Beiträge zur Biologie der Uredineen

falls gut inficiert werden kann. Das ist aber, wie wir gesehen haben, nicht der Fall, vielmehr ergab unser Infectionsversuch (IX, Nr. 1) nur ein sehr schwaches Resultat. Nichtsdestoweniger kann man aber wohl sagen, daß innerhalb eines gewissen Rahmens bei Uromyces caryophyllinus die Specialisation mehr von der Verbreitung der Nährpflanzen abhängig ist, als von deren Verwandtschaft; sofern wenigstens die von den Systematikern durchgeführte Verteilung seiner Wirtsspecies auf die Gattungen wirklich der Verwandtschaft den richtigen Ausdruck gibt! In dieser Hinsicht besteht ein scharfer Unterschied gegenüber Puccinia Pulsatillae, für die wir unten zeigen werden, daß die Specialisation sehr genau mit der systematischen Gruppierung der Wirte zusammenfällt, aber zu deren geographischen Verbreitung keine nähere Beziehung erkennen läßt.

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Some Suggestions as to the Phylogeny of the *Ascomycetes*¹).

By

ERNST A. BESSEY, East Lansing (Michigan).

It was an early suggestion of SACHS²) that the Ascomycetes and Florideae were closely related, with the implication that the latter, or rather the ancestral forms of the latter, were the plants from which the former were descended. DE BARY³) on the other hand, and with him many others, while recognizing the many points of similarity between these two groups preferred to derive the Ascomycetes from some of the Phycomycetes. As is well known BREFELD also had a somewhat similar standpoint, differing however from that of DE BARY in his denial of the presence of sexuality in the Ascomycetes as well as in many of the features of his classification. The researches of STAHL upon Collema and THAXTER⁴) upon the Laboulbeniales have led many to incline toward the

1) Read before the Botanical Society of America at the Cleveland meeting, Dec. 31. to Jan. 3., 1913.

2) Lehrbuch der Botanik, 4. Auflage, 1874, p. 288.

3) Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria (English edition) 1887, p. 236-237.

4) THAXTER, R., Contributions towards a Monograph of the Laboulbeniaceae, Part I (Mem. Am. Acad. of Arts and Sci. 1896). — STAHL, E., Beiträge zur Entwicklungsgeschichte der Flechten, Leipzig 1877.

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Floridean origin of the *Ascomycetes* so that now the number of botanists of this faith is fairly large.

I will attempt to give a very brief résumé of the chief points that would support this hypothesis. First and foremost, as SACHS pointed out, the two groups possess in common that type of reproductive structure that may be called a "spore fruit". Whereas in the *Phycomycetes* the result of sexual fusion is the production of a thick walled oospore or zygospore, in the Florideae and Ascomycetes, the fertilized oogone (or carpogone) grows out into series of cells, few or many in number, often associated with sterile cells from other sources and leading to the production of the final reproductive structures, carpospores in the one group, asci containing ascospores in the other. I will revert later to the details of this process in the two groups. In the second place, these two groups show many points of similarity, vegetatively. Thus in the Laboulbeniales as pointed out by THAXTER and by FAULL¹), Pyronema according to CLAUSSEN²) and many higher fungi and lichens according to MEYER³) and others, the septa of the hyphae are perforated by a single fairly large pit which permits of protoplasmic connection between adjoining cells. In the Ascomycetes and in the lower Florideae, the structure is prevailingly filamentous and, for a large part, the growth of these filaments is terminal. There is also a strong tendency for the cells of the filaments to become plurinucleate with age altho they often remain uninucleate. The gelatinization of the walls so prevalent in the Florideae is frequent in the higher fungi but not by any means widespread.

In two great particulars however, the groups under consideration are very different, namely, their mode of nourishment and the structure of their ultimate reproductive cells. The Ascomycetes are without exception, hysterophytes (i. e. dependent upon external sources for their organic food) while the *Florideae* are typically holophytes. No traces of chloroplasts are to be found in the Ascomycetes while they are regularly present in the Red seaweeds. However, there are a number of *Florideae* which show transitions from the holophytic to the hysterophytic condition. Thus, many are simply epiphytes, apparently using other seaweeds only for a place of attachment. Many of these indeed show a tendency on the part of the holdfast cells to penetrate rather deeply into the tissues of the supporting plant. This becomes very marked in the endophytic species, some of which apparently are merely room - parasites, apparently obtaining none of their organic food from the plants they inhabit: while others, though still retaining apparently functional chloroplasts, are certainly somewhat parasitic in that the cells of the host plant bordering upon the filaments of the parasite are killed or at least emptied of their reserve food materials. These examples lead to the case of Harveyella *mirabilis*, which is like the last mentioned except that it contains no chloroplasts. It is in fact a fungus, physiologically. Its hyphae branch through the host like those of a fungus and indeed the external cushion

¹⁾ FAULL, J. H., The Cytology of Laboulbenia chaetophora and L. gyrinidarum (Annals of Botany, April 1912, 26, 325-355; pl. 37-40).

