

THE SUBOPERCULATE ASCUS—A REVIEW*

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The suboperculate nature of the asci of the Sarcoscyphaceae is discussed, and it is concluded that it does not exist in its original sense, and further that the Sarcoscyphaceae is not closely related to the Sclerotiniaceae.

The question of the precise nature of the ascus in the Sarcoscyphaceae is important in connection with the treatment of the taxonomy of the Discomycetes. The family Sarcoscyphaceae has been established as a highranking taxon, the Suboperculati, by Le Gal (1946b, 1953), on the basis of its asci being suboperculate. Furthermore, the Suboperculati has been regarded as intermediate between the rest of the Operculati, The Pezizales, and the Inoperculati, especially the order Helotiales, and its family Sclerotiniaceae (Le Gal, 1953). Recent views on the taxonomic position of the Sarcoscyphaceae are given by Rifai (1968), Eckblad (1968), Arpin (1968), Kimbrough (1970) and Korf (1971).

The Suboperculati were regarded by Le Gal (1946a, b) as intermediates because they had both the operculum of the Operculati, and in addition, beneath it, something of the pore structure of the Inoperculati. In the Suboperculati the pore structure is said to take the form of an apical chamber with an internal, often incomplete ring-like structure within it. Note that in this case the spores on discharge have to travers a double hindrance, the internal ring and the circular opening, and that the diameters of these obstacles are both smaller than the smallest diameter of the spores. Therefore, the spores have to be forced through a double hindrance; this seems rather improbable.

There may be other reasons for accepting the Sarcoscyphaceae as a high ranking taxon, but what I am going to maintain here is that the suboperculate nature of their asci, as first described, is not a good reason, since, in my opinion, few if any of its members have asci that are suboperculate in the way described by Le Gal. Furthermore, I am going to suggest that if this suboperculate nature of their asci is denied, in fact very little remains to place the Sarcoscyphaceae in close phylogenetic relationship to the Sclerotiniaceae.

The term 'suboperculate ascus' was introduced by Le Gal (1946a). Later the same year, Le Gal (1946b) stated that the term 'paraoperculate ascus' introduced by Chadefaud (1946) covered the same thing. The term 'suboperculate' has been accepted by everybody. (Nannfeldt, 1949, Korf, 1957, Denison, 1965, Rifai, 1968,

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Eckblad, 1968). Le Gal (1946a) first described the phenomenon in *Cookeina sulcipes* while Chadefaud (1946) described the same phenomenon, as the paraoperculate ascus, in *Sarcoscypha coccinea*. In *Cookeina sulcipes* the suboperculate ascus was described by Le Gal (1946) as having a three layered ascus wall. Within an enlargement of the middle layer the apical chamber is formed.

In a later paper, Le Gal (1946b) gave more detailed descriptions and drawings of the suboperculate ascus of a number of species, all belonging to the family Sarcoscyphaceae. In this paper the suboperculate ascus is stated to have two wall layers, and she appears now to regard the *Cookeina* ascus as two-layered too. The ascus wall has been demonstrated to be two-layered also in several operculate genera not belonging to the Sarcoscyphaceae, viz. *Ascobolus* and *Saccobolus* (van Brummelen, 1967), *Thelebolus* (Kobayasi *et al.*, 1967). I have also seen the double wall on electronmicrographs in *Gyromitra esculenta* (unpublished).

According to Le Gal (1946b) there are three different types of suboperculate asci in the Sarcoscyphaceae.

The first type is found in a number of species now belonging to the genera *Pseudoplectania*, *Pithya*, *Urnula*, *Plectania*, *Wynnea* and *Sarcoscypha*.

In all these genera the inner wall layer is said to become thicker at the top of the ascus, and the apical chamber to be formed within this thickening. Within this chamber again is formed an internal ringlike structure which is considered to correspond—according to Le Gal—to the internal pore canal of the ascus apex of many inoperculate Discomycetes.

In the second group, consisting of the tropical genera *Phillipsia*, *Cookeina* and *Boedijnopeziza* the apical chamber is said to develop, not within the inner layer, but between the two layers. In the case of *Phillipsia* at least it appears from her drawings that the ring-like structure is reduced to a thickening on the inside of the circular opening left by the operculum. The third group, represented only by *Urnula geaster*, or more correctly, *Chorioactis geaster*, differs only slightly from the latter type.

In her paper on the Discomycetes of Madagascar Le Gal (1953) also described the suboperculate apical apparatus of some genera closely associated with the Sarcoscyphaceae, viz. *Phaedropezia* Le Gal, and *Midotiopsis* Henn., and of *Rutstroemia nummiformis* (Pat.) Le Gal of the Sclerotiniaceae.

The hypothesis that the Sarcoscyphaceae form a taxon intermediate between the Inoperculati and the Operculati, or more especially between the Sclerotiniaceae and the Pezizales was in the main based on these findings.

I hasten to assure that the thickened inside of the opening of the ascus of *Phillipsia* I have also seen. In fact this thickening or apical pad was clearly described and illustrated by Boedijn (1953). The lid itself is also thickened on the inside.

If this type of apical 'apparatus' is what is generally understood by a suboperculate ascus, I do not deny its existence. But it should be remembered that in this case the apical chamber has disappeared, and also the internal ring like structure within it. With its disappearance the double hindrance of the spore discharge vanished too. What is left is a thickening of the operculum and the opening itself.

