THE IMPORTANCE OF THE GONIDIA TO THE CLASSI-FICATION OF THE LICHENS

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More than 70 years have elapsed, since, in 1866, de Bary enunciated the hypothesis that Lichens are dual organisms, the socalled gonidia being Algae. As about 1899, the year when N ylander died, the dual nature of the Lichens had become generally accepted, lichenologists have had 40 years to realize the consequences of this theory. Nevertheless even now opinions differ widely. While practically all botanists admit that a Lichen is composed of a Fungus and an Alga, most lichen-taxonomists apply, perhaps for a good deal unintentionally, the species-name to the consortium, while others emphasize the necessity of restricting the specific and generic names to the Fungus. Reinke, Wainio, Zahlbruckner and Keissler may be regarded as adherents of the first procedure; Sernander, Fink, Clements and Nannfeldt of the second. While the attitude of Zahlbruckner c.s. is perhaps largely due to practical considerations, As a hin a recently advocates this conception as a logical consequence of the dual nature of Lichens: "Aus der dualistischen Natur der Flechten muss man aber eine Flechten-Art A (Pilz) + B (Alge) als verschieden von der A + B' betrachten". But, in my opinion, the very fact of the dual nature of Lichens leads to the conclusion that a Lichen is no more a species than a plum pocket is one. In general, as stated above, it seems to me that the acknowledgement of the consortium as specific is semiconscious, and rests on practical reasons. Nannfeldt remarks that Wern e r, for instance, has used specific names as well for the Lichen as for the Fungous component. In many cases, it must be admitted, the procedure though arbitrary, is perfectly harmless. Lichen taxonomy is obliged to use other methods than taxonomic mycology, the vegetative thallus being often as important a feature as the fructification: and with the thallus, one naturally describes the gonidia, though for practical reasons the description remains as a rule incomplete. If the Fungus is strictly monophagous, the presence of a special gonidial partner may be regarded as a character of the Fungus. In many cases, however, especially in groups where the consortium bears a primitive character, difficulties arise. The latter regard not only the delimitation of the species, but their place in the classification as well.

There are numerous instances of Fungi living either without or with gonidia, or with different kinds of gonidia. As long ago as 1866, Fries remarked that it would be unnatural to bring Peltigera aphthosa and P. malacea or Pannaria brunnea and P. hypnorum in different genera. The same holds good, for instance, for Peltigera canina and P. variolosa. Reinke argues that the species containing Cyanophyceae and those containing Chlorophyceae might have developped independently, and placed in all these cases the second species in a different genus. But if this procedure is applied, it strikes one that almost or perhaps quite identical species are divided indescriminately over both groups. It appears, for instance, that even the subdivision of Peltigera in Peltidea and Eupeltigera can not be accepted. In such derived groups as *Peltigera* it happens but rarely that in one species widely different gonidia are met with, and the presence of Algae belonging to the same genus can only be demonstrated by cultivating them. In this connection the forms of Parmelia caperata (Jaag) and of Xanthoria parietina (Warén) must be mentioned. As a hin a has suggested that chemical differences in morphologically identical Lichens might be due to physiological differences in the gonidia, but, as Thomas has demonstrated now that parietin, one of the substances which have always been considered as specific for definite consortia, is produced in pure cultures by the Fungi Caloplaca murorum and C. elegans, this hypothesis seems rather doubtful.

Among the Caliciaceae numerous examples show that in this group the gonidia have no value for the taxonomy. So the classic case of *Coniocybe nivea*, which occurs with or without gonidia; in the latter instance it lives either as a parasite or as a saprophyte, and is called *Roesleria hypogaea*. Other genera and species belonging to this group too occur sometimes with, and sometimes without gonidial Algae.

The genus Cora splendidly demonstrates the difficulties arising from the idea that the consortium should be regarded as specific. Wainio and Zahlbruckner distinguish the genera Cora and Dictyonema, the first having Chroococcus (Scytonema?) cells, arranged in a distinct layer as gonidia, the latter Scytonema cells, not arranged in a layer. Now Möller has demonstrated that it

is always the same Fungus, and sometimes the same individual which associates with these Algae, so giving rise to both Lichens. He found the Fungus also fruiting without gonidia. It is hitherto unknown to which genus Cora belongs. Whether Möller thought that Cora should be accepted as the generic name of the Fungus is not clear. At any rate the name Cora is applied to the Lichen as well. In the procedure followed by Wainio in his paper on the Finnish Coniocarpeae, the Fungus, however, would belong to another genus, and then one individual of a Basidiomycete might belong to three genera. And this is not the end of the difficulties: both of Cora and Dictyonema there are more species. Fruiting material is rare, and the descriptions of different authors are sometimes contradictory, but it seems probable that the species of the Lichengenus Cora, if studied by a modern mycologist, would prove to belong to different genera. So one Basidiomycete belongs to three genera, and at least one of these genera may comprise some other ones.

