

7] Recent Developments in the Systematics of Pathogenic Fungi

by BRYCE KENDRICK*

ABSTRACT

Since 1968 six large-scale compilations and/or syntheses of almost 600 "good" form-genera of Hyphomycetes have appeared, elicited after a 50-year hiatus by the irruption of developmental concepts onto a scene previously dominated by morphology of mature organisms. But ontogeny is no taxonomic panacea, and the best treatments are now eclectic, since only a developmental process that leaves its mark on the mature organism, or is always associated with other conspicuous features, is taxonomically useful. Of seven ways in which a chain of conidia can develop, most are easily diagnosed retrospectively; in the others we must still rely on unique form, superbly illustrated. Of 600 "good" form-genera of Coelomycetes, only 200 have been ontogenetically investigated, and some important genera of pathogens—*Ascochyta*, *Diplodia*, *Septogloeum*—with hundreds of species, are still dismally heterogeneous. *Septogloeum*, for example, has species with solitary, annellidic, annellidic and sympodial, phialidic, and meristem conidium ontogenies. Most such problems should be solved in another decade. In Ascomycetes, lysigenous or schizogenous centrum development is consistently associated with the more easily detected bitunicate asci, and if ascospores are phragmosporous or dictyosporous, odds are greater than 9 to 1 that they occur in bitunicate asci.

Full development of many fungi involves both sexual and asexual states, often separated in time and space. Only when data derived from *all* phenotypic expressions of a fungal genome (the "perfect" fungus) are correlated with comprehensive ecological data can we approach a rational taxonomic system.

INTRODUCTION

The logo designed for this symposium shows a tree of life with three main branches, presumably representing three Kingdoms—Plantae, Protista and Animalia. My own interpretation is closer to the Five-Kingdom scheme

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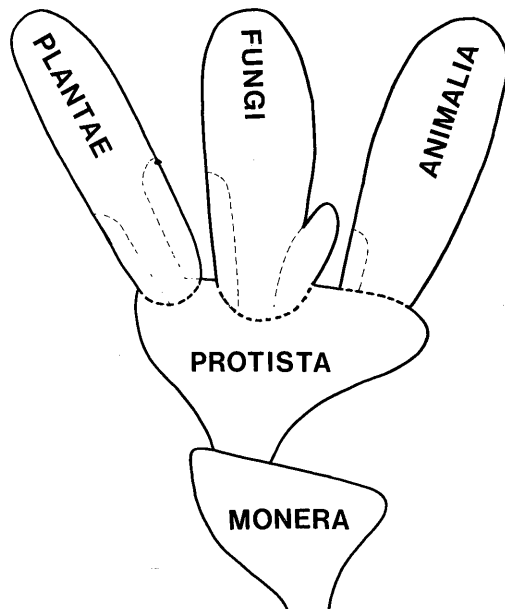


Figure 7.1. Diagram of the Five-Kingdom scheme proposed by Whittaker (20).

(Fig. 7.1) proposed by Whittaker (20), in that I consider the Fungi to have achieved the status of a separate Kingdom. Perhaps, in deference to my hosts, I can compromise by thinking of the fungi as essentially protistan that have invented a unique form of modular domestic architecture—the tubular hypha—which protects its living contents, and greatly facilitates the exploration and penetration of substrates. This most successful strategy, combined with their enzymatic versatility, has made the fungi of first rank importance in the decomposition of the enormous amounts of plant debris—estimated at 85 billion tons per annum—produced in the terrestrial habitat. They are also second only to the arthropods in their depredation on living plants.

Over a third of all fungi (and a majority of plant pathogens) belong to the great Subdivision Ascomycotina. Many members of this group produce asexual mitospores called conidia* that serve as dispersal units, and many of these asexual phenotypes exist independently of the sexual phenotype. If one finds an unknown insect larva, proper care and feeding will usually result in its arriving at identifiable adulthood. Conidial fungi are not so predictable. The vast majority of them have not yet been connected to the

*A reasonable definition of the term “conidium” is the following: A specialized, non-motile asexual propagule, usually caducous, not developing by cytoplasmic cleavage or free-cell formation (9).

sexual states (indeed, many of them may no longer be capable of producing sexual states), and so we have been forced to classify them independently.

These conidial fungi are known collectively as the Form Subdivision Deuteromycotina. This large group is initially split into two Form Classes: the Hyphomycetes, which produce their conidia from exposed conidigenous cells, and the Coelomycetes, which form their conidia within some kind of protective structure.

As every plant pathologist knows, many destructive plant pathogenic fungi are found among the Deuteromycotina. Need I do more than mention a few Hyphomycetes such as *Fusarium*, *Helminthosporium*, *Botrytis*, and *Cercospora*, or Coelomycetes such as *Ascochyta*, *Colletotrichum*, and *Septoria*, to make my point? But for over half a century no up-to-date, accurate, comprehensive taxonomic treatment of this group was produced. This deficiency inevitably led to incorrect identifications. Over the years these grew into misleading generic concepts that have had plenty of time to become firmly established.

THE FORM CLASS HYPHOMYCETES

Fortunately, the situation has been considerably ameliorated during the past decade, at least as far as the Hyphomycetes are concerned, by the publication of six large-scale syntheses and compilations: Barron (3), von Arx (1, 2), Ellis (5, 6), Kendrick (9), and Kendrick and Carmichael (10). Further volumes will appear in 1978. What triggered this avalanche of useful books? My guess is that it was some seminal work on the part of Hughes (7), who saw clearly that the systematics of the Deuteromycotina was being seriously held back by its excessive reliance on characters of mature morphology, a doctrine enshrined in the monumental works of the great 19th century Italian mycologist, Saccardo, and even inherent in the concept of the *Form* Subdivision Deuteromycotina.