²⁾ CLAUSSEN, P., Zur Entwicklungsgeschichte der Ascomyceten, Pyronema confluens (Zeitschr. f. Bot. 1912, 4, 1-64; figs. 1-13, pl. 1-6).

³⁾ MEYER, ARTHUR, Die Plasmaverbindungen und die Fusionen der Pilze der Florideenreihe (Bot. Ztg. 1902, 60, 139--176; pl. 6).

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of tissue in which the carpospores are borne shows a remarkable similarity to the apothecium of some *Lichen* I do not want to be understood as advocating any claim for *Harveyella* in the ancestral line of the *Ascomycetes* but I wish to show that the modern *Florideae* are capable of giving rise to parasites with many of the fungal characteristics. If this is possible with recent *Florideae* it does not seem reasonable to deny the possibility of the more primitive *Florideae* having given rise to a hysterophytic offshoot that eventually, became the *Ascomycetes*.

The most difficult objection to overcome is the ascus. No living Red seaweed is known in which such a structure is present. True, it has been suggested that the tetraspore mother cell represents an ascus and the tetraspores four ascospores. An additional point of similarity is the fact that in both structures, viz. tetrasporangium and ascus we find the occurrence of a reduction division. However, in view of the association of the tetrasporangium with a type of alternation of generations such as appears not to occur among the fungi except in the Uredinales, and of the totally different origin of tetrasporangium and ascus morphologically, I feel that we must for the present look elsewhere, unless we are to suppose that the ancestors of the Ascomycetes suffered a shortening of the tetrasporic generation and combination of it with the sporophytic structure arising from the fertilized carpogone, so that the sporogenous filaments from the carpogone, instead of terminating in carpospores came to terminate in tetrasporangia (asci). Perhaps Nemalion which does not possess an intercalated tetrasporic generation may give us a hint as to the possible origin of the ascus. In this form the fusion nuclei formed by the division of the fertilized nucleus of the carpogone are diploid in character. The rather short sporogenous threads are also composed of cells with diploid nuclei. WOLFE 1) has found, however, that the end cell of each sporogenous filament, the cell from which the carpospores are budded off, shows the haploid number of chromosomes in the divisions which give rise to the carpospores. He found no indication of tetrad formation or of the two nuclear divisions always considered as essential to the reduction of chromosomes. Possibly the carpospores thus produced contain the haploid number of double chromosomes and on germination make the typical reduction divisions or possibly these take place just back of the cells on question. In either event those cells in which this occurs show considerable homology to the asci which are cells produced near the ends of filamentous outgrowths from the fertilized carpogone, within which the reduction division takes place. Perhaps the retention and further division of the products of this division within the ascus so as to form eight or even more ascospores is connected in some way with the changed manner of spore distribution. In the seaweeds the comparatively large carpospores are easily transported by the water while the airdispersal is more efficacious with smaller spores, such as the ascospores.

In the *Florideae* the union of the nuclei takes place in the carpogone. The sporogenous threads, then, contain daughter fusion nuclei. In some of the *Ascomycetes* doubt has been thrown recently upon the occurrence of this union within the carpogone. Indeed CLAUSSEN, SCHIKORRA

¹⁾ WOLFE, J. J., Cytological Studies on Nemalion (Ann. of Bot. 1904, 18 [Oct.], 607-630; 1 textfig., pl. 40-41).

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and FAULL¹) deny this fusion for the carpogone and appear to show, for the forms with which they worked, that paired but not united nuclei pass out into the ascogenous threads, dividing by conjugate division but not uniting until the ascus is formed. Yet in this case each pair of nuclei has, between them, the diploid number of chromosomes, the union of chromatic matter taking place in the *Ascomycetes* as in the *Florideae* in the synapsis connected with the reduction division. The fundamental difference is that in the one case the chromatin masses destined for union at synapsis are in separate but closely associated nuclei, while in the other case they lie within the same nuclear membrane. Where this change occurred, whether as the hysterophytic habit was being assumed or earlier or later one can scarcely venture to guess in a matter the whole of which is to so large an extent pure speculation.

