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A REASSESSMENT OF THE CYPHELLACEAE[1])

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A suitable subtitle for this paper would have been "The rise and fall of a family". What is usually called the *Cyphellaceae* is an instructive example of a situation not uncommonly encountered in the current systematics of mycology: a family retained in a traditional sense by some mycologists and considered by them as good a family as any, while others are convinced that it is nothing but a handy bin from which part of the contents has already been taken out and disposed of by scattering it over various groups, but which is still needed for keeping what remains. We do not yet know what to do with this considerable remainder, mainly because the published accounts are inadequate and the species have not yet been scrutinized anew in the light of present-day taxonomic requirements.

In order to understand the basic idea of the *Cyphellaceae* the type species may be briefly introduced. The fact that *Cyphella digitalis* was originally described as *Peziza digitalis* is telling, and one could not do better than characterize it as a 'discomycete' with basidia, viz. a cup-shaped fruit-body with the hymenium lining the smooth inside or 'disk'. If one were pressed to form an opinion about its taxonomic position from a dried, not annotated collection and without the aid of the microscope, one would even now, very likely, dispose of it as a discomycete. However, there is little doubt that in nature the cup is directed downward at least when mature, in contradistinction to the average discomycete in which the hymenium containing the asci is directed upward. This difference is a reflection of the two modes of violent spore discharge inherent in the hymenomycetous basidium and ascus; it has been explained through Buller's well-known researches. The cups in the various species are not always typically cup-shaped; in a number they are more or less tubular or else more flattened and even disk-like.

Once their true nature was recognized these discomycete-like basidiomycetes had to be reclassified in the system of the *Hymenomycetes*. Since the hymenium is smooth, the '*Thelephoraceae*' became the receptacle for the species with more or less scattered fruitbodies (*Cyphella*). In other species the fruitbodies may be so densely crowded that together they simulate the pore layer of the '*Polyporaceae*'. In *Solenia* (correct name, *Henningsomyces*) the 'tubes' are seated directly on the substratum. In *Stromatoscypha* (originally *Porotheleum*) they are

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crowded on a well-defined membranous stroma, common to a colony. Hence these fungi became to some authors members of the '*Polyporaceae*'.

This was, roughly, the situation when PATOUILLARD (1900), after preliminary steps by Quélet and Schroeter, decided to assemble these discomycete-like *Hymenomycetes* into a taxon (subtribus) of their own. He admitted the genera *Aleurodiscus*, *Cytidia*, *Cyphella* (fused with *Solenia*), *Porotheleum*, *Punctularia*, and *Phaeocyphella*. Later mycologists usually kept to Patouillard's circumscription except for some minor alterations, such as the exclusion of *Aleurodiscus*, and still more unanimously, of *Punctularia*. After some time the taxon was raised to the rank of a family, a simple definition of which runs: tube-, cup-, or disk-shaped fruitbodies with the smooth or slightly wrinkled basidial hymenium lining the inside, viz. the concave to flattened or even slightly convex disk.

The assignment of *Punctularia* to the cyphellaceous fungi was unexpected. Patouillard was the first to discover that the knobs and folds of the hymenial surface (often likened to that of typical species of *Phlebia*) of the resupinate fruitbody were not really what they appeared to be, but were distinct cushions covered by the hymenium and separated by narrow, sterile troughs. This led him to conceive the only species he knew as comparable to *Stromatoscypha* but with convex rather than concave individual fruitbodies seated on a common subicular layer.

It sometimes does not take long after a family has become established to attract elements that tend to obscure its original character: it then grows out *par enchaînement*. This happened in this case, too. Thus, *Fistulina* was assigned to the family. Another introduction was *Chlorocyphella*, believed to be a lichenized cyphella. At a much later stage followed the genera *Campanella*, *Leptoglossum*, *Arrhenia*, *Rimbachia*, and *Flavolaschia*. In this way various elements were added that considerably departed from the straightforward original conception: for instance, some of these elements had laterally stalked caps, and others a strongly veined to almost lamellate or even tubulate hymenium. With these additions the family was raised to the rank of a suborder and divided into three families, *Cyphellaceae*, *Leptotaceae*, and *Fistulinaceae*. However, none of these innovations has found much general support.

Let us briefly examine some of these accretions. As soon as a relationship between two groups of the magnitude of rather diversified families is postulated it is apt to become a two-way traffic bridge. This is what also happened in connection with the *Polyporaceae*, of which *Fistulina* has been considered a good example by many mycologists up till to-day.