Why, asked Hughes, should we base our whole taxonomic scheme on the frozen moment that is represented by maturity? Why not trace the entire developmental process and see if useful characters emerge? This wasn't exactly a new idea—Hughes didn't *invent* development any more than Darwin invented evolution. The French mycologist Vuillemin (17, 18, 19) had made some very perceptive observations at the beginning of this century, but he was ahead of his time, and his ideas were effectively buried for nearly 50 years. But after the Second World War had brought increased awareness that molds can be very important to man—not solely as plant pathogens, but as destroyers of textiles, and as producers of antibiotics—the time was ripe. Hughes proceeded to do for Deuteromycete ontogeny what Darwin had done for evolution: he fleshed out the idea with a mass of meticulous observations. These have since been extended, intensified, and refined by many other mycologists. Fungal systematists hoped that, with

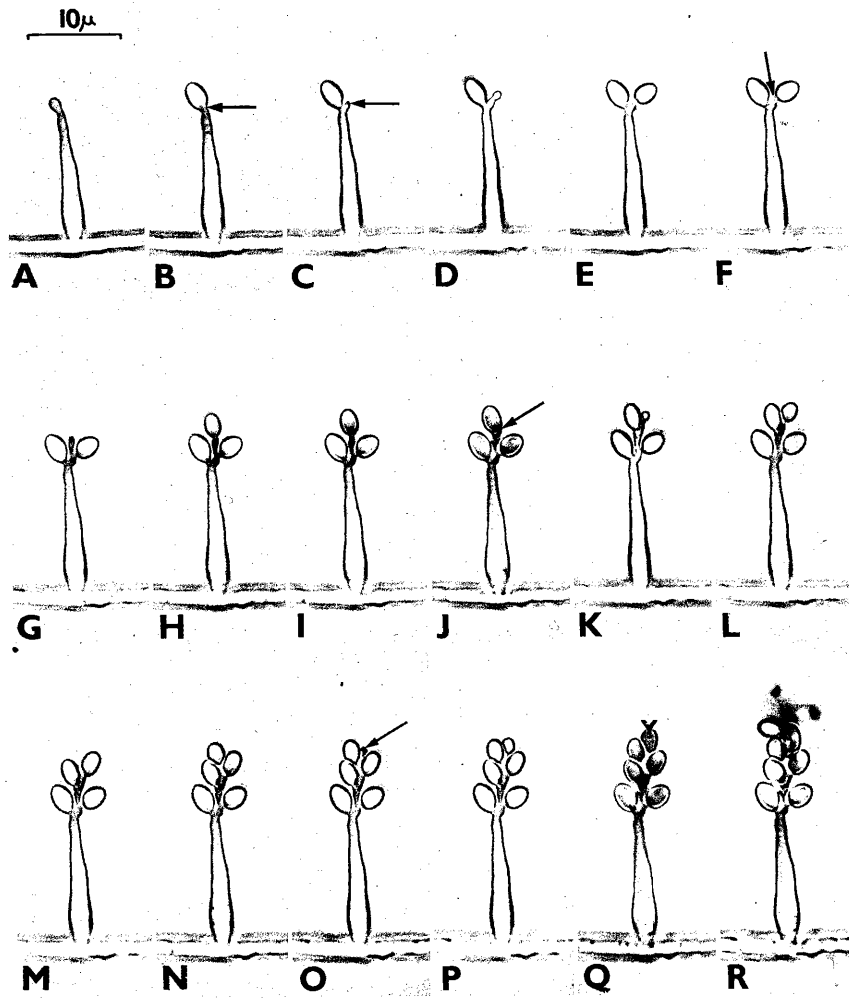


Figure 7.2. Time-lapse photographs of sympodial proliferation of the conidiogenous cell during repeated conidiogenesis in *Tritirachium album* Limber (from Kendrick, ref. 9).

