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TAXONOMY OF OPERCULATE DISCOMYCETES: SYNTHESIS*

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A general consideration is given on various aspects of the taxonomy of Operculate Discomycetes. The thesis is advanced that the genus, rather than the species, may represent the basic evolutionary unit. More detailed considerations are devoted to a few topics, for instance to the systematic position of the genera *Cyttaria* and *Medeolaria*.

It is no accident that here at this First International Mycological Congress a special session on Taxonomy of Operculate Discomycetes should be convened, for the time was ripe. As you have already heard today, there are a large number of active workers seriously applying themselves to the problems of taxonomy in this most intriguing group of fungi.

Nevertheless, the great strides forward in taxonomy of Operculate Discomycetes can be traced back, in nearly all instances, to the brilliant analyses of the cup fungi by three mycologists publishing a century ago: the great French master, Émile Boudier, the brilliant Swiss mycologist Leopold Fuckel, and the Scandinavian giant, P. A. Karsten. All three possessed not only the ability to discern species, a quality of all great mycologists, but had in addition that rare gift of rearranging the pieces of the puzzle to provide a classification giving an insight into relationships. That some of the genera that they proposed have fallen by the wayside, or have proven to be polyphyletic in the ensuing century, should in no way diminish our admiration for their ability to recognize affinities, often decades or even a century ahead of their time.

As taxonomists we are usually prepared to utilize any data, from whatever source, which will help us to separate groups – the process of *analysis* so essential in recognizing species, for example—or, conversely, that will help us in uniting taxa into higher categories, genera, tribes, families, orders—the process of *synthesis*. We who are actively concerned with the Operculate Discomycetes are at that fortunate moment in time when several distinct disciplines have come to focus upon the same materials, as some of our speakers today have already pointed out. The thrust of my comments today is that, without disparaging the importance of analysis and the importance of discerning species and infraspecific taxa, our real business of the moment is synthesis.

I know that I speak for all of the panel of this session in voicing our regret that

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Mme Le Gal was unable, by reason of her health, to attend and participate today. For her studies, detailed and precise, have formed for all of us a solid foundation upon which to test our ideas of classification. The genera and many of the families which she has adopted, for which she would be the first to acknowledge her debt to the pioneering work of Boudier, were all delimited by classical morpho-taxonomic procedures. In the 25 years since she published her arrangement in the "Recherches sur les Ornementations Sporales des Discomycètes Operculés" only a few groups have seen significant changes, and these were the very groups which she recognized needed critical study. But in those 25 years new tools have been brought to bear, particularly:

1) critical microanatomical study of the apothecium, advocated by Starbäck, von Höhnel, and above all by Professor Nannfeldt,

2) cultural studies such as those outlined today by Professor Paden, and a few days ago at another session at this congress by Professor Hennebert,

3) studies of nuclear numbers in ascospores, paraphyses, and cells of the vegetative mycelium, provided us most recently by Professor Berthet,

4) ontogenetic studies of ascocarp development, quiescent since the initial studies by Corner, but as you have noted today in the papers by Dr. van Brummelen and by Professor Kimbrough, attaining new importance in the Ascobolaceae and Theleboleae,

5) ascus wall characters, a current area of interest of several investigators, and

6) chemotaxonomic and physiotaxonomic studies of various sorts, including the blueing reaction of certain asci in Melzer's Reagent and Dr. Arpin's critical analysis of carotenoid pigments in our group.

What is really impressive, at least to me, is that the accumulation of the data, admittedly by no means complete, has in almost all instances *reinforced* the Boudier-Le Gal classification of Operculate Discomycetes. Each independent discipline, potentially capable of telling us that our groups delimited by traditional morphological procedures are fictions or arrays of artificially arranged taxa, instead has pointed to real biological relationships at the generic and higher levels.

This is not to say there are no longer problems for us to consider! We have not so perfected our classification that we can now proceed merely to a catalogue of the species within each genus, and for a search for infraspecific variants, as is the case with some of our phanerogamic colleagues. But to my mind we have reached, in the Pezizales, a point of validity in our classification which allows us to recognize families and infrafamilial groups that are biologically sound. As new facts emerge, I feel it is safe to predict that the general outline of our classification will remain unchanged.

