

XIV.—*On the Reproductive Organs of the Lichens and Fungi*
(First Part). By M. L. R. TULASNE*.

AMONG the various products originating on the thallus of the Lichens, the black points to which the attention of botanists has been recently directed by M. Itzigsohn, are not those least worthy of thorough examination. Long known to lichenographers, these points have been taken sometimes for parasitic Fungi of the order Pyrenomycetes, sometimes for anomalous fructifications, or even for peculiar species of Lichens. With regard to their organization, M. von Flotow, who seems to be the last who has spoken of them, appears to consider them as little utricles filled with a mucilage in which swim cylindrical corpuscles of extreme tenuity, animated with a molecular motion. In his eyes these corpuscles are spores in a rudimentary condition, destined however subsequently to become perfect reproductive organs. M. Itzigsohn, on the other hand, has been induced to regard the points in question as antheridia analogous to those of the Mosses and Hepaticæ, and the corpuscles they contain as animalcules endowed with a movement of translation. He affirms that these corpuscles become developed, like the spermatozoids already known, within lenticular cells seemingly imbedded in the green tissue of the Lichen. Like MM. Kützing and Von Flotow, I have not been able to witness the vital motion attributed to these corpuscles, even by employing the means recommended for the purpose; and far from seeing them originate in special cells like the spermatozoids of the Muscinæ, I have satisfied myself that they are developed on the surface of a basidigerous *hymenium*, and owe their origin to an acrogenous vegetation.

Whatever resemblance there may be, at first sight, between the black or brown points in question and the antheridia of the stemless *Jungermannia* for instance,—that a kind of mucilage, a white, gray, or brownish pulp is poured out by both,—the elements of this substance and the structure of the organ in which it is elaborated are unlike in the two cases. In the Lichens, the pulp effused from the thallus is composed solely of linear bodies which are very short and slightly curved, or more elongated and thin, either strongly curved into an arc or more or less flexuous; but these corpuscles never appear to present cilia or appendages of any kind, and their confused movements do not differ from the molecular trembling described by Mr. Brown; in a word, they do not possess the characters which distinguish those singular beings engendered in antheridia properly so-called.

They differ no less, as I have said, in their mode of develop-

* Translated from the *Comptes Rendus* for March 24, 1851.

ment. The globule or conceptacle which produces them is imbedded in the thallus of the Lichen, commonly beneath an obscure point or a prominence which reveals its presence. Sometimes it possesses special walls, and may be extricated entire from the tissue in which it seems to grow as a foreign and parasitic body (for example, in *Parmelia physodes*); more frequently it is intimately connected with the parenchyma of the Lichen, and its form only marked there by its peculiar colour. In other Lichens it is divided into a number of loculi, sinuous cavities, by various processes, or more or less perfect partitions. Whatever may be the internal organization, it opens on the surface by a rounded pore, little converging slits or irregular chinks.

The corpuscles which emerge through these orifices originate like acrogenous spores, isolated or twin, upon the cells which form the internal walls of the globule, or laterally from moniliform filaments, or various processes lining the cavity. Sometimes a long filament, which becomes divided into a variable number of corpuscles, becomes developed in place of one of these corpuscles. This genesis has nothing really in common with that of the spermatozoids, which all originate in the interior of special cells, from which they disentangle themselves soon after their exit from the antheridium. But the circumstance that approximates the corpuscles in question to true spermatozoids is their equal tenuity; for, with a thickness which appears scarcely equal to a thousandth of a millimetre, the majority measure not less than three thousandths of a millimetre in length; some are eight or ten times as long, but no thicker.

Taking into consideration the whole of the characters presented by these point-like conceptacles, which I propose to call *spermogoni*, one would be inclined to regard them as foreign bodies on the Lichen, as parasites upon its thallus, analogous to the *Septoria*, *Phyllosticta*, and other minute Fungi which live upon fading leaves, aware of course that these latter possess an organization almost identical with that just described. Yet there will be hesitation in deciding thus, when it is recollected how frequent these *spermogoni* are on the thallus of almost all Lichens, a frequency sometimes so great as to exclude all normal organs of fructification (I have seen examples in *Endocarpon fluviatile* and *E. hepaticum*); that is to say, if the ascigerous apothecia alone deserve this name. The examples furnished by *Verrucaria* and analogous genera have also much weight on the question. It may be ascertained in *V. atomaria*, that its apothecia, when observed at a certain age, inclose at the same time and in great numbers both corpuscles wholly resembling those contained in the *spermogoni* of other Lichens, and fertile spores of the well-known structure. It is further observable that the development

of these corpuscles (which might be called *spermatia*) precedes that of the spore-bearing cells, for the young apothecia are densely filled with the first before the second have acquired a recognizable form. On the dissociated thallus of *V. epidermidis*, seminiferous perithecia and other smaller conceptacles containing only the linear corpuscles or *spermatia* occur scattered and intermingled, and it is impossible to avoid regarding those two kinds of perithecia as belonging to one and the same plant.

