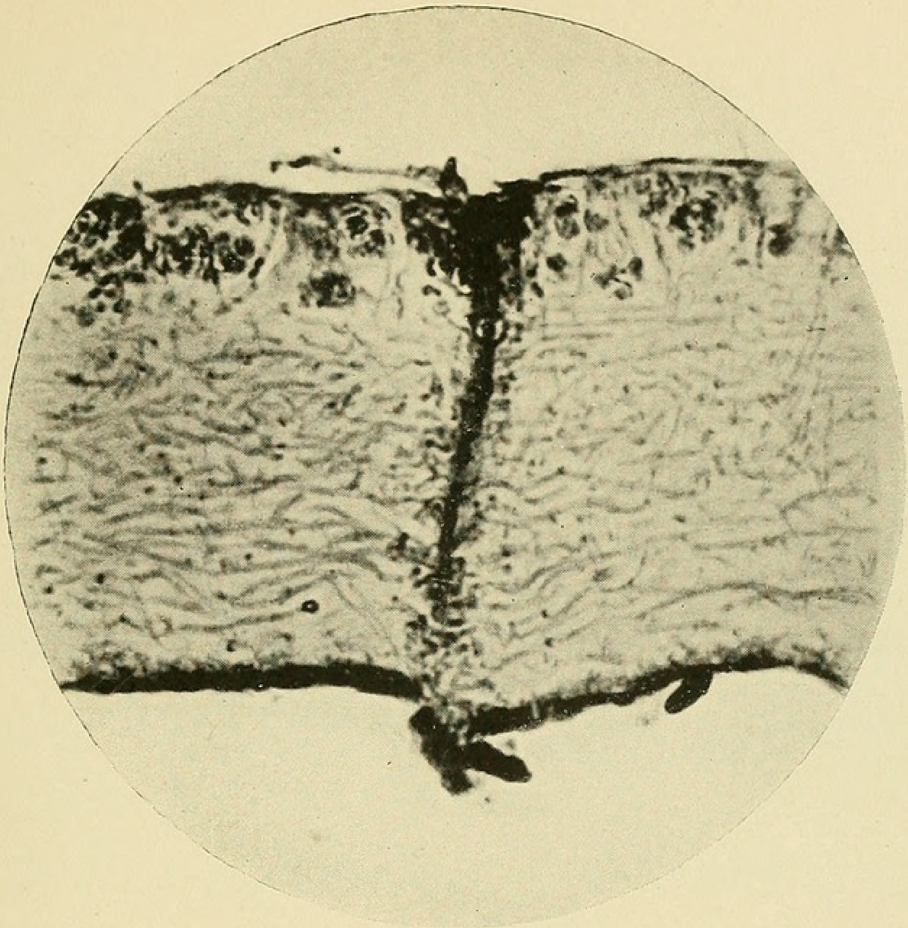
Absorption pore of *Parmelia tiliacea*, Ach., x 300.

Figure 2.