TABLE I. CHARACTERS OF SARCOscyPHACEAE AND SCLEROTINIACEAE COMPARED

| | Sarcoscyphaceae | Sclerotiniaceae |
|---------------------|--|---|
| mode of nutrition | saprobic | parasitic |
| substrate | epixylous | not epixylous, except <i>Rutstroemia</i> , <i>Martinia</i> |
| mycelium | plurinucleate | plurinucleate |
| sclerotia or stroma | not, except in <i>Wynnea</i> | common |
| apothecia | hairy | glabrous |
| colour | Yellow, orange, red, black | yellowish-brown |
| paraphyses | mostly plurinucleate except " <i>Sarcosoma</i> ", <i>Urnula</i> , <i>Pseudoplectania</i> | uninucleate, except <i>Sclerotinia tuberosa</i> |
| asci | long | short |
| asci | cylindrical | clavate |
| asci | nonamyloid | amyloid |
| asci | aporhynque | aporhynque or pleuro- rhyne |
| ascospores | large | small |
| ascospores | one-celled | mostly one-celled |
| ascospores | hyaline | mostly hyaline |
| ascospores | globose, ellipsoid often inaequilateral | ellipsoid, sometimes slightly inaequilateral |
| ascospores | plurinucleate | uninucleate, except <i>Sclerotinia tuberosa</i> 2-6 <i>Ciboria batschiana</i> 1-2 |
| conidial states | mostly none except <i>Verticicladium</i> <i>Conoplea</i> | common <i>Botrytis</i> , <i>Monilia</i> etc. |

Furthermore, this type of opening is definitely known only from the genera *Phillipsia*, *Cookeina*, and *Boedijnopeziza*, but may occur also in the monotypic genera *Geodina* and *Aurophora*, which both are closely related to *Phillipsia*. It may occur in a few other genera too.

Of the existence of the suboperculate ascus in the original sense, I have so far seen no corroboration in the literature in the form of a description, drawing or photograph based on personal studies. True, there are several records of suboperculate asci in new species and genera, *Galiella* (Korf, 1957), *Geodina* (Denison, 1965), *Aurophora* (Rifai, 1968), *Neourrnula* (Paden & Tylutki, 1969), *Korfiella* (Pant & Tewari, 1970) and *Thindia* (Korf & Waraitch, 1971). In none of these cases, however, is there any drawing or photograph of the apical apparatus. What features of the ascus are referred to by the term suboperculate, has not been described.

I have studied in detail only few species of the Sarcoscyphaceae. But I have studied two of them, *Pseudoplectania nigrella* and *Sarcoscypha coccinea*, and especially the former in detail. The asci of *Pseudoplectania* I have studied for three years without finding

the slightest indication either of an apical chamber or of an internal ring. Judging from Le Gal's drawing (1946b, Fig. 2, 2) the internal ring of *Pseudoplectania nigrella* would be approximately 8 microns wide and 3 microns thick, i.e. clearly visible even in a light microscope. In *Sarcoscypha coccinea* the structure is described as much smaller, although not at all of a submicroscopical nature. The asci have been studied fresh in water mounts or in various media, or stained. The result is the same.

In these two genera the suboperculate apparatus of the ascus is nonexistent. On the basis of these negative results in two central genera, I feel that fresh evidence for the existence of this structure is now necessary. The most satisfactory evidence would be longitudinal sections of the ascus studied in light and electron microscope. This sort of evidence has not yet been produced, probably because of the technical difficulties in obtaining such sections.

It is necessary to keep in mind that I distinguish between two types of asci in the Sarcoscyphaceae.

I. The *Phillipsia*—*Cookeina* type, in which the operculum itself and the rim of the opening of the ascus is thickened. There is no apical chamber and there is a single hindrance to the spores. This type I accept. In my opinion this type of ascus should not be termed suboperculate, since this would amount to a virtual redefinition of the term considering the sense it was originally given by Le Gal (1946a).

II. The *Pseudoplectania* type, where there should be both the operculate opening, and beneath it a second hindrance, the internal ring. I do not believe that this type exists.

On the other hand I will, of course, not deny that the ascus of the Sarcoscyphaceae possesses a series of peculiar characters. Few of these characters are found in the asci of all species, however.

The asci are often thick-walled and often very long and with a flexuous narrowing base, which is aporhynque, according to Berthet (1949) i.e. without croziers. In some genera the operculum and opening is oblique and thickened on the inside. In a few genera all asci ripen simultaneously. The spores are often inaequilateral and often with longitudinal or transverse ridges or striations which are not stained by cotton blue or similar dyes, and are mostly plurinucleate (Berthet, 1964).

These characters together with the characters of the excipulum (see Nannfeldt, 1949, Le Gal, 1953, Rifai, 1968, Eckblad, 1968) the epixyloous habitat and the tropical distribution of several genera certainly gives the family or families (Korf, 1971) a somewhat exotic image.

I am, however, quite unable to see that these characters point to a relationship with the Sclerotiniaceae or for that matter, with any other group of the Inoperculati. In Table 1, I have confronted a number of characters of the Sarcoscyphaceae and of the Sclerotiniaceae. Very few of the characters are the same, mostly they are different.

My conclusion is then—in the absence of positive evidence—that the Suboperculati as a whole do not possess a suboperculate apical apparatus as originally defined, and that lacking this—there is no reason to seek a phylogenetic relationship between the Suboperculati and the Inoperculati.

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