These examples may suffice to show that, although perhaps many Lichenfungi are strictly monophagous, the taxonomist should be constantly aware, that others may be polyphagous, and that in that case the gonidia are a character of the consortium only. Or again, the Fungus may be monophagous, but there may exist different races, living with different gonidial commensals. In mycology in this case one would speak of biologic forms and I see no reason for not doing so in lichenology. It seems advisable to use the term f.g. — forma gonidialis — for all such cases where one Fungus associates with different Algae, forming different Lichens. The term should be used as well for monophagous races living with different gonidia as for the various combinations of polyphagous ones. It, consequently, does not cover the term biologic race, which indicates a special property of the Fungus, whereas f.g. merely means that the Fungus lives with a specific Alga. It is more or less a concession to those lichenologists who regard the consortium as specific, but it is rather harmless, as it prevents the splitting of well established genera. It is, moreover, inevitable, as it is often impossible to know whether the Fungus is mono- or polyphagous.

From several sides it has been emphasized that the classification of the Lichens should be based upon the Fungus constituent (Sernander, Fink, Nannfeldt, Feldmann a.o.). In vol. 8 of "Pflanzenfamilien" Zahlbruckner has, indeed, to a certain extent given preference to the fungous characters. But, as Feldmann observes, among the Gymnocarpeae even some Pyrenomycetes, because of their thallus structure, have found a

place. Especially the Pyrenocarpeae however have been dealt with in a manner which leaves nothing of the fungous system. While Clements and Shear admit but the family of the Verrucariaceae, the group is divided by Zahlbruckner in 16 families, of which one, the Strigulaceae, does not figure in the key on p. 63. This is a pity, for in the midst of the other families, which are for a good deal characterized by the gonidia only, the Strigulaceae to whom no less than 4 different genera of gonidia are allowed, would make a striking effect. Feldmann, in an interesting note concerning some errors committed by Keissler in the determination of the gonidia of some Pyrenocarpeae, mentions the presence of Hyellacells in Arthopyrenia litoralis for which, if one proceeds like Zahlbruckner, a new family should be created. One asks alarmed if there be really no other differences for e.g. the genera Arthopyrenia (Pyrenulaceae), Pseudarthopyrenia (Pyrenidiaceae) and Xanthopyrenia (Xanthopyreniaceae), but a difference in the gonidia? It looks indeed as if there is nothing else. But then, what reasons has Keissler to write: "Maszgebend für die Abgrenzung (der Pyrenulaceae) der Pyrenocarpeae sind hauptsächlich die Gonidien, denen hier für die Unterscheidung der einzelnen Gruppen eine besondere Bedeutung zukommt", etc.? One can say exactly the same of any character which one has a priori chosen as the only sound one. One could f.i. divide the Uredineae in genera or families, according to their hosts. This would (if one excepts the aecidial generation) do well for the genus Melampsora. But what if this knowledge would be applied at random to other rusts, bringing Uromyces Festucae in one genus with Puccinia Festucae, and U. Poae in another with P. Poge?

Mention should be made here of the results obtained by C hodat, Warén and Jaag, as these results have been adduced by Keissler (l.c., p. 8) in suppport of a classification of the Pyrenocarpeae based on the gonidial constituents. By isolating gonidia from a number of Lichens, especially Parmeliae and Cladoniae, these authors have shown that each species has its own specific gonidia. Differences may be present however in gonidia from the same species of Lichen, if the latter has been collected in distant localities. The differences between gonidia from various Cladoniae are smaller than those between Cladonia- and Parmelia-gonidia. So, in Cladonia and Parmelia, a difference in fungous structure is correlated with a difference in gonidia. But differences in the gonidial constituent do not necessarily involve differences in fungous structure. Why then should this be otherwise in the Pyrenocarpeae?

Moreover, Raths, in a recent paper, supplies data on the Caliciaceae where the gonidial specificity is less pronounced. As in all these investigations the starting point is the structure of the fungous component, why then infer from the results that this structure is without importance?

From these few examples (see also Nannfeldt) the desirability of basing the classification of the Lichens on their fungous components, may be sufficiently clear. It is certainly practical for floras and the like to deal with the Lichens as a whole, but the classification within the group should be based upon the fungous characters. As regards the delimitation of species and genera, the application of the term f.g., as suggested above, might lead to uniting numerous genera which actually are scattered over different families but which naturally belong together.

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Fig. 1. Manihot saxicola Lanj. Voltzberg, Sept. 1933.

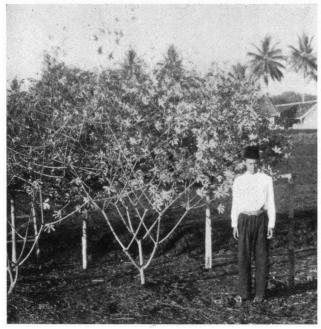


Fig. 2. Manihot saxicola Lanj. Plant raised from seed at Buitenzorg.