Persoon was the first to compare *Solenia* (*Henningsomyces*) with the resupinate species of *Polyporus* (viz. the modern artificial genus *Poria*). The separate fruitbodies are often elongate to cylindrical and when densely arranged they do closely resemble porias. Fries went a step further and classed *Solenia* as well as *Porotheleum* (*Stromatoscypha*) in

the *Polyporaceae*. The theoretical implication behind this was that *Solenia* had free tubes represented by the individual fruitbodies which are directly seated on the substratum; *Porotheleum*, free tubes on a quite distinct, membranaceous subiculum common to the whole colony; and that in *Fistulina* the subiculum was replaced by an extremely well-developed laterally stalked fleshy-fibrous and succulent cap, but all the same also bearing free tubes. The bridge that served Fries to transfer *Solenia* and *Porotheleum* to the neighbourhood of *Fistulina* and into the Polyporaceae has been used by some modern authors to transfer *Fistulina* into the *Cyphellaceae*.

Another quite remarkable two-way bridge is between the *Cyphellaceae* and the *Corticiaceae*; it may be called after *Aleurodiscus*. This genus has gradually become more and more a storehouse of corticiums with some kind, any kind, of so-called paraphyses. It is not this artificial genus *Aleurodiscus* I have in mind, but the one as recently redefined, in which the development of the basidia and amyloid spore-wall play an important role in the generic character. The type species is *Aleurodiscus amorphus*, originally held to be a small cup-fungus: in outer appearance it is certainly like a discomycete and hence cyphellaceous. If one gradually extends the genus *par enchaînement* it appears quite justifiable to penetrate more and more into the crowd of cyphellas and to enlist in *Aleurodiscus* such fine, big, cup-shaped fungi like *Cyphella vitellina* from South America. One also realizes to his astonishment that the very type species of *Cyphella* itself (*C. digitalis*) is in certain features very similar to these cup-shaped species of *Aleurodiscus*. Patouillard was quite correct, one would conclude, to make *Aleurodiscus* a genus of the '*Cyphellaceae*'. However, surveying the species of *Aleurodiscus* in another direction one soon comes across such species as *A. aurantius*, a fungus with completely 'resupinate' (effused) fruitbodies and in all respects ideally corticiaceous and belonging to the '*Thelephoraceae*' of the traditional classification. It was natural that some authors placed *Aleurodiscus* in its entirety, as well as *Cyphella* reduced to its type species, in the '*Thelephoraceae*' or in a segregate thereof, the *Corticiaceae*—and thus excluded *Cyphella* from the '*Cyphellaceae*'.

Another example is the *Leptoglossum* bridge. *Leptoglossum* reminds one of *Aleurodiscus* in so far that it is partially typically cyphellaceous in the traditional sense. The smallest of its species (let us call it *Cyphella muscicola*, but this is not the correct name) is more or less cup-shaped, and has a smooth hymenium. It very closely resembles young fruitbodies of *L. retirugum*. Next come the species that have been placed in a distinct genus *Leptotus*, now fused with *Leptoglossum*. They are *Leptoglossum retirugum* and *L. lobatum*; both are initially dorsally attached and finally attain far bigger dimensions and have a pronounced tendency to throw their hymenium into folds which may become radially arranged and in appearance somewhat gill-like with cross-veins. Then follows *Leptoglossum muscigenum* with a distinct but short lateral stalk; then *Omphalina rickenii* with erect, centrally stalked fruitbodies and folds well enough developed to include it in the

agarics; and finally we arrive at *Pleurotus acerosus* with gills in *optima forma*. All these species have the same hyphal structure, the same general form of spores of about the same dimensions; the same brownish or greyish-brown colours with corresponding membrana-pigments encrusting the outer hyphae; and the same habitat, for they are all moss-loving. The series appears so perfectly coherent that all its species are now placed by some authors in the single genus *Leptoglossum*.

So far about some examples of the relatively late influx of genera which do not well conform to the traditional character of the *Cyphellaceae*. On the other hand it has not yet been fully realized that if a broadly conceived family of Cyphellaceae is to be maintained, the genus *Schizophyllum* has carefully to be weighed for admission. It is now classed as a genus of gill-fungi but this is not correct. The so-called split gills which characterize the genus are morphologically not at all comparable to the gills of the agarics. The fruitbody is in origin typically cyphellaceous but soon it becomes complicated by proliferation of radially outgrowing marginal lobes. Two adjacent sides of two grown out marginal lobes pressed together form together a 'split' gill. In addition adventitious split gills may also be formed in the hymenial surface.