Though some of the many problems which confront us have already been discussed today by the participants in this program, let me briefly indicate some of the areas that seem to me to call for critical work.

First and foremost, the microanatomy of the apothecium still needs intensive study in most of the genera of Operculate Discomycetes. Too few species have been

critically examined for us yet to base our classification on what may be very useful anatomical details of taxonomic importance at the generic and higher levels.

Though I remain a staunch advocate of the monographic approach to taxonomy, I am also convinced that species analysis is, at times, not as critical a necessity for the advancement of our knowledge as is the understanding of genera, tribes, and even families. Too long, to my mind, has the concept of the species as the basic unit of evolution gone unchallenged. I am convinced from my own studies, and from the work of others on various groups of plants and animals[1], that the basic evolutionary unit may be groups of species, in some cases recognized as subgenera, genera, or even groups of genera. Natural selection, unquestionably to my mind the major evolutionary factor, may as well affect groups of species as it does individual species. Because real genera are physiologically related, through their evolutionary ancestry, in *many* attributes, they may evolve simultaneously in one direction or another under the stress of a particular natural selection pressure. We need not assume in the classical way that a single species evolves to form a new species or genus, but rather may take a broader view, that related species simultaneously respond and change with time. It is for this reason that I advocate intensive study of what constitute generic, as opposed to specific, characters. Such characters cannot, therefore, be arbitrarily chosen, but must reflect phylogeny. Species, when aggregated into genera on the basis of phylogenetic similarity, begin to make a valid classification.

Clearly, we must avoid excessive generic splitting. Our colleague, Professor Berthet, recently wrote me of his very real concern that there seems to be a tendency, at least in the Sarcoscyphineae, to recognize a separate genus for nearly every species. I must admit that I share his concern. For how many genera with one or a few species can we tolerate with, say, a *Conoplea* imperfect state? We know it in *Urnula*, in *Plectania*, and in *Korfiella*, and I suspect, unlike Professor Paden, that in time we shall find a species of *Pseudoplectania* that also yields a *Conoplea* imperfect state. Have we not gone too far in recognizing so many genera of similar Discomycetes when perhaps one, *Urnula*, would suffice?

Though it seems fair to state that there is rather general agreement today on generic limits in the Pezizales, clearly there are points of real disagreement. For example, as taxonomists we disagree among ourselves on the generic limits of the *Discina-Neogyromitra-Maublancomyces-Paradiscina-Gyromitra-Pseudorhizina* complex of genera. To the non-specialist on Discomycetes, our taxonomic indecision in this area must seem incredible, compounded by the fact that these are large fungi, not infrequently collected, and for which names are therefore actively sought in our books and papers.

In 1970 I proposed the tribe Boedijnopezizeae within the Sarcoscyphaceae,

[1] The thesis that I am advancing here, that the genus may represent the basic evolutionary unit, in not wholly new. I thank my student, Mr. Paul Powell, for calling to my attention the recent paper by Darlington (*1971*) on group selection in carabid beetles, a beautifully executed case in point.

based on three genera, *Boedijnopeziza*, *Cookeina* and *Microstoma*, differing from all other members of the Pezizales in having their asci maturing simultaneously within the apothecium. In all other genera of the order—and in my recent classification (Korf, *1972*) I recognized over 90 genera—asci mature *seriatim*, that is to say, asci of various ages and states of maturity will be present in any mount. I know of only one other case of simultaneous ascus maturation among Discomycete-like fungi. This is in the genus *Cyttaria*, the type and only genus of the Cyttariaceae, a family shunted about from Pyrenomycetes to Operculate Discomycetes to Inoperculate Discomycetes in various classifications. This peculiar genus is found only parasitic on the southern hemisphere beeches of the genus *Nothofagus*. It produces large, spherical or pyriform ascostromata, usually in clusters on a swollen canker of a branch or trunk. Each ascostroma produces 20 to 100 or more large cavities lined with a hymenium. In the species I have studied, these asci are all at the identical stage of development in any one apothecial cavity, but each cavity will be at its own developmental stage. The ascostroma is thus not an apothecium, but a compound structure bearing individual apothecia. The asci are cylindrical, flattened at the apex, which is thickened in youth and provided with a broad apical ring which, in some species, turns blue in Melzer's Reagent. The ring is sufficiently large that it recalls that seen in many species of *Peziza*, rather than the tiny blueing pore seen in many Helotiales. The thin, flattened apex ruptures, sometimes giving the appearance of an operculum, but whether one should call such asci operculate or inoperculate remains, at least for me, an unanswered question. The ascospores of *Cyttaria* recall in their form those of the Pezizales rather than of the Helotiales. But pycnidia, perhaps better thought of as spermagonia, are found in young ascostromata of at least some species of *Cyttaria*, and no member of the Pezizales is known to produce either pycnidia or spermagonia. Despite the simultaneous ascus maturation recalling that in the Boedijnopezizeae, I think it best to treat the Cyttariaceae as a separate order, Cyttariales, and to place it in the Inoperculatae, probably representing a line of development quite unrelated to the Helotiales, Phacidiales, or Ostropales, and not too divergent from the Pezizales.

I would also call your attention to another anomalous fungus which appears to have affinities with the Operculate Discomycetes. This is the monotypic genus *Medeolaria*, described by that master discerner of the odd fungus, Roland Thaxter, almost exactly 50 years ago. It occurs on the stems of a small, North American, herbaceous wild plant in the woods, *Medeola virginiana*, where it causes fusiform swellings and a shortened internode. Through these swollen areas the previously completely internal hyphae emerge in a palisade of paraphysis-like elements, among which eventually are formed asci with 8 huge, brown ascospores, flattened on one side and longitudinally ribbed as in *Phillipsia* or *Wynnea*. To the best of my knowledge, the fungus was never again collected until last year, when a former student, Dr. Donald H. Pfister, and I made a special trip to search for it in one of three areas where Thaxter had reported it. After searching in vain for six hours among thousands of *Medeola* plants, we luckily were able to find several diseased

plants bearing the *Medeolaria* in various states of development. We are, however, scarcely any closer to a knowledge of the life history of this peculiar parasite than we were before, and our hope of studying the asci and their dehiscence mechanism was frustrated by the discovery that they disappear very early in development. The large, inequilateral, ribbed asospores recall, among Ascomycetes, only those of the Sarcoscyphineae, yet the parasitism and simple structure of the ascocarp, little more than a felt of asci and paraphyses, lead me to propose that *Medeolaria* deserves not only a separate family, but a new order, Medeolariales, of which it is the sole representative. Needless to say, I hope that some of my colleagues here will take up the study of Thaxter's fungus, to prove its relationships and to determine whether I am justified in assigning it a position close to the Pezizales despite its evanescent asci, for which no operculum has been demonstrated.

Lack of an operculum is all that has kept us today from treating the order Tuberales in our discussions, for here is another group that very clearly represents probably the closest relatives to the Pezizales that we know. Loss of a functional operculum is surely to be expected when an Operculate Discomycete takes to an underground life and to dispersal of its ascospores by some other means than air dispersal. The selection pressures to retain the complex apical mechanism of the operculum, operating on all members of the Pezizales, no longer affects such a fungus when its spores have a suitable means of dispersal by some other agent. Despite the lack of an operculum, those of us who work with Operculate Discomycetes are content to include the Tuberales among the Operculates!

In summary, let me note that it is our good fortune to be working in the area of Operculate Discomycetes. Our genera appear, for the most part, to be sound. Our groups of genera, at several taxonomic levels, also appear to have a basis in phylogeny. The challenges to us are to refine our system, to apply the new techniques as they appear – the scanning electron microscope being a current example –, but also to proceed with the detailed study of all of our taxa to ensure that they are biologically defensible.

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