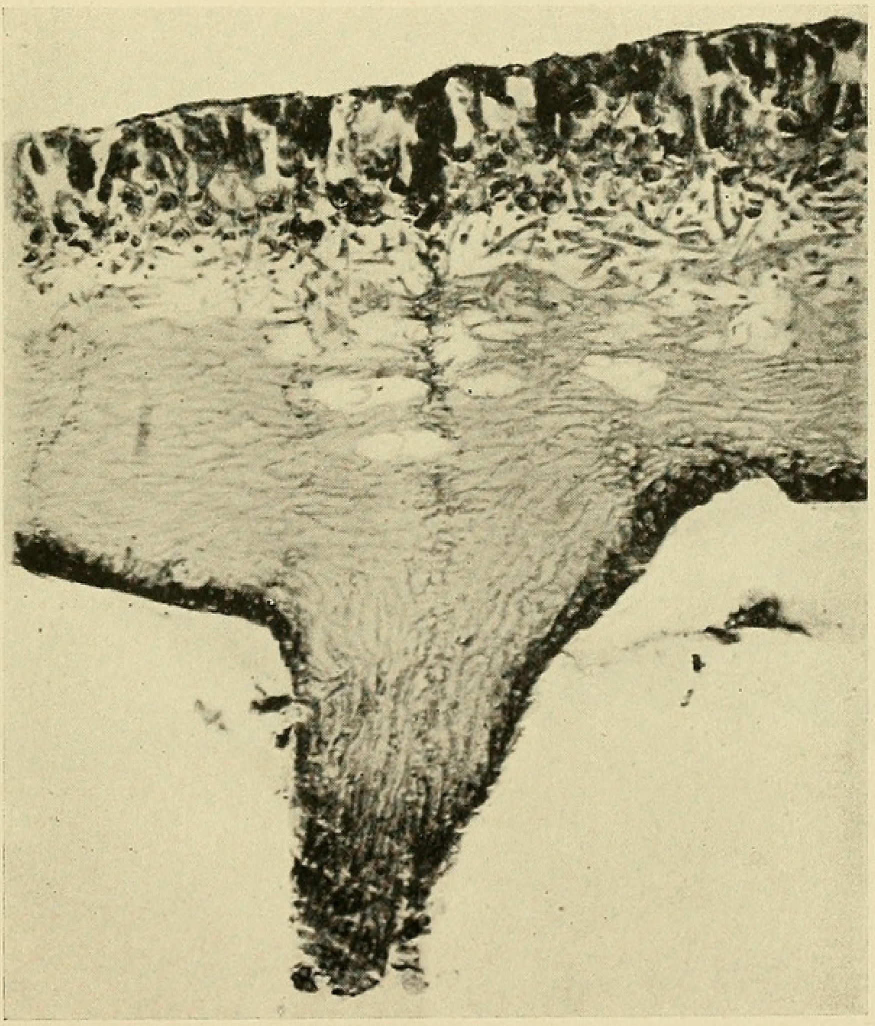
Absorption pore of *Parmelia placorhodiodes*, Nyl., x 300.

Figure 3.



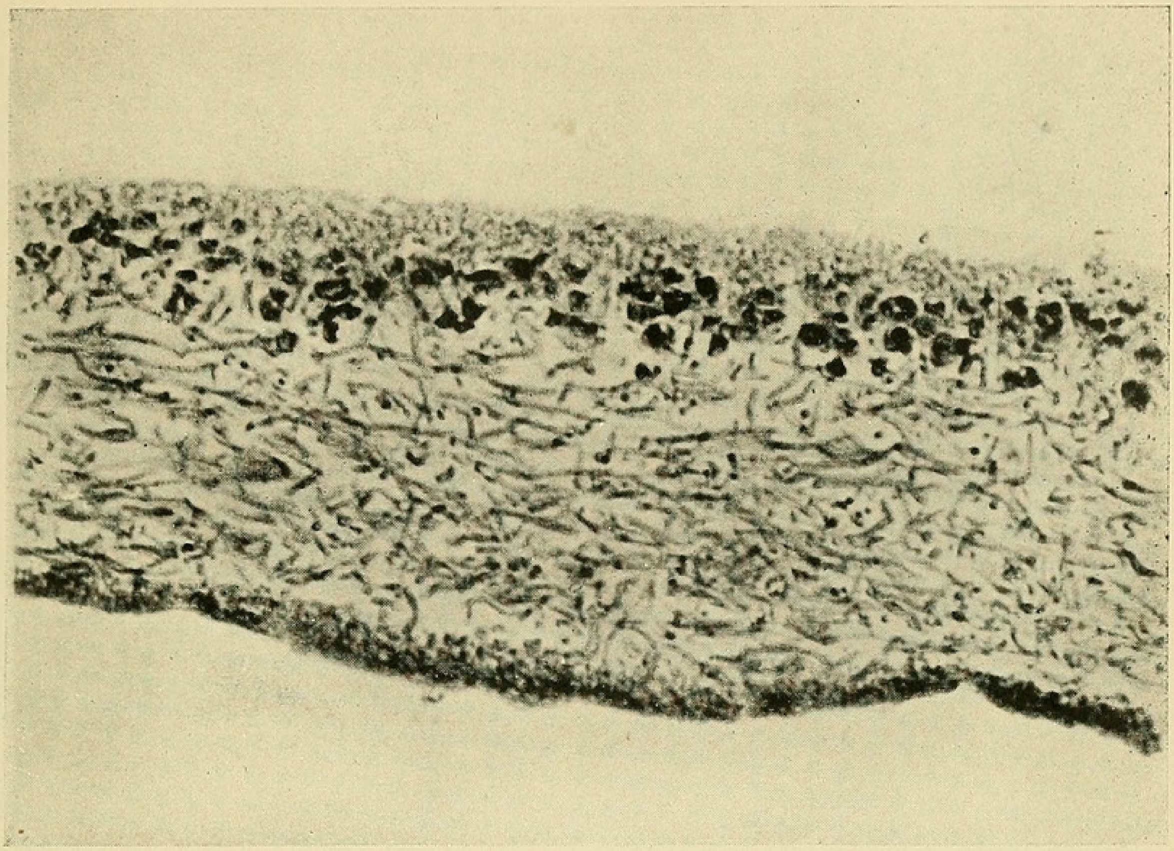
Absorbent pore of *Parmelia tinctorum*, L., x 300.