But let us return to the more restricted and traditional circumscription of the family and recall a diagram published in 1925. It expressed the phylogenetic relationships as they were thought likely by its author. How important this family looks from an evolutionary point of view! It appears as a knot that connects various lines of evolution, viz. (i) toward the *Polyporaceae* through *Stromatoscypha*, (ii) toward the *Cantharellaceae* through *Leptoglossum* (iii) toward the Hymenolichens through *Chlorocyphella*, and (iv) from the *Corticiaceae* in a wide sense through such genera as *Cytidia* and *Cyphella*. Can this scheme stand the test of time after 40 years?

Before answering this question it may be pointed out that some of the genera should never have been included. Apparently they were unknown to the maker of the diagram from personal experience. *Chlorocyphella* has no basidia; it is a genus of imperfect fungi or lichens. Thus, any connection with the Hymenolichens must be given up. The presence of *Hypolyssus* in this scheme is based on a palpable error and it should be left out of further account, too.

As we saw, accepting a close connection with the Polyporaceae is very tempting indeed. Still less difficult is assuming close connections between such genera as *Cytidia* and various *Corticiaceae*, particularly if one places *Aleurodiscus* in the latter family. As to the relationship with the *Cantharellaceae*, this was suggested by the wrinkled or veined hymenium of some species of *Cyphella* when well developed, and by taking the *Cantharellaceae* in a broad and artificial sense. If one restricts that family to those species of *Cantharellus* and *Craterellus* with stichic basidia, then any relationship with the *Cyphellaceae* becomes difficult to defend. However, the *Cantharellaceae* may well be replaced in discussions by the *Agaricales*, for *Leptoglossum* is obviously closely re-

lated to some species that are definitely typical agarics rather than species of *Cantharellaceae*. Thus, there should be little doubt that if the naturalness of the *Cyphellaceae* is postulated it would be outstanding for its many-sided relations to various other families.

If the *Cyphellaceae* were a natural group . . .! The same situation could theoretically also readily be explained by assuming its artificiality. If one includes in a single family the kangeroo, the kangeroo rat, and other leaping mammals and considers them to form a natural taxon of closely related genera, one will get a situation comparable with what has been inferred for the *Cyphellaceae*.

Both the cupulate habit and the smooth hymenium that are the leading characters of this family may be explained as end stages in processes of reduction. Although the typical agarics are centrally stalked, many groups include elements with cupulate fruitbodies, a phenomenon that is coupled with the substratum, viz. stalks of plants, stems of trees, rotten wood, leaves, mosses, instead of the ground. It is also plausible to derive orbicular, but strictly effused, fruitbodies of the *Corticium* type through appressed-peltate ones, from the flattened cupulate fruitbody of 'cyphellaceous' genera as *Cytidia*.

The cyphellaceous or discomycete-like habit is encountered in practically all groups of *Hymenomycetes*; thus, the *Auriculariaceae* have the genus *Hirneola* (the Jew's ear); the *Tremellaceae*, *Exidia*; the *Dacrymycetaceae*, *Femsjonia*. If no special attention had been paid to their basidia these genera might well have been included in the *Cyphellaceae*, too. This shows that the cup-shaped fruitbody has originated along many convergent lines of development.

Even when the cupulate habit is not in evidence in the fully developed fruitbodies of certain agarics it still may occur in the initial stages. A good example is *Pleurotus* (= *Phyllotus*) *porrigens*. If the fruitbody initials were to stop growing out at a very early stage, a good cyphella would result. Would the derivative be the type of a new genus? That depends on what one would know about its genesis. Those who would know how the derivative came into being would presumably call it a new, much reduced species of the same genus; those who would not be informed about the actual relationship would be likely to place it in a different genus and perhaps even in a different family. The situation that one is actually aware in advance about the genesis of such a derivative is hardly ever realized and the taxonomist will have to fill up this gap in his knowledge by acting as a detective and gather his evidence from a detailed examination of his material, mainly by carefully studying the microscopical and chemical features.

The very existence of such series as *Leptoglossum* and *Aleurodiscus* is proof of the existence of the process of transmutation from one ecological type into another. In the *Leptoglossum* case the transmutation of the shape of the fruitbody goes hand in hand with the transmutation of the hymenium from lamellate to smooth, or vice versa. Another example of such a series, this time a very short one is *Mniopetalum*—if it is really a natural unit. It contains two cupulate

species of which one (*Mniopetalum globisporum*) has s smooth hymenium and the other (*Agaricus bryophilus*) a typically lamellate one.

Considerations like these have lead to the working thesis that the *Cyphellaceae* is a standard example of an artificial family, and that as much of its contents as possible should be driven out along all the available as well as several new bridges to other groups of *Hymenomycetes*. Some of these bridges impress one at the moment as well-constructed and solid; others appear still rather ramshackle; and still others are positively perilous, or still under construction.

One of the main difficulties which has to be attended to preceding an orderly exodus is unmixing the cocktail: all of the few traditional genera appeared thoroughly artificial, too. A lot of splitting up and re-classifying into smaller genera has recently been done and has resulted in about twenty or so new genera. This process is still taking its course and with it the rapid deflation of the family. As yet it is not possible to predict that some of the residual contents consist of one or more smaller independent families.

The intention of this paper is not to discuss one by one all groups that have absorbed former elements of the Cyphellaceae. A brief mentioning of some examples additional to those already mentioned may suffice. One of the earliest, and now rated as one of the safest, is the bridge through which *Lachnella* (in a strongly emended sense) was driven out to occupy a position in the neighbourhood of the agaric genera *Chaetocalathus* (cupulate) and *Crinipellis* (centrally stalked). In its wake follow *Cyphellopsis* and perhaps still other genera. The fusiform bodies occurring in the hymenium of *Lachnella villosa* and other species are in my opinion young basidia rather than cystidioles. Exactly similar basidioles are very rare among the agarics except in some groups with one of which *Lachnella* is now actually associated.

Resupinatus is an agaric genus with small to minute cupulate fruitbodies. If one takes away the gills, which may be few, one has constructed species that would find their place in the cyphellaceous genus *Stigmatolemma* as recently emended, redefined, and excluded.

The outside of the fruitbody of the cyphellaceous genus *Calyptella* is occupied by appressed hyphae which form botryose or simpler patent excrescences. The same structures we find also in some of the non-amyloid spored species of the agaric genus *Mycena*; the resemblance of the total of microscopical and chemical features is so suggestive that a close connection between the two genera may be accepted as very likely.

In many of these fungi with so strongly reduced fruitbodies the most important characters are often to be found in the hairs (terminal cells) clothing the outside of the cups. The number of genera that can be recognized by a close and detailed study of these hairs is rapidly increasing. Most of them are suspected to be related to such genera as *Marasmius* and *Crinipellis*. One sometimes feels like a pedlar going from genus to genus, from door to door, with his often limited notes to find response. In those groups of agarics where, for instance, the microscopical details of the cap are well studied one will succeed

occasionally, but contact cannot be established except when the details at both sides are worked out rather carefully and extensively.

What will happen to the original type genus of the '*Cyphellaceae*'? After it was excluded it was disposed of as part of, or placed in the neighbourhood of, *Aleurodiscus*, a genus that itself was stowed away for convenience's sake in that artificial assemblage now called *Corticiaceae*, a name which for nomenclatural reasons is likely to be suppressed in the future. And when its contents are reclassified a mycologist will come across the genus *Cyphella* to which an early family-name is tied. I certainly would not be surprized if the name were to be taken up again to act as a crystallization centre for a family very different from the one that was originally called by exactly the same name. It may well happen that within a few years we will be able to watch the rise of a family of *Cyphellaceae* once more.

REFERENCES

DONK, M. A. 1959. Notes on 'Cyphellaceae'. I. Persoonia **1**: 25–110.

————. 1962. Notes on 'Cyphellaceae'. II. Persoonia **3**: 331–348.

————. 1964. A conspectus of the families of Aphyllophorales. Persoonia **3**: 199–324.

LOHWAG, H. & L. FOLLNER. 1936. Die Hymenophore von *Fistulina hepatica* Annls mycol. **34**: 456–464.

PATOUILLARD, N. 1900. Essai taxonomique sur les familles et les genres des Hyménomycètes. Lons-le-Saunier.

PILÁT, A. 1925. Monographia Cyphellacearum čechosloveniae. 1. . . . La partie générale. Spisy přirod. Fak. Karl. Univ. No. 28: 52 pp.

SINGER, R. 1945. The *Laschia*-complex (Basidiomycetes). Lloydia **8**: 170–230.

————. 1962. The Agaricales in modern taxonomy. Second, fully revised edition. Weinheim.