A TEXT-BOOK

OF

GENERAL LICHENOLOGY,

WITH DESCRIPTIONS AND FIGURES OF THE GENERA
OCCURRING IN THE
NORTHEASTERN UNITED STATES.

BY

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VI. PERIOD.

From Schwendener (1868) to Reinke (1894).

This is by far the most important period in the entire history of lichenology. It is marked by the recognition of the true nature of lichens and their classification as modified fungi. Since most of the literature of this period is readily accessible I shall not review it at length and shall limit myself to a very brief outline of the work done during this period, mentioning only a few of the leading investigators.

The most important work of the period was the discovery of the dual nature of lichens. That is, a lichen consists of a fungal and an algal portion associated in an intimate organic union. Although Schwendener is generally credited with having made known this discovery, it must not be forgotten that the preparatory work was done in the preceding period; also that Schwendener did not at first believe in the dual nature of lichens. Not until the year 1868 (79) did he express the opinion that the gonidia of various lichens corresponded to certain low forms of algae. His conclusions of that time may be summarized as follows:

1. There is no direct proof of any genetic relation between the gonidia and the hyphal elements.

2. The cell-walls of the gonidia have a different chemical behavior from the membranes of the hyphae; the former react similarly to those of algae, the latter similarly to those of fungi.

3. As to structure and development the various forms of gonidia correspond to different forms of algae. The resemblance is so close that in many cases a given isolated gonidium cannot be distinguished from the corresponding alga. The algal types are as follows:

(a) The majority of heteromerous lichens (*Usnea*, *Bryopogon*, *Evernia*, *Physica*, *Anaptychia*, *Imbricaria*, *Parmelia*, etc.), contain species of the algal genus *Cystococcus* Naeg. (*C. humicola* and related forms).

(b) Some other heteromerous lichens contain species of *Pleurococcus* Menegh. (*P. vulgaris* and related forms).

(c) In *Rocella* we find the algal genus *Exococcus* Naeg.

(d) *Omphalaria* and other lichens with blue-green gonidia contain various representatives of the Chroococcaceae as *Gloeocapsa*, *Chroococcus*, and perhaps other related forms.

(e) The Collemaceae are associated with *Nostoc*.

(f) *Ephebe* and related genera with *Stigonema*. (*Ephebella Hegetschweileri* with *Scytonema*.)

(g) *Hormogonium* and *Cystocoleus* are associated with an alga belonging to the Confervaceae.

(h) *Graphis*, *Opegrapha* and related forms are associated with *Chroolepus*.

4. The development of the spore never proceeds further than the protothalloid stage, perhaps because of the absence of the requisite algae.

5. There is a great similarity between the lichens and the pyrenomycetous fungi.

Schwendener issued a communication on the algal types of lichens in the following year (81). It is accompanied by colored plates illustrating most of the lichen-algae. Famintzin and Baranetzky (23, 24) demonstrated experimentally that the gonidia of heteromerous lichens, such as *Physcia*, *Evernia*, *Cladonia* and *Peltigera*, as well as some of the gelatinous lichens, as *Collema*, are capable of developing apart from the thallus, even producing zoospores like the unicellular algae. In spite of this fact these investigators concluded that the gonidia were not algae, and further expressed the opinion that perhaps many of the unicellular algae were simply free lichen-gonidia.

Woronin (103) demonstrated that the gonidia of *Parmelia pulverulenta* never produce hyphal filaments, but always develop into new gonidia; or, what is the same thing, the free gonidium which is neither more nor less than a species of *Cystococcus* develops into new colonies of algae. He thus opposes the view held by Baranetzky and Famintzin and favors the theory of Schwendener. Rees (74) demonstrated that the hyphae developed from the spores of *Collema glaucescens* will not mature unless associated with *Nostoc lichenoides*; in the absence of such an association the young hyphae soon perish. A few years later Bornet (15, 16) isolated and determined specifically the algae which enter into the composition of a large number of lichens. He also described the method by which the hyphae envelop the algae, as well as the mutual benefit derived from the intimate association of algae and fungi. Similar observations were made by Treub (94).

These and other experiments demonstrated beyond a doubt the

dual nature of lichens. They also demonstrated that this association was not like that of ordinary parasitism, but rather formed a union for mutual benefit, thus enabling these plants to exist where neither of the components could exist alone. This association was known as consortism (Reinke), or symbiosis (de Bary).