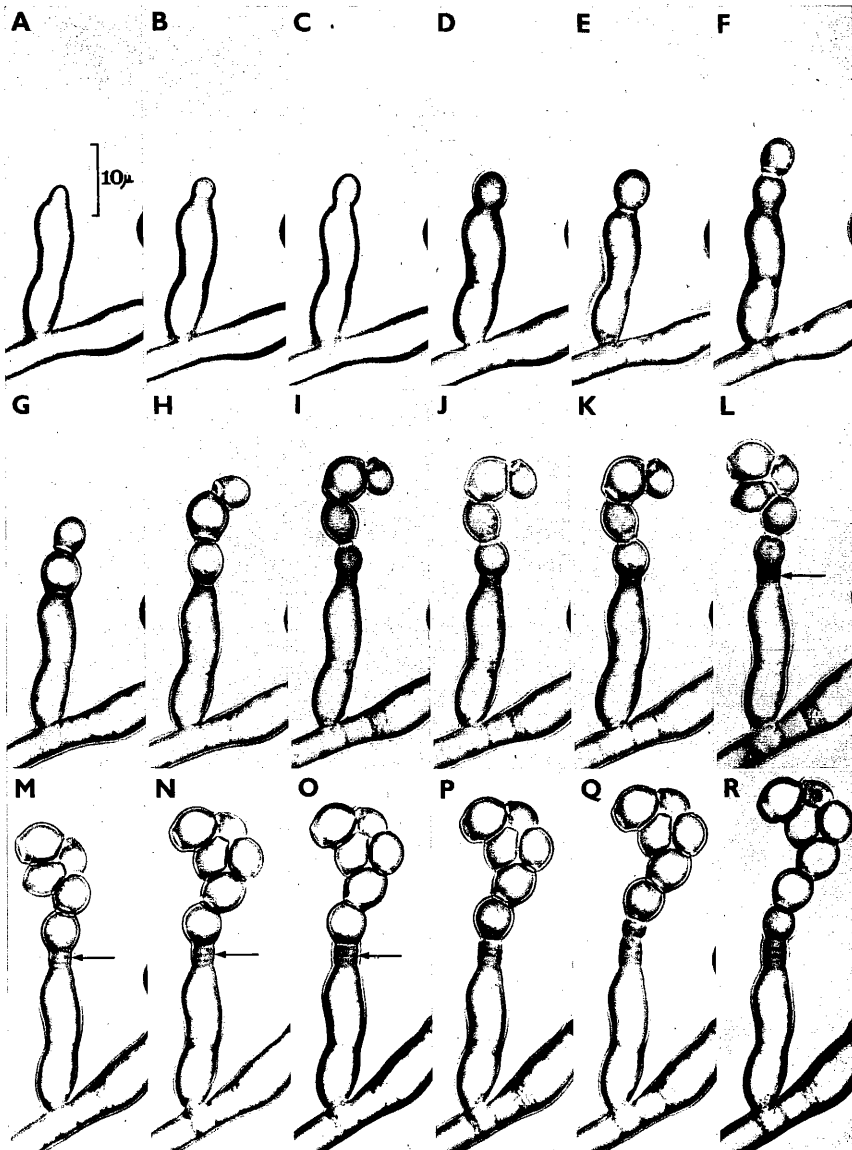


Figure 7.3. Time-lapse photographs of percurrent proliferation of an annellide during repeated conidiogenesis in *Scopulariopsis brevicaulis* (Sacc.) Bainier (from Kendrick, ref. 9).

the advent and adoption of developmental characters—the recognition of the many different ways in which conidia can be formed singly, synchronously, or successively—a whole new and more ‘natural’ classification would emerge. I must admit—and this is one of the key points I want to make—that this has *not* happened. Despite the scores of papers published about conidium ontogeny, no workable classification based on development has been proposed, and I am convinced that none will be.

Was the whole developmental concept a chimera, a mirage? Not at all. Despite certain current excesses, the benefits accruing to mycology from the ontogenetic movement have been impressive. Despite disappointments, we have some important new characters to use. In the most extensive compilation of Hyphomycete genera yet attempted, Kendrick and Carmichael (10) adopted a very pragmatic philosophy. If developmental characters could be reasonably easily discerned under the light microscope, they would be applied. If mature morphology were diagnostic, then *it* would be used. This eclectic system has already made it easier to identify a Hyphomycete to the genus level than ever before. From the practical point of view, we know that no one will do a time-consuming developmental study of an organism or examine it with an electron microscope, just to identify it. That is why I have deliberately refrained from using electron micrographs to illustrate this chapter. The only kind of developmental feature fit for general use is

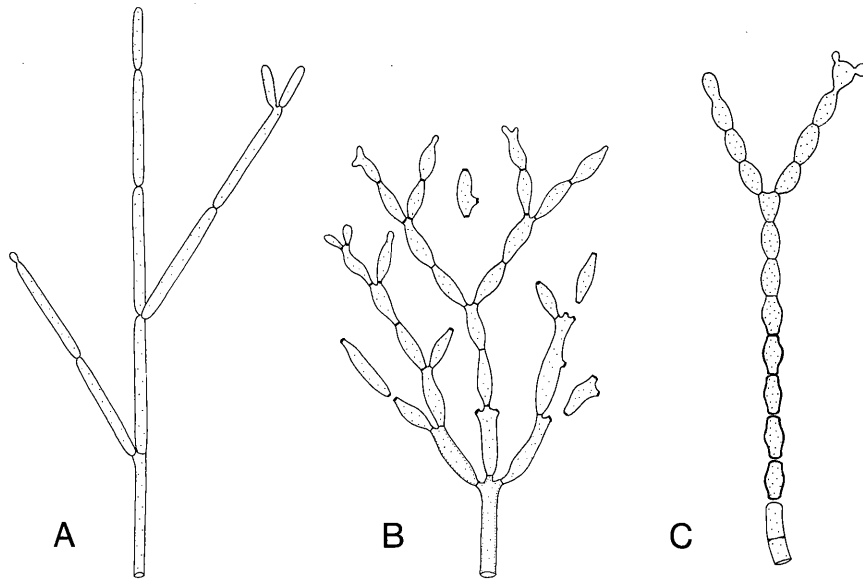


Figure 7.4. Acropetal chains in (A) *Fusidium griseum* Link, (B) *Hyalodendron* sp, and (C) *Monilia cinerea* Bonorden. Note the diagnostic young conidia forming at the tip of some chains.

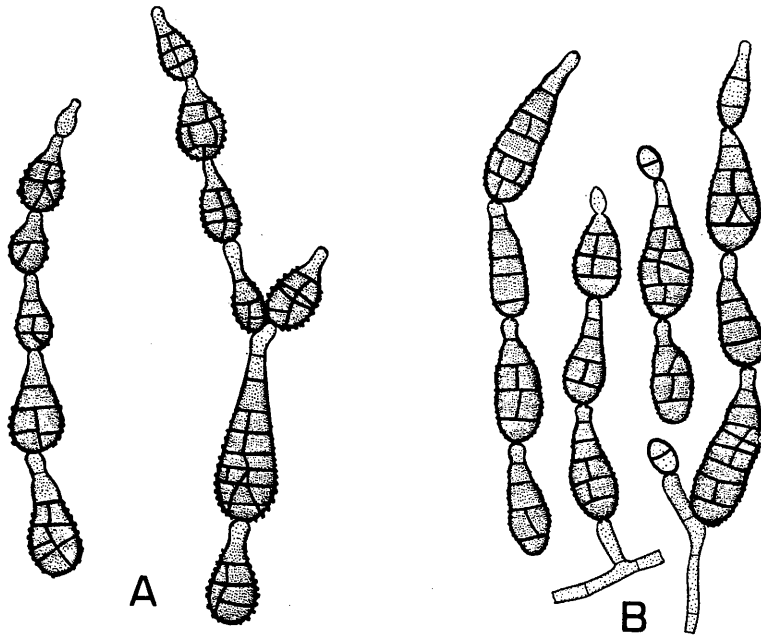


Figure 7.5. Acropetal chains of dictyoconidia in (A) the *Alternaria* state of *Pleospora infectoria* Fuckel and (B) *Alternaria alternata* (Fr.) Keissler (after Ellis, ref. 5).

the kind that leaves its mark on the mature organism or structure, or is invariably associated, for historical (evolutionary) reasons, with other easily recognized features.