An examination, both of other crustaceous Lichens (e. gr. *Urceolaria scruposa*, *cinerea*, *Lecanora atra*, *circinata*, *Placodium murorum*, *radiosum*, *Squamaria lentigera*, &c.) and of foliaceous Lichens (e. g. *Parmelia tiliacea*, *aipolia*, *Acetabulum*, *Gyrophora hirsuta*, *pustulata*, *Loboria pulmonacea*, *Sticta glomulifera*, *herbacea*, &c.), will in like manner show that the Itzigsohnian corpuscles or *spermogoni* which occur in them must belong to them; and it is impossible to doubt that they are peculiar organs of these plants, unfairly neglected by lichenographers hitherto. This opinion may be expressed with the more assurance since it is by no means the case, as M. von Flotow imagines, that these organs occur only on certain Lichens, for they are found upon so great a number that the list of the species which appear to be devoid of them is probably very limited.

On the other hand, the extreme dissimilarity of form and size existing between the *spermatia* and true spores, the constancy of these differences, and above all, the mode of generation peculiar to each of these organs, render the idea that the *spermatian* corpuscles are imperfect or young spores, altogether improbable. If this be so, neither perhaps does their extreme tenuity allow us to suppose that they are organs of fissiparous or gongylary reproduction, the Lichens being moreover furnished very abundantly with organs of this nature in their gonidia and the gemmæ of various forms of which these are the principal elements. Thus these reflections tend to increase the probability of the opinion which regards, with M. Itzigsohn, the brown points observed by him as organs of the male sex in the Lichens. But it must not be concealed that their little analogy, in regard to structure, with the antheridia of the Algæ and Muscineæ, is unfavourable to their assimilation with these organs. So that just as the nature and true functions of the latter seem destined to be for a long time more or less problematical and questionable, this will doubtless also be the fate of the *spermogoni* in the history of the Lichens. At the same time it is doubtful whether their dissimilarity from the antheridia already known is a sufficient reason for denying the function attributed to them; for, if among those there are some which are similar, as the antheridia of the Mosses to those of the Ferns, others, such as the antheridia of the Algæ

and those of the Salviniaceæ, have scarcely any parity of structure either between themselves or with the former.

Perhaps the study of the Lichens alone may not procure sufficient data for the solution of the question of the nature and physiological functions of the *spermatia*: this doubt has led me to make some researches in the class of Fungi, the results of which, joined to those previously obtained by observations exclusively devoted to the Lichens*, indicate, if I am not deceived, that the latter, in spite of the name *aërial Algæ* which has been applied to them, are connected with the Fungi by an affinity much closer than has been generally believed.

(Second Part. †)

The great resemblance between the spermogonia of the Lichens and the *Pyrenomycetes* of the genus *Septoria* or their allies, leads to the suspicion that these little Fungi are not, as is generally supposed, autonomous productions—that they do not represent, alone, an entire vegetable species; and since several of these have been described sometimes as *Sphæria*, sometimes as *Septoria*, it is probable that they have been observed at different epochs of their development, and that each of these ambiguous *Septoriæ* corresponds to a peculiar *Sphæria* or other thecasporous *Pyrenomyces*, which succeeds it and forms with it but a single species of Fungus. What would be true of the *Septoriæ*, should extend to a great number of other genera of *Pyrenomycetes* or of *Coniomycetes*, which in like manner would comprise only the dissociated members of species composed of several terms. This assertion is in fact now borne out by several proofs.

The *Cytisporæ*, which have so much analogy to the *Septoriæ*, were called by Tode *Sphæria cirrhifera*, and in the most recent classifications are placed near the *Sphæria* or confounded with them. The reason of this is not to be sought in their organization, which differs extremely from that of the *Sphæria*, but far rather in that remarkable correspondence, noted by M. Fries, between certain species of these two genera of Fungi. Patient research will show that this correspondence is a much more general fact than has been imagined, and it sufficiently authorizes the belief, that far from being the total expression of a species of Fungus, each of the *Cytisporæ* represents merely a particular state of a Fungus which subsequently presents itself under a more perfect form as a true *Sphæria*, or at least as a thecasporous *Sphæriacean*. It will be found that this is the real state of the

* Vide l'Institut, xviii. année, p. 16; or, Bull. de la Soc. Philomathique, 1850, p. 26.

† Comptes Rendus, March 31, 1851.

case in *Nemaspora*, *Micropera*, *Polystigma*, *Ascochyta*, and many other genera comprehended in the *Cytisporaceæ* or *Phyllostictææ*. Thus, to cite only a few examples, *Nemaspora Ribis* belongs to *Sphæria Ehrenbergi*, N., *Polystigma rubrum* to *Polystigma fulvum*, a thecigerous Fungus, *Micropera Drupacearum* to *Sphæria Leveillei*, &c.