There were also a large number of investigators engaged in the study of the morphology as well as the physiology of particular groups of lichens as well as of lichens in general. We will mention a few of these. Stahl (89, 90) made a special study of the spermagonia. His conclusions were that in *Collema* the spermatia are the male reproductive organs. The female reproductive organ known as the carpogone after being fertilized by the spermatia develops into the apothecium. It is interesting to note that this form of sexual reproduction was observed only in *Collema*. Recently Sturgis has apparently verified Stahl's results (93). Further investigations are necessary to establish Stahl's theory. A number of investigators have demonstrated that the spermatia will develop a hyphal network, even developing new spermagonia. This would seem to prove that spermatia are true spores instead of sexual organs. The most important work in regard to the physiology of lichens was done by Jumelle (44). This author gave us the first reliable results of observations made on the exchanges of gases in fruticose and foliose as well as in crustaceous lichens. He found that the exchange of O for CO_2 is independent of the substratum and dependent upon sunlight and moisture, and also that this gaseous exchange varies greatly in different lichens. An excess of moisture reduces carbon-assimilation. Respiration in some lichens still goes on at very low temperatures, — 10° to — 40° C. Lichens can also resist much higher temperatures than phanerogams. For instance, respiration was still active when the lichen was exposed for one day to a temperature of 45° C., three hours at 50° C. and one-half hour at 60° C.

Among the systematists we will mention Tuckerman,[1] who considered Körber's system the most useful and adopted it in his classification of the North American lichens; his diagnoses are carefully given, accompanied by spore-measurements. With Nylander he considered the spermagonia of great importance in classification. A number of new species were described. He also issued a work

[1] Tuckerman, E. Synopsis of North American Lichens. Part I. 1882. Part II. 1888.

on the genera of lichens and their relationships,[1] which is, however, unsatisfactory, because the author did not seem to have any clear conception of genera. Leighton's manual of English lichens[2] has no commendable features; the spore measurements are quoted; his diagnostic terminology is a peculiar mixture of English and Latin. Körber's and Nylander's methods of classification were referred to in the previous period. Hué published a list of exotic lichens,[3] from which it is safe to estimate that nearly five thousand species and varieties were known at the time. Of this number some are no doubt duplicates. It must be remembered also that a host of varieties, sub-varieties and forms were described. It is at present impossible to state the actual number of authentic species.

Schwendener and his followers uniformly agreed to classify lichens as fungi. To this the systematists objected very strongly. Naturally, they also objected to Schwendener's theory as to the true nature of lichens. In fact, all through this period we find the morphologists and physiologists pitted against the systematists; the former earnestly endeavoring to get at the life-history of the various lichens, the latter refusing to recognize the discoveries made by the former and continuing the work of arbitrary classification. The work of Jatta[4] deserves special mention. He precedes the descriptions of the lichens of southern Italy by a discussion of the anatomy and biology of lichens, and adds a number of colored plates illustrating the principal morphological characters. It is not complete, but it is a work contributing much to the scientific evolution of lichenology.

The use of lichens in the arts, in medicine and in the household was still continued. Great improvements were made in the method of using the various lichens in the dye industries. For further particulars the student is referred to three little works on the uses of lichens by Magnin[5], Henneguy[6] and Porcher[7]. As far as the medicinal uses of lichens are concerned we find that the allopathic school

[1] Tuckerman, E. Genera Lichenum. Amherst. 1872.

[2] Leighton. W. A. The Lichen-flora of Great Britain, Ireland and the Channel Islands. Shrewsbury. 1879.

[3] Hué, A. M. Lichenes Exotici. Paris. 1892.

[4] Jatta, A. Monographia Lichenum Italiae meridionalis. Trano. 1889.

[5] Magnin, Dr. A. Les Lichens utiles. Lyon. 1877.

[6] Henneguy, Dr. F. Les Lichens utiles. Paris. 1883.

[7] Porcher, F. P. The Medicinal, Poisonous and Dietetic Properties of the Cryptogamic Plants of the United States. New York. 1854.

has practically abandoned them as being too unreliable in their effects. In Bartholow's Materia Medica (1884) we find that only *Cetraria Islandica* is recommended to be given as a stomachic tonic, "but only to be prescribed when the more efficient remedies are not well borne." The homeopathic school of medicine still recommends certain lichens in a few diseases, for example, *Sticta pulmonaria* in lung troubles. Other lichens are given in whooping-cough, etc.

VII. PERIOD.

From Reinke (1894) to the Close of 1896.

I may be justly criticised for recognizing this as a period, since Reinke's propositions have not been generally accepted as correct. It can not, however, be denied that his conclusions are based upon sound argument and should, therefore, mark the beginning of the period in which lichens are recognized as a distinct class of plants; such recognition being based upon physiological considerations. In his article on "Die Stellung der Flechten im Pflanzensysteme" (75, III) Reinke endeavors to demonstrate that lichens are autonomous structures. He recognizes and admits all the facts established by Schwendener and his followers, but maintains that lichens are physiologically as well as morphologically sufficiently distinct from both fungi and algae to be recognized as a distinct class. Although the lichen-algae may be cultivated artifically this does not indicate that lichens should be considered as fungi parasitically associated with algae. The fact remains that when either of the symbionts is removed the lichen no longer exists; its autonomy is destroyed. The difference between the school of Schwendener and that of Reinke is principally a difference of opinion as to what constitutes autonomy. Tubeuf (96) states that in mutualism we have a union of fungus and alga which produces an individual wholly different from either of the components and *entirely distinct* as to *form*, *requirements* and *conditions* of life. This intimate nutritive association of two or more originally distinct organisms, which is typically met with in lichens, Tubeuf designates as *individualism*. According to this definition lichens should, doubtless, be treated as a distinct class.

It will be remembered that Tuckerman and others of the previ-

ous period maintained that lichens formed a distinct class of plants. But Tuckerman and Reinke had entirely different conceptions as to the nature of lichens. The former did not believe in their dual nature and, therefore, could not form any true idea as to the relation they bear to other groups of plants, the fungi and algae in particular. For that reason we are justified in stating that Reinke was the first to indicate the true position of lichens in the vegetable kingdom.

Lindau (53) is opposed to Reinke's views and strenuously upholds the theory of Schwendener. As has already been indicated, the future must decide which theory will prevail.

Reinke also pointed out the polyphyletic origin of lichens (75, III, IV). The various groups (usually generic) of lichens are derived from different fungal ancestors. Usually several fungal ancestors have become associated with the same algal type, or the same fungal type may have become adapted to different algal types. Reinke has proposed a system based upon this polyphyletic relationship, which, when more perfected, will form the first approximately natural system of classification for lichens. As this author states, to study the exact phylogenetic relation of lichens to fungi and algae, is one of the important works of the future.

Fünfstück (32) has investigated the fatty secretions found within crustaceous rock lichens. His conclusions are briefly summarized as follows: Calcivorous crustaceous lichens vary greatly as to the depth to which they penetrate the substratum; the endolithic forms have a deficient algal layer as compared with the epilithic forms; the fatty deposition increases with the increase of the gonidial layer, but has no genetic relation to it; the fatty substance is deposited in the hyphae lying within the substratum; fat is deposited only in lichens growing upon a substratum bearing carbonates; the formation of the fatty substance is very likely initiated by the decomposition of the carbonates.

Lindau (54) has also issued the first of a series of communications on the morphology and physiology of lichens. Part 1 treats of the growth and mode of adhesion of crustaceous bark lichens. He concludes that the hyphae never penetrate the intact cells of the substratum. He has also considered the question whether lichens have or have not an injurious effect upon trees (54). He comes to the conclusion that they have no injurious effect upon trees growing under normal conditions. Only when the trees are growing in poor

soil, or when too closely crowded, can a profuse development of lichens have an injurious effect.

Of the systematists of this period we will mention only Crombie.[1] In his classification of British lichens this writer has adopted Nylander's system. He does not recognize Schwendener's theory and divides the lichen-algae into gonidia, gonimia and gonidimia. His diagnostic terminology is that peculiar mixture and combination of English and Latin so much employed by English systematists of this as well as of the preceding period.

We shall conclude this historical review with a brief reference to fossil lichens; so far there is no reliable record of any such remains. There is, however, little doubt that lichens existed during former geologic ages. No records are left for the same reason that we have few authentic records of fossil algae and fungi, that is, lichens are not sufficiently resisting to become fossilized. Excavations of prehistoric cave dwellings (Germany) have revealed the presence of lichens (*Cladonia rangiferina*) among the bones of various animals and the stone implements, which would indicate that man of that early period had already made some economic uses of them.

[1] Crombie, British Lichens, I., 1895.