Figure 4.



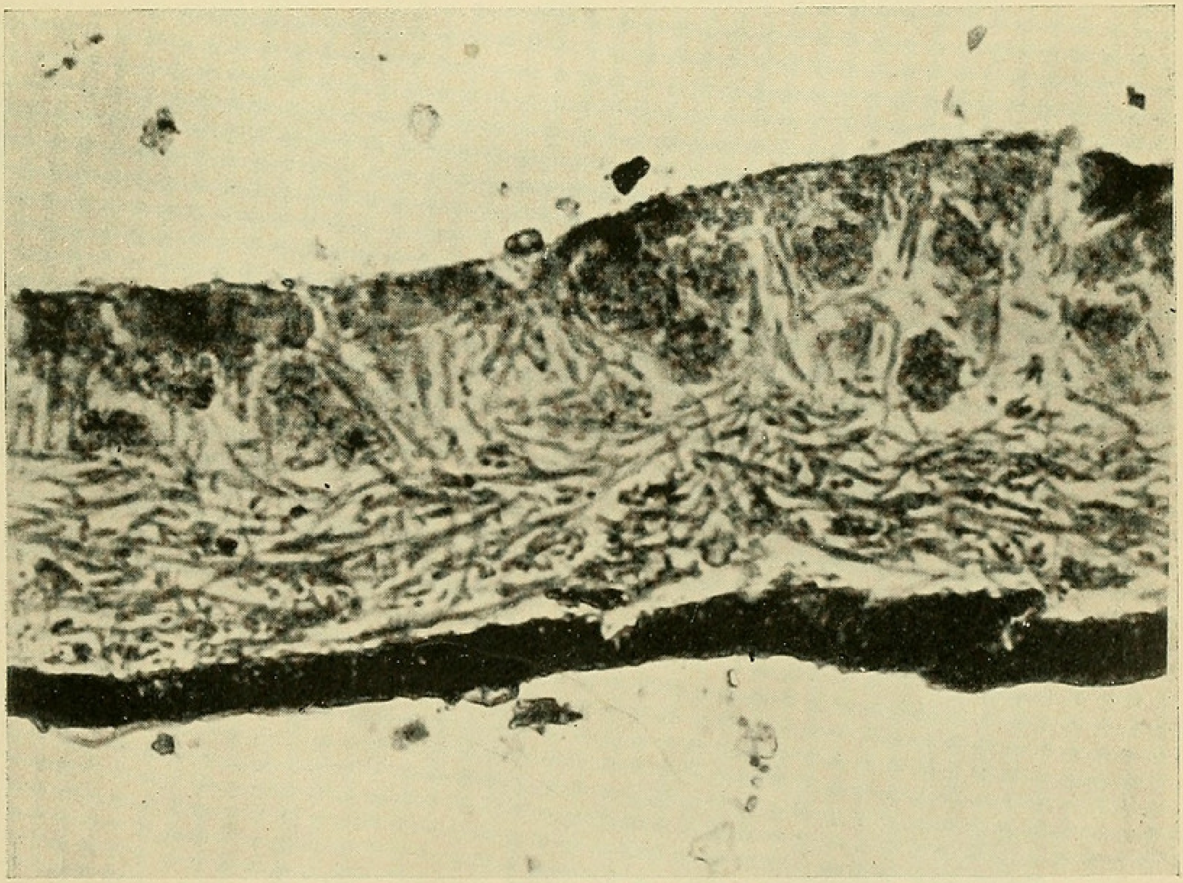
Absorbent pore of *Parmelia limbata*, Laur., x 300.

Figure 5.



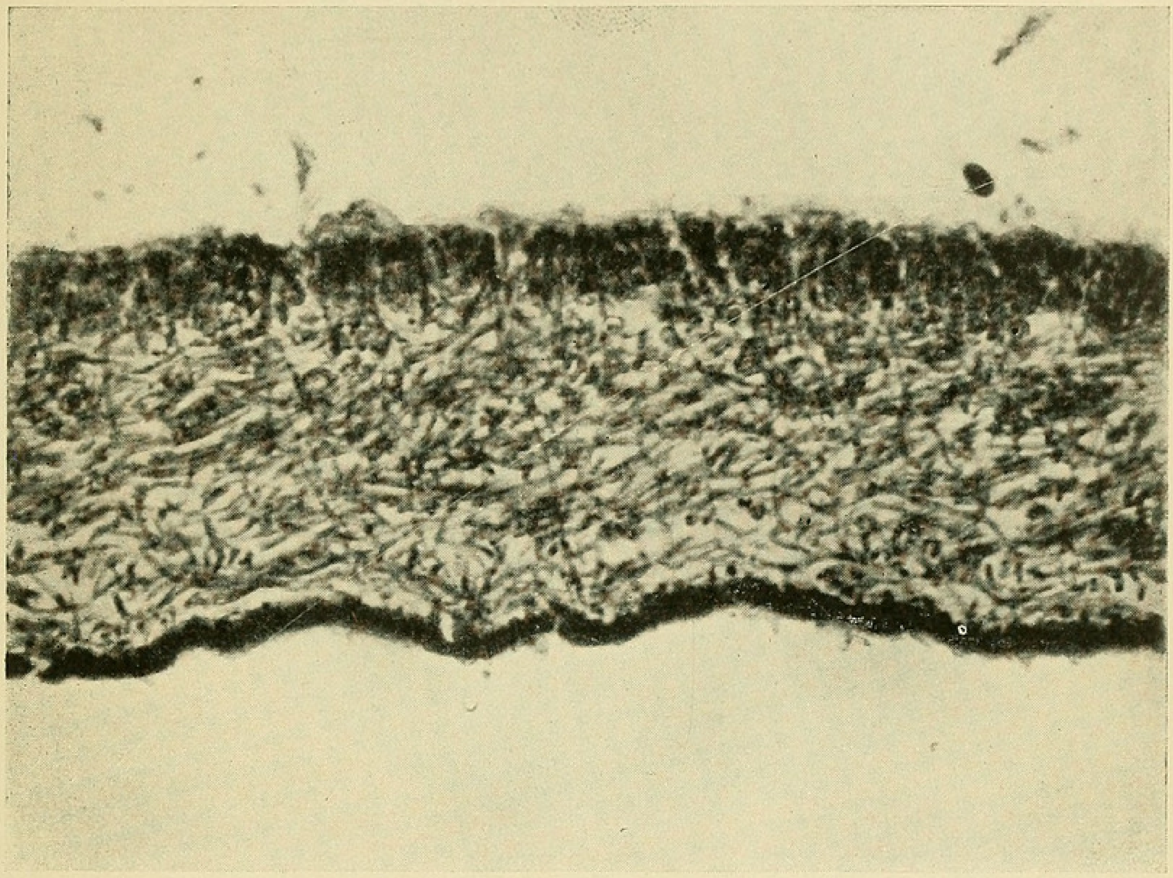
Thallus of *Parmelia laxa*, Mull. Arg., x 300.

Figure 6.



Thallus of *Parmelia cetrata v. sorediifera*, Wain., x 300.

Figure 7.

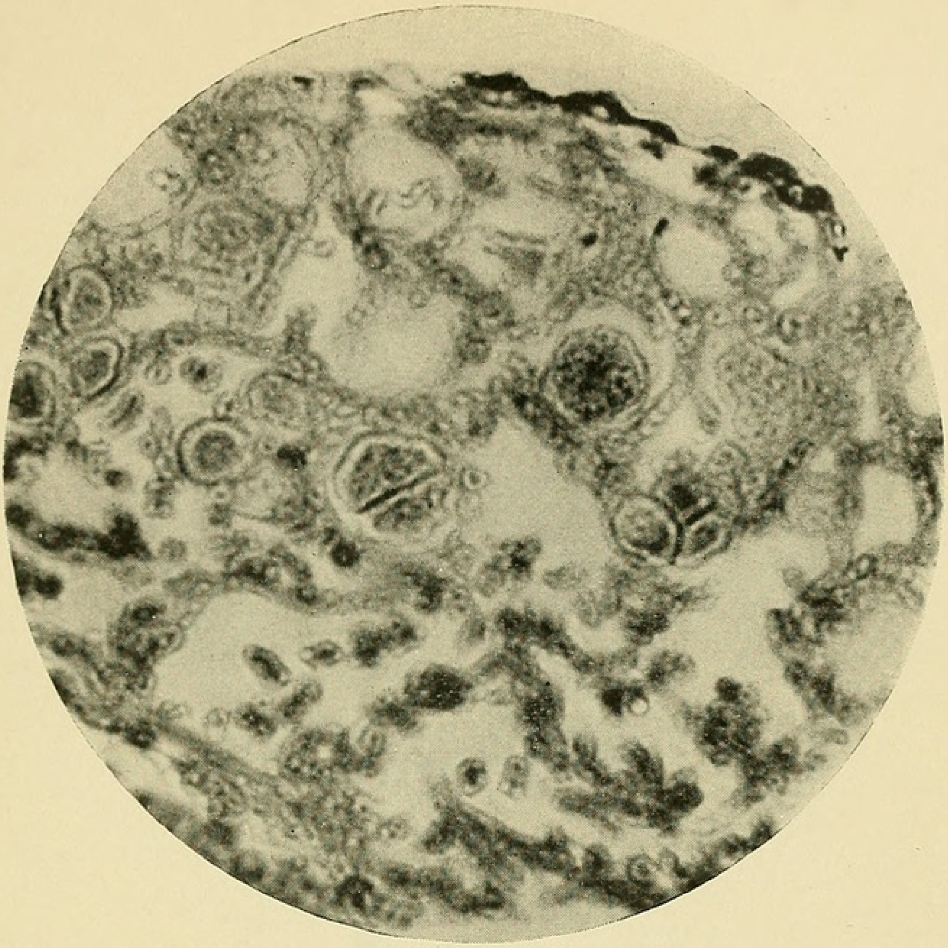


Thallus of *Parmelia latissima,* Fee, x 300.

Figure 8.

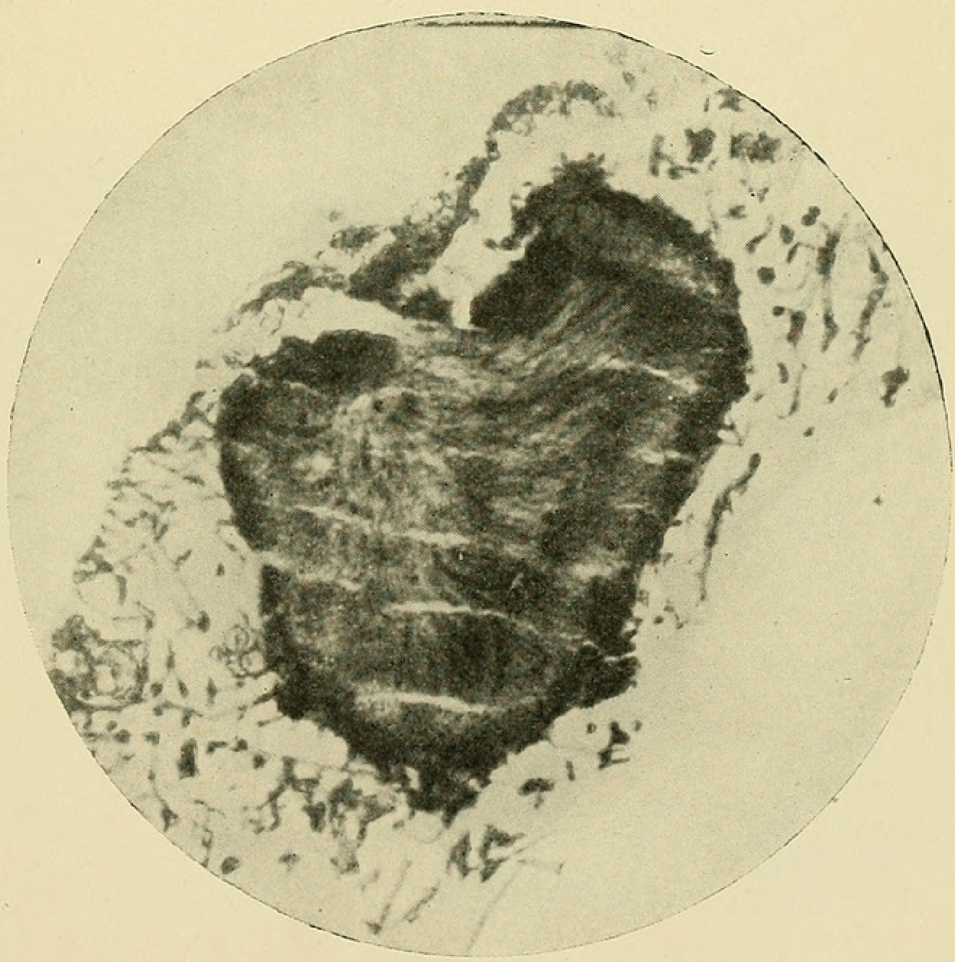
Symbiosis of hyphæ and gonidia, *Parmelia placorhodioides,* Nyl.

Figure 9.



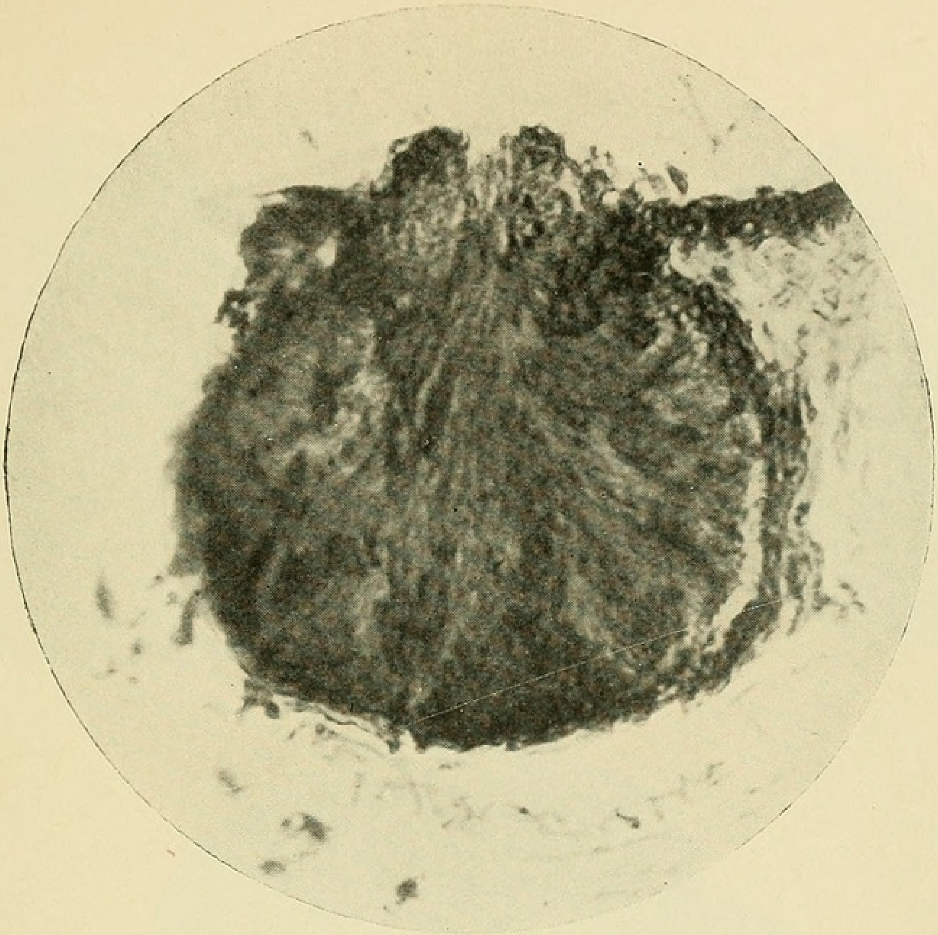
Gonidia (*Polycoccus*) in the act of dividing, x 770.

Figure 10.



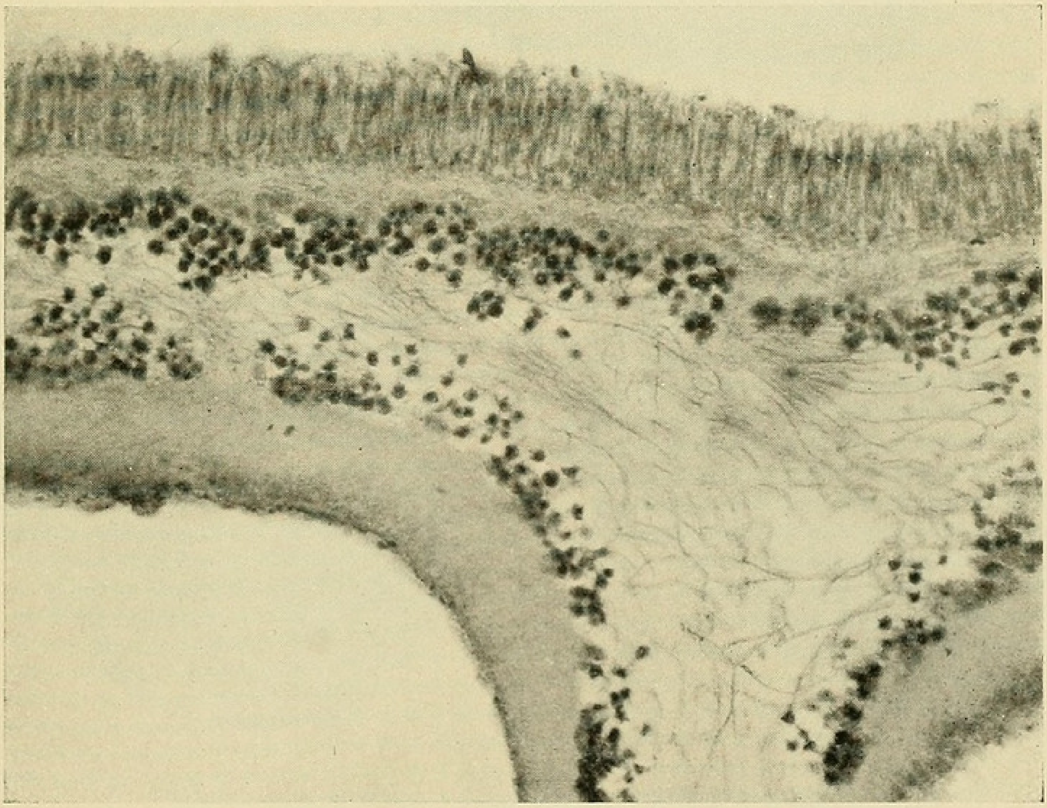
Section of Spermagonium, showing wall and remains of the original hyphal coil or scolecite, x 300.

Figure 11.



Spermagonium showing Ostiole, x 300.

Figure 12.



Apothecium of Lichen with double layer of Algæ.

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Shirley, John. 1918. "The Thallus of the Genus Parmelia." *Papers and proceedings of the Royal Society of Tasmania* 53–68.

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