Assuming now that it may be likely that the primitive Ascomycetes had a Floridean ancestry we must naturally seek for the most primitive Ascomycetes among those forms with structures most nearly like those of the Algae in question. These we find in the Lichens related to Collema, as well as in the Laboulbeniales. In both of these groups the occurrence of non-motile sperm cells and trichogynes has often led to the belief in the relationship of these fungi to the Red seaweeds. Collema is of especial interest in view of the discovery by Miss BACHMANN²) that in one species the sperms are not set free from the antherid but are sought out by the trichogynes which partially wind around them and then fuse with them. This forms an easy transition to the types like Pyronema where the antherid forms no sperm cell at all but fuses directly with the trichogyne. By a gradual reduction of the latter we approach types like the Erysiphaceae in which a trichogyne is lacking.

Even in the *Florideae* the trichogyne is sometimes a separate cell from the carpogone. This is strongly marked in the case of those *Ascomycetes* in which this organ occurs, it often containing four to six or mere cells. The formation of a several celled ascogonium, the cells of which may fuse more or less is perhaps an indication that the ancestral *Florideae* were of the type in which auxiliary cells were present. This is of course mere surmise until the nuclear phenomena in forms with a true ascogone have been worked out fully.

Based on the foregoing I would suggest that the algal ancestors of the Ascomycetes were Floridean in nature, probably inhabitants of fresh water, that were first epiphytic, then endophytic and finally parasitic within colonies of Nostoc. They gradually emerged and acquired the power of land life in connection with this or similar hosts. The most primitive spore fruit, then, of the Ascomycetes would be the apothecium such as found in Collema or similar Lichens, a structure resembling the cystocarp of many red seaweeds. In the one direction this type of structure became more and more perithecioid, until we have a true perithecium. This progressed further to the closed structure of the Erysiphaceae and the spore fruits such as occur in Aspergillus, the Tuberaceae

¹⁾ CLAUSSEN, l. c. — FAULL, l. c. — SCHIKORRA, W., Über die Entwicklungsgeschichte von *Monascus* (Zeitschr. f. Bot. 1909, 1, 379—410; 3 Textfig., 2 Taf.).

²⁾ BACHMANN, FREDA M., A New Type of Spermagonium and Fertilization in *Collema* (Ann. of Bot. 1912, **26** [Jy.], 747-760; pl. 69).

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etc. In the other direction there was a further development of the apothecial type resulting in the typical *Pezizales*, *Helvellales* etc. By reduction, such forms as *Exoascus* arose from this type.

In some of these lines of development the formation of a separate antherid was gradually omitted, the sexual fusions taking place now between nuclei all of which originated within the carpogone.

I can not refrain at this point from urging the strict homology between the ascus, and the teliospore of the Uredinales. In both cases a union of two cells gives rise to one or several, ascogenous filaments, within which the cells are binucleate. At or near the end of such a filament cells arise within which the two nuclei unite, forming the young ascus or teliospore as the case may be. In this cell now begins the reduction division, leading to the production within the ascus of four or mostly eight ascospores, and in the teliospore (in some Uredinales) or in an outgrowth from it (promycelium), of four cells which may form germ tubes directly but usually form secondary spores, the so-called sporidia or basidiospores. By the same token the spores of the Ustilaginales and even the basidia of the Basidiomycetes are perhaps homologous to the ascus, and these groups, too, are probably derived from the Ascomycetes.

Protascus colorans, a new genus and a new species of the Protoascineae-group; the source of "Yellow-grains" in Rice.

By

P. C. VAN DER WOLK, Buitenzorg (Java). (With 1 col. plate.)

1. Introduction.

One of the most fearful calamities in the trade-rice of some countries, viz: — the rice which is exported from the Indies to the European market for consumption — is the appearance of the so-called "yellow grains". If a handful of rice be taken out of such an infected lot then "yellow grains" immediately come into view here and there. It is the endosperm that looks yellow. Now, it is no usual yellow colour that these same grains exhibit; the colour inclines a little to be brownish; so, one is more disposed to speak of brownish-yellow grains; sometimes there is an overlying deep orange glow. In all cases the grains are of a deep-yellow colour, a yellow fonce, so that one may without doubt speak of "yellow grains".

This phenomenon of "yellow grains" is not a matter of general spreading; but in the countries where it is endemic, it is in the highest degree dreaded by the rice-producers. Rice which has only just been harvested does not immediately exhibit yellow grains. They only appear in rice which has been garnered for a long time in large heaps. The yellow-colouring process progresses very slowly. It is not until after several months have elapsed that one has the chance of finding yellow

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