Perhaps I should be more specific. If a conidiogenous cell produces a succession of conidia by sympodial proliferation, the appearance of that cell will be permanently changed (Fig. 7.2). The visible changes are frequently diagnostic. If a conidiogenous cell, in producing each new conidium, proliferates vegetatively through the scar left when the previous conidium fell off, the appearance of that cell, too, will be permanently changed. Such a cell is called an annellide (Fig. 7.3). If conidia are produced in chains that grow at the tip (acropetal chains), the presence of a young conidium at the distal end of some of the chains will usually tell us exactly how those chains were formed (Fig. 7.4). Even large, muriformly-septate conidia like those of *Alternaria* (Fig. 7.5) are formed in acropetal chains.

Many molds have been described as having "catenate conidia," or "conidia in chains," and until fairly recently this was thought to be sufficiently diagnostic. But of course those chains were not all produced in the same way. Conidial fungi have evolved no fewer than seven methods of conidial chainmaking. It is convenient to divide them into the four "successive"

methods, which add one conidium at a time, and the three “concurrent” methods, in which more than one conidium in the chain is formed at a time. I have already mentioned two of the “successive techniques,” the acropetal chain, and the chain produced by some annellides. A third is the chain produced from a conidiogenous cell that doesn’t change in length even after producing a large number of conidia (Fig. 7.6). This sausage-machine type of approach is adopted by open-ended conidiogenous cells called phialides, and the youngest conidium in this kind of chain is always at the bottom, having just been extruded by the phialide. Such a chain is called a basipetal chain to distinguish it from the acropetal chain which extends at the top. Phialides and annellides can both produce basipetal chains, and although these two kinds of conidiogenous cell are now considered to be developmentally related, they look different after conidiogenesis, and can therefore be used as bases for form genera.

If the annellide gets longer as it produces conidia, and the phialide stays the same length, could there be a cell that gets shorter as it produces conidia? Indeed there could be, and there is. The so-called retrogressive conidiogenous cell blows out a short segment of itself to produce each conidium, and as the chain gets longer, the conidiogenous cell becomes gradually shorter (Fig. 7.7).

Now let us consider the chains in which two or more conidia develop concurrently. First, there are the meristem conidia. In this kind, several conidia are developing at the same time, though each is at a different stage of development, with the most mature at the top, and very young conidia, hardly differentiated from the cells of the conidiophore, at the bottom (Fig. 7.8). In this case it is hard to tell just where the conidiophore stops and the chain of conidia begins: there is a diffuse meristematic zone which gives these conidia their name. Conidial states of the powdery mildews belong here.

Second, there are the random chains which result when a hypha disarticulates at the septa to form conidia. This disarticulation gives rise to what we call fission arthroconidia (Fig. 7.9). As a variation of this process, every other cell of a hypha or conidiophore degenerates and dissolves, while the alternate cells metamorphose into conidia (alternate arthroconidia, Fig. 7.10).

If we can find ways of recognizing, after the fact, which kind of development has taken place, and show other people how to recognize it, we have considerably increased the taxonomically useful information that can be readily extracted from many fungi.

Sometimes, as with the telltale signs left by sympodial proliferation, or the conspicuous collarete present on many phialides (Fig. 7.11), this information is easy to communicate, if critical illustrations are available, and identification becomes easy. But in other cases, as with the often extremely inconspicuous scars on annellides, or the easily misread phenomena associated with holoblastic-retrogressive conidiogenesis, recogni-