Any one attentively following this constant succession of the same fungous productions upon the same *mycelium* will naturally suppose that they are determined by a law, and that a necessary relation exists between these vegetable forms; but it will be found difficult to believe that they are so many different creations, parasitical upon one another, and it will be more readily supposed that they are connected by some other bond. A proof that this bond is that which exists between the members of the same body or the individuals of a single species, is furnished by the species of *Tympanis* and *Cenangium*, which are kinds of cespitose or coalescent *Pezizas*. The *stroma* of these Fungi, before giving birth to the thecigerous cupules or disks, produces abundantly upon its surface, borne upon *basidia* of various forms, not only naked spores, but also extremely slender cylindrical corpuscles, exactly like those emitted from the *spermogoni* of the Lichens, the *Septoriæ*, many of the *Cytisporæ*, and other analogous Fungi. The same corpuscles are observed also upon the edge of the cupule of various species of *Cenangium*.

In *Rhytisma*, a thecasporous genus, of the order *Discomycetes*, each species, so to speak, possesses a kind of precursor in a *Melasmia*, or Fungus with acrogenous spores, which plays towards it the same part as the *Cytisporæ* and their analogues do in relation to the *Sphæriæ*. According to what Mr. Berkeley says, *Asteroma Ulmi* should be a sort of *Melasmia* to *Dothidea Ulmi*. Several species of *Hysterium* and *Phacidium* are also joined to *Leptostroma*, which evidently belongs to them.

With reference to some genera of the *Coniomycetes*, it has long been suspected that the *Melanconia* and their allies are only *Sphæriæ* in a certain state of alteration (*Sphæriæ corruptæ*). M. Fries, following Link, has raised doubts as to their autonomy, but no one has yet shown, by a sufficient examination of their mode of increase, what they really are, that is to say (like *Stegonsporium*, *Didymosporium*, *Stilbospora* and analogous genera), the gonidia of various *Sphæriæ* (e. g. *Sphæria stilbostoma*, *fava-cea*, &c.). The majority of the *Tuberculariæ* also represent the *stroma* of certain *Sphæriæ* (v. g. *S. cinnabarina*, *S. coccinea*, &c.), and their spores must also be received as the gonidia of the latter. A very exact comparison can be made between the spores of the *Tuberculariæ* and the dissociated elements of the articulated filaments, which by their union constitute the pulvinules called by

the name of *Dacrymyces Urticæ*, or the margin of the *Peziza fusarioides*, which is merely the perfect condition of the same fungus. *Tubercularia persicina*, Dittm. (*Æcidium exanthematum*, Ung.) and other analogous productions live intermingled with *Uredines* and *Æcidia* when the *sori* of these entophytes are scattered (e. gr. *Uredo Euphorbiæ*, *suaveolens*, *Æcidium Cichoracearum*, *Euphorbiæ*), or they occupy the centre of the area bounded by these *sori* when they are circular (e. c. *Uredo compransor*, *Mercurialis*, *concentrica*, *Æcidium Grossulariæ*, *crassum*, *Convallariæ*, *Paridis*, &c.); in like manner punctiform productions, which, like *Æcidium exanthematum*, might well represent the spermogoni of the *Uredineæ*, are constantly developed upon the opposite surface of the patch borne by *Ræstelia cancellata*, *Centridium Sorbi*, *Cydoniæ*, &c.

Among the Fungi most decisively proving the thesis now proposed, are the *Sphæriæ*. *S. Laburni*, Pers., is a very complete species; its ascophorous *perithecia* arise like those of a large number of *Sphæriæ*, around a cytispore with a whitish cirrhus, mixed, in addition, on the same *stroma* with conceptacles lined by a basidigerous *hymenium*, which would be referable to the genus *Sporocadus* or one of its analogues. Thus *Sphæria Laburni* possesses three kinds of reproductive organs, viz. normal endothecal spores, acrogenous spores very like the fruit, those of the *Sporocadus*, and lastly other spores equally acrogenous, but very different and exceedingly slender, namely those of the *Cytispora*. In *Sphæria hypoxylon* and other *Xylariæ*, I have as yet seen only two kinds of spores, namely the black endogenous spores which are known to belong to them, and in the second place the white seminules which cover the young branches of the *stroma* with a fine dust. These seminules arise singly from a naked *hymenium*, clothed with short, straight *basidia*. *Dothidea ribesia* is more complete; on the upper face of its pulviniform *stroma* it produces white seminules like those of the *Xylariæ*, and in the substance of its parenchyma little cavities become excavated here and there, producing upon their walls acrogenous corpuscles resembling the seminules of the *Septoriæ*. Finally, it is known that it also possesses an innumerable quantity of superficial conceptacles filled with eight-spored *thecæ*.

The multiplicity of reproductive organs in all these Fungi requires the invention of a few new words to distinguish them from each other. The term *spores* remaining attached to the most perfect, those developed in the *thecæ*, without relation of continuity with the parent plant; we may apply the name of *stylospores* to those which originate naked, that is to say, from linear stalk-like cells analogous to the *basidia* of the *Agaricineæ*. Then the more delicate seminules, the generation of which is also

acrogenous, should receive, like the Itzigsohnian corpuscles which they wholly resemble, the name of *spermatia*, which merely conveys the idea of a body destined, in some manner or other, to the office of reproduction.

M. Fries applies the name of *conidia* to all the reproductive bodies which are not, as he thinks, normal spores, so that after the foregoing statements, this designation would embrace very dissimilar organs. I would propose to restrain the application of it to the *gemmae* properly so-called, if it be agreed to regard as such the reproductive cells which arise directly from the *mycelium* (as in the *Erysiphes*, *Ascophoræ*, and other *Mucedineæ*) and appear to correspond especially to the *gongyli* of the *Muscineæ* and *Hepaticæ*. Leaving to it the general acceptation, the term *conidia* would be employed whenever it is impossible to determine the nature of a reproductive body which it is required to describe. The difficulty of this problem will appear when the fungus under examination does not present the different kinds of reproductive organs united; but then analogical reasoning will be usefully adopted. If, for example, *Melasmia*, the precursors of *Rhytisma*, are compared with the first condition of *Tympanis*, there will be an inclination to regard the seminules of these *Melasmia* as *spermatia*, rather than as *stylospores* of the future *Rhytisma*. *Sphæria Laburni* furnishes the interpretation of all the *Sphæria* constructed upon the same plan; its *cytispora*, like that of its congeners, will represent the receptacle of the *spermatia*, and its *sporocadus* the stylosporous *perithecia*.

Another difficulty will be found in reuniting the elements of a single species of Fungus when they are not met with associated together in nature. If the Fungi above-named prove that these elements are often assembled together, so that there can be no doubt of their natural relations; there are others which would show in different degrees the dissociation of the different constituent terms of the species. For example, we find the yellow *stroma* of *Sphæria stilbostoma* sometimes fertile at the same time in ascophorous *perithecia* and in *Melanconium* (*conidia*); sometimes, on the contrary, devoid of one or other of these productions. The same is true of the *stroma* of *Sphæria favacea*, although, more frequently, it developes the *Sphæria* and their *conidia* isolated. In *Sphæria nivea*, we find on the same area, circumscribed by the black margin of the *mycelium*, *cytisporous* tubercles and tubercles producing *Sphæria*; we also find, but much more rarely, tubercles which are *cytisporous* only in part, one half giving birth to thecigerous *perithecia*. The *stroma* of *Sphæria castanea*, N., most frequently presents the *perithecia* and the *cytispora* united; yet it commonly produces the latter to the exclusion of the former, or *vice versâ*, and does not enter into the

class of the *Sphæriæ*, among which the *cytisporæ* always accompanies the ascophorous conceptacles (e. g. *Sphæria leucostoma*, *ambiens*, *corticis*, *pulchella*, *Leveillei*, *profusa*, &c.).

It may be suspected that certain *Sphæriæ* do not exist at all, or are only met with commonly under the three principal forms which they may take on. In *Sphæria Laburni*, even, the stylosporous form (*Sphæropsis*, *Sporocadus*) is as frequent as, if not more common than, the perfect thecigerous state. *S. sapinea* appears to be known only with acrogenous spores, yet it is sometimes combined with its *cytisporæ*. *S. Oreades*, *atrovirens*, *Hederæ*, and a crowd of others, commonly present themselves with merely a gongylary reproductive apparatus. Hence it might be concluded with much probability, that the group of the *Sphæropsides* and that of the *Cytisporacei* (which claim a great number of *Phyllostictæi*) include a number of *Pyrenomycetes*, the perfect states of which are to be sought among the *Sphæriaceæ* properly so-called, and which consequently must one day be united to them, when persevering investigations shall have clearly made known the constituent elements of each species.

Finally, there is a constant fact to which it is still desirable to call attention, namely the order of development of the different terms of which we believe the species of Fungus to be composed. It is such, that the *spermatia* which may be contemporaneous with the *stylospores* always precede the appearance of the perfect or thecigerous form. This anterior development may take place even several months before, as is seen in the *Rhytismæ* which only ripen their *spores* in spring, while their *spermatia* (*Melasmia*) are developed at the close of the preceding summer. Without in any way prejudging the nature and office of these *spermatia*, it is impossible to avoid remarking that they precede the *endothecal spores* in the same manner as the *antheridia* of the Ferns or *Equiseta* precede the origin of the seminiferous capsules of those plants.

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