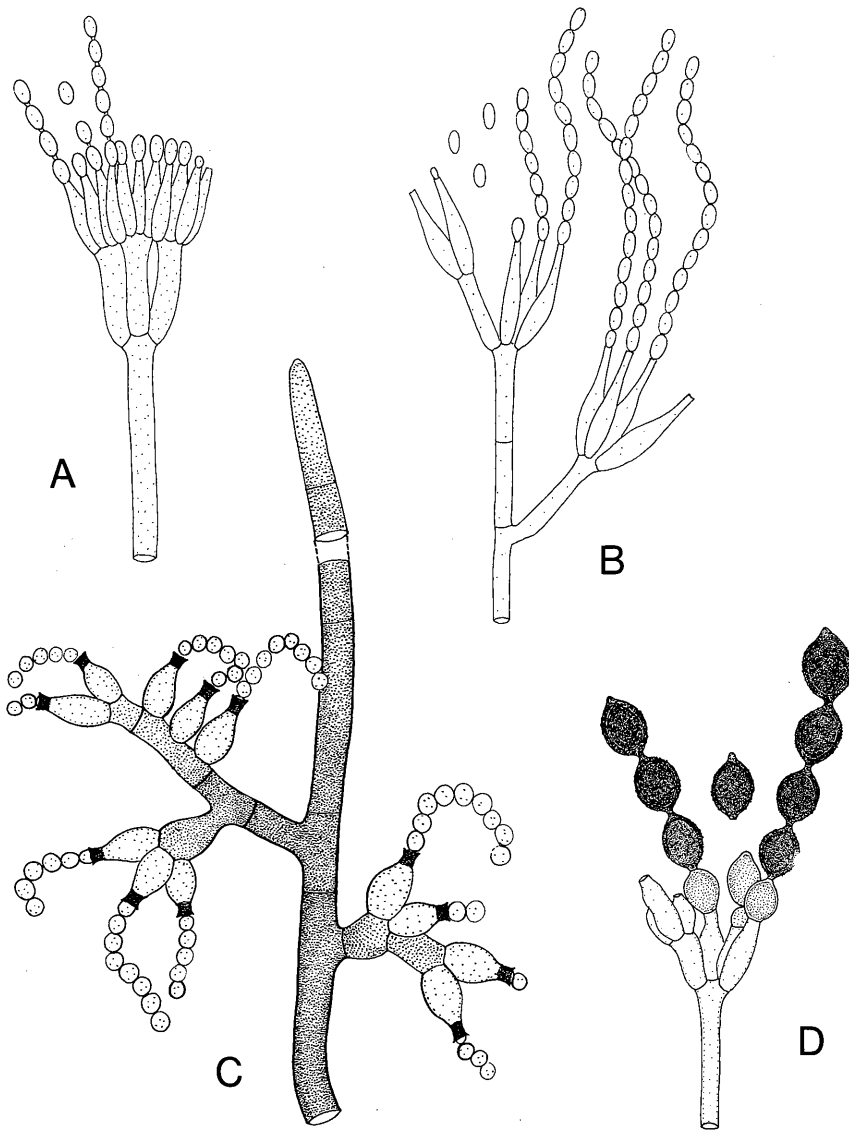


Figure 7.6. Basipetal chains of conidia being produced by phialides in (A) *Penicillium* sp, (B) *Paecilomyces varioti* Bainier, and (C) *Angulimaya sundara* Subram. and Lodha, and (D) *Phialomyces macrosporus* Misra and Talbot (after Kendrick and Carmichael, ref. 10).

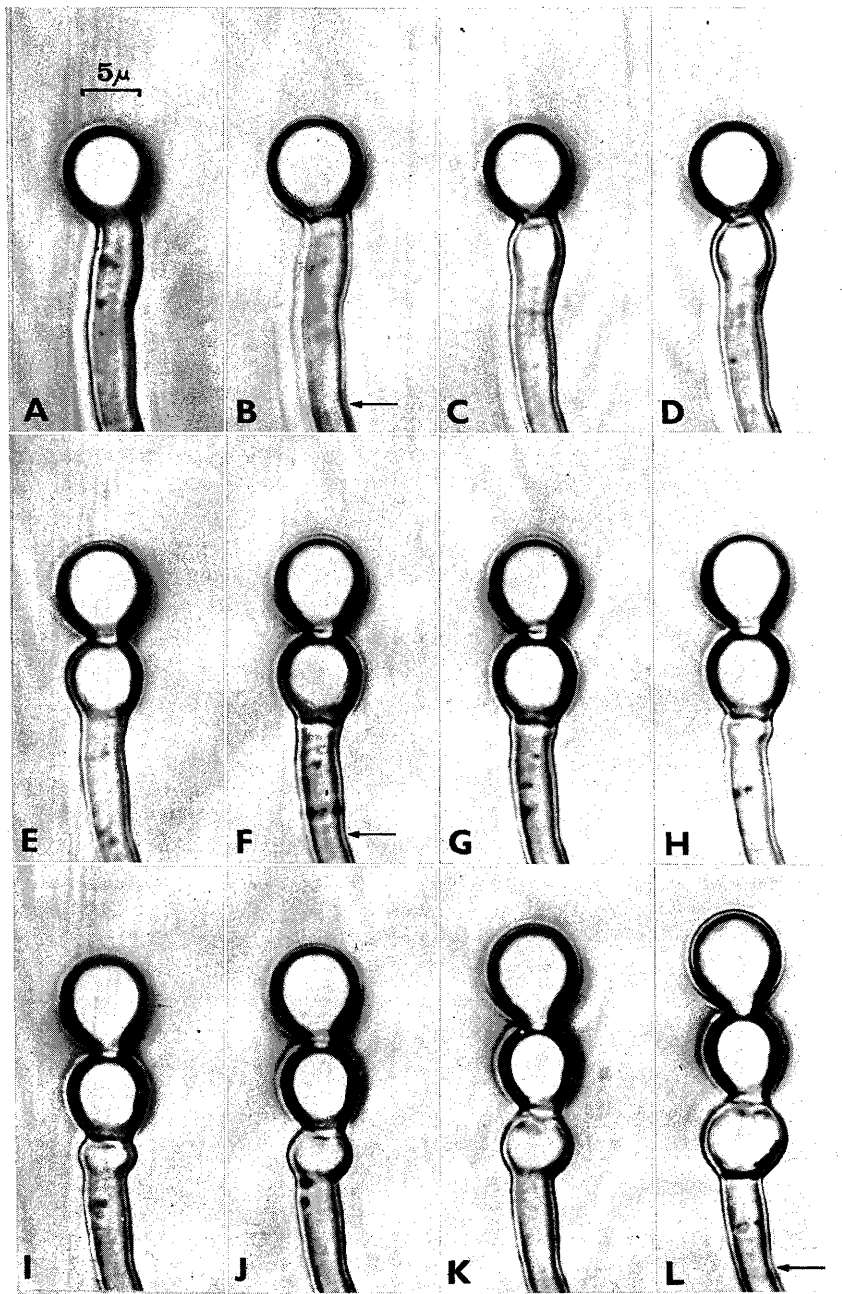
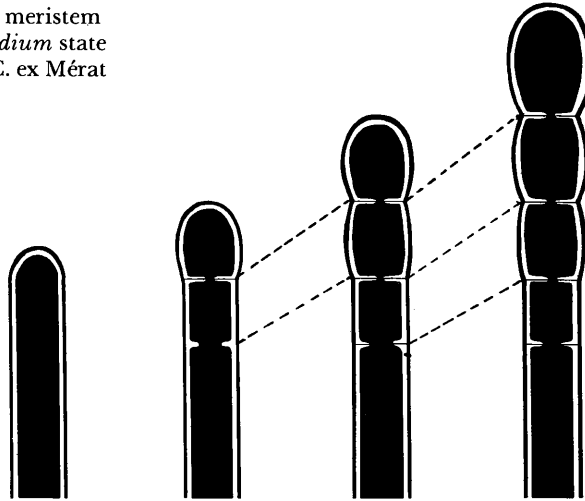


Figure 7.7. Time-lapse photographs of retrogressive conidiogenesis in the *Basipetospora* state of *Monascus ruber* Van Tieghem. The arrows indicate a reference point (from Kendrick, ref. 9).

Figure 7.8. Diagram of meristem conidiogenesis in the *Oidium* state of *Erysiphe graminis* DC. ex Mérat (after Kendrick, ref. 9).



tion of developmental phenomena may call for more critical observations than many practicing plant pathologists have time to make. In such cases we can only hope that truly accurate, life-like illustrations may prove sufficiently diagnostic—that a number of morphological differences, each small in itself, may add up to a unique facies. Certainly, even if one is unaware of their fine developmental criteria, one is unlikely to confuse the annellidic *Spilocaea* state of *Venturia inaequalis* (Cooke) Winter (the apple-scab fungus), or the synchronous blastoconidia of *Botrytis cinerea* Pers. ex Pers., with anything else. Other difficulties confronting those who would establish classifications based on development can be briefly listed as follows:

- 1) Some ascomycetous genera produce more than one conidial state. Species of *Ceratocystis* produce conidial states assignable to no fewer than 16 form genera (16). These conidial states not only differ in morphology, but also exhibit five different kinds of conidium ontogeny. This may indicate heterogeneity in *Ceratocystis*, but that will not explain all the difficulties inherent in this situation.
- 2) Members of the same form genus of Hyphomycetes have been reliably connected to widely differing sexual states. This may be explained by convergent evolution of conidial states, but it is a real (if natural) obstacle to the establishment of an integrated classification.
- 3) Some conidial fungi are themselves pleomorphic, producing two (or occasionally more) morphologically and developmentally different conidial states on one mycelium (for example, *Doratomyces stemonitis* (Pers. ex Fr.) Morton and Smith, and *Echinobotryum atrum* Corda; *Chalara elegans* Nag Raj and Kendrick (14) and its unnamed chlamydosporic state—the latter pair formerly known under the single binomial *Thielaviopsis basicola* (Berk. and Br.) Ferraris).
- 4) Some conidial fungi can switch from one method of conidiogenesis to another

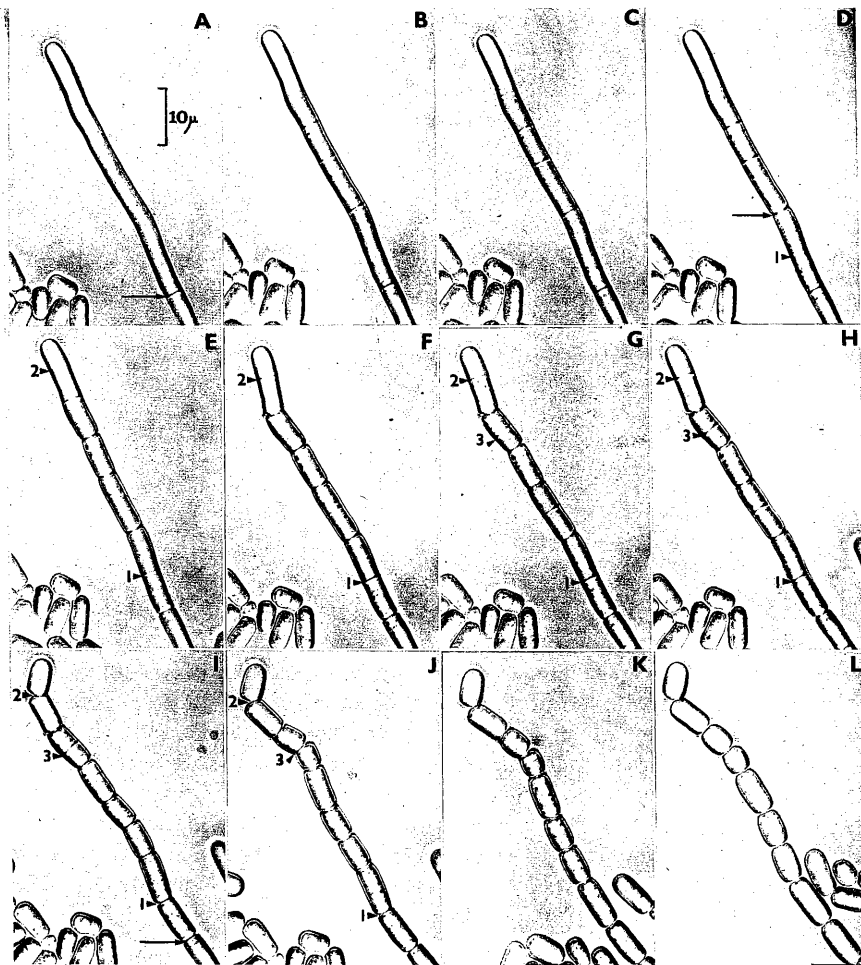


Figure 7.9. Time-lapse photographs of a "random" chain of fission arthroconidia forming in *Geotrichum candidum* Link ex Pers. (from Kendrick, ref. 9). Note that the sequence of formation of conidia (in some cases indicated by numbers) is neither acropetal nor basipetal.

(for example, *Spiropes melanoplaca* (Berk. and Curt.) M. B. Ellis and *Chionomyces meliolicola* (Ciferri) Deight. and Piroz.—sympodial to annellidic).

I emphasize that developmental characters in most cases have not replaced the more traditional morphological features such as branching, shape, septation, and color, but have supplemented them, and have helped systematists to produce a body of useful and accessible literature on identification. Taxonomists would welcome feedback from the applied mycolo-

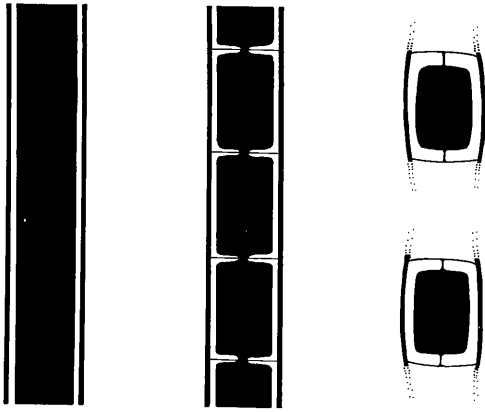


Figure 7.10. Diagram of alternate arthroconidia formation in *Coremiella ulmariae* (MacWeeney) Mason (after Kendrick, ref. 9).

gists who must now try to use these books, and for whom they are written. Dr. Carmichael and I completed our comprehensive compilation of Hyphomycete genera in 1971. It was published in 1973, and gave coverage of over 1500 generic names, of which we accepted just under 600 as "good." Since 1971 about 240 new generic names have been published. The appearance of our fully illustrated compendium apparently reassured many authors that their "new" taxa were indeed unique. (Sometimes when a genus has been described as new, this has meant only "new to the author"—it *should* have meant that the author knew and could confidently rule out all extant genera.) In addition to this spate of new names, a number of formerly poorly understood older names have now been satisfactorily interpreted. Thus we have undertaken to produce a completely revised, up-dated and expanded version. We hope, but without conviction, that this second edition will last longer than the first.

THE FORM CLASS COELOMYCETES

We formerly divided the Coelomycetes into two Form Orders: the acervular fungi, Form Order Melanconiales, and the pycnidial fungi, Form Order Sphaeropsidales. As the anatomy of more and more Coelomycetes was studied, so many intermediate and aberrant forms were found that we now prefer to call all Coelomycete fructifications "conidiomata." Many genera were published with deficient descriptions and no illustrations. Perhaps this, and the fact that the fifth edition of the *Dictionary of the Fungi** lists over 1,000 generic names for Coelomycetes, daunted taxonomists, because the group was neglected for even longer than the Hyphomycetes. The number of "good" Coelomycete form genera can still be only roughly estimated, but T. R. Nag Raj (personal communication, 1977) suggests that

*Ainsworth, G. C. 1961. Commonwealth Mycological Institute, Kew, Surrey. 547 pp.

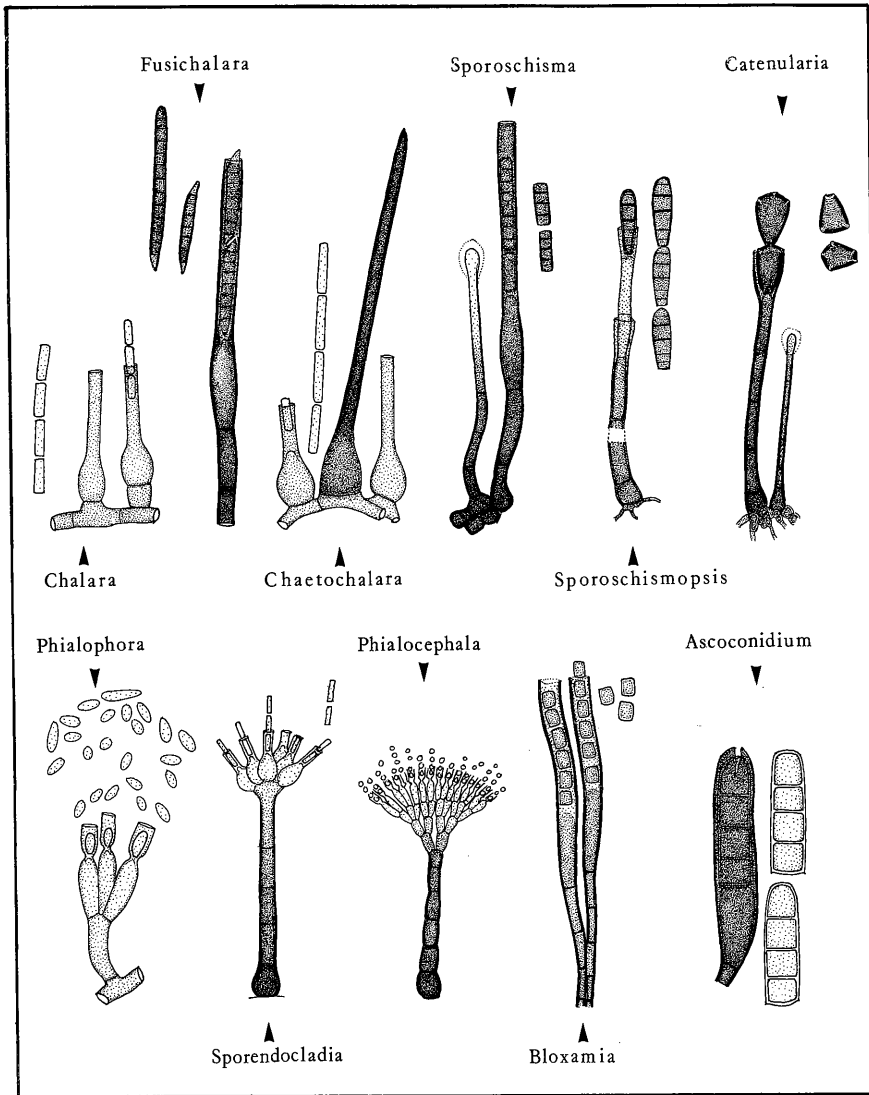


Figure 7.11. Variation in collarete morphology among some phialidic Hyphomycetes (after Nag Raj and Kendrick, ref. 14).

there may be as many as 600. This makes the group, despite the fact that far fewer mycologists concern themselves with it, of a size and complexity comparable to the Hyphomycetes.

The critical reevaluation of generic concepts in the Coelomycetes is going ahead slowly but surely, and we feel that in about another decade they will rest on a firm developmental-anatomical foundation. But at present, accurate developmental and anatomical data are available for only about a third of the genera. Plant pathogenic genera such as *Ascochyta*, *Diplodia*, and *Septogloeum* contain several hundred “species” each. They are obviously dismally heterogeneous, and that means bad, genera. *Septogloeum* is known to contain species with five different patterns of conidium ontogeny—annellidic, solitary, sympodial plus annellidic, phialidic, and meristem—and it will be some time before this particular mess is cleaned up. Nag Raj (personal communication) is investigating the genus *Ceuthospora*, and finds that species formerly attributed to this genus should be disposed in *Coleophoma*, *Dothichiza*, and *Cytospora*.

This kind of information may not be immediately useful to applied mycologists, but I hope they will tolerate our efforts to establish order rather than condemn us because we can't yet produce an over-all classification for them. Clearly, if the process is to be speeded up, more money must be spent on good Coelomycete taxonomists.

THE SUBDIVISION ASCOMYCOTINA

Although many areas of Ascomycete taxonomy are still controversial, some concepts are regarded as established beyond dispute. One of these is that at some time early in Ascomycete evolution a dichotomy occurred between forms producing enclosed ascomata in which the cavity containing the asci was “built-in” during the development of the ascoma, and other forms in which the cavity developed secondarily by dissolution or splitting apart of tissue at the time the asci arose. Again, it is unlikely that anyone trying to name an ascomycetous plant pathogen will do a detailed study to find out which kind is which, because it is much easier to make the decision on the basis of another character altogether—whether the asci themselves are unitunicate or bitunicate.

Painstaking work has shown that ascomata with secondary (lysigenous or schizogenous) cavities always contain bitunicate asci. The constellation of associated characters here is even more extensive—the ascospores in bitunicate asci are usually septate, and they are usually shot out of the ascus one at a time rather than in a single burst. Both of these characters help to differentiate them from the unitunicate Ascomycetes. We can go even further: if ascospores are phragmosporous (having two or more cross-walls), or dictyosporous (with septa running transversely and longitudinally), the odds are at least 9 to 1 that the fungus is one of the bitunicates: ascospore septation is, of course, even easier to observe than the bitunicate ascus.

For some excellent discussions of the implications of developmental characters of the ascoma, I refer you to E. S. Luttrell's accounts published in 1951, 1955, and 1973 (11, 12, 13).

THE SYNTHESIS

The Deuteromycotina are not a part of the main taxonomic classification of the fungi. How can they be? They include conidial states of Ascomycetes, Basidiomycetes and, in the opinion of some, Zygomycetes. We group these conidial states into form genera largely for convenience in identification. The species included in any particular form genus must have a high level of morphological and, one hopes, developmental similarity, but they may not be related by descent. There can be no guarantee of that. So it is impossible or at least misleading, to propose many higher taxa, such as families, for them. Conidial states can only take their place in the main classification when they are linked to their sexual states (if such exist), and we can talk about the "whole fungus."

When I was first introduced to the mysteries of mycology, I gained the impression that the classifications of the Ascomycotina and Basidiomycotina were in good order, while that of the Deuteromycotina was chaotic. Things have changed! Families and Orders of Ascomycetes and Basidiomycetes have been juggled around with amazing dexterity, and even created and abolished with a wave of the pen. Those of us who work with the Deuteromycotina once felt that if we could make connections between the conidial fungi and their sexual states, the sexual classification would help us to put our house in order. Now I think the Ascomycete and Basidiomycete specialists need us almost as much as we need them. In 1971 Kendrick and Carmichael (10) noted sexual state connections for about one-quarter of the "good" Hyphomycete form genera—one or more Ascomycete genera were noted as states for 133 form genera, and clamp-connections or named Basidiomycete genera were noted for 25 form genera. Kendrick and Watling (unpublished data) have almost doubled the number of form generic names applied to Basidiomycete conidial states, and our continuing revision of the listing of form-genera shows that Ascomycete connections are now known for about one-third of the "good" form genera.

By the time this book appears, a determined attempt at interpretation of the known connections will have been made. Experts with various backgrounds will have met at the second Kananaskis Conference (Kananaskis, Alberta, September 1977). Here's an example of subject matter: Gary Samuels, collaborating with Amy Rossman at The New York Botanical Garden, concluded that present generic separations of Nectrioid fungi, which are based on ascospore septation, are essentially unnatural, and that well-defined groups (genera?) can be delimited by using a combination of characters, but emphasizing perithecial wall structure and conidial state. Not only have Samuels and Rossman been able to reorganize the perithecial

fungi, but they can also define form genera for the conidial states and suggest possible origins and variations of these. Clearly, in this particular exercise each classification—the sexual and the asexual—benefits from the other. In Chapter 11 of this volume E. S. Luttrell ably expounds how this same cross-fertilization process has affected the taxonomy of *Helminthosporium sensu lato*.

THE FUTURE

Morphology. Much remains to be done in the straightforward, classical descriptive mode. The rate of publication of new taxa is still increasing, and I am sure it will be at least a century (all other factors remaining favorable) before it slows down. The general standard of description and illustration has improved in recent years, but much still remains to be done in the way of training mycologists to communicate their taxonomic findings with the completeness that only loving care and consummate skill can achieve.

Development. The development spectrum of the Deuteromycetes is now well understood, but the full integration of ontogeny into the classification will take many more years, since hundreds of genera and thousands of species still await reexamination.

It is now obvious that fungi sharing a particular mode of conidiogenesis are not necessarily closely related. We have had to accept the obvious corollary of this—most, if not all, techniques of producing conidia have arisen more than once. We do not yet know how many times, and I think it will be difficult to find out with any degree of certainty. But we must try.

In the Coelomycetes, we can expect advances in our understanding when detailed studies are made of the mode of origin of the cavities on conidiomata—are they original, or are they lysigenous or schizogenous? We can answer that question for very few genera at present. Yet the relevance of a comparison between conidiomatal cavities and ascomatal cavities is obvious.

Connections. The number of connections established between sexual and conidial states is growing rapidly, and now represents a significant fraction of known fungal taxa. But the process of establishing connections is painstaking and uncertain, and my own belief is that many common conidial fungi have lost the ability to reproduce sexually (probably because it is no longer adaptive, and because they are heterokaryotic and can undergo genetic recombination via the parasexual cycle). In addition, the known connections are concentrated in certain Orders of Ascomycetes, (for example, Hypocreales, Eurotiales, Pezizales) while other Orders have few or no known conidial states (for example, Ostropales, Coronophorales, Lecanorales, Tuberales, Myriangiales). This may be due to taxonomic neglect, or to difficulties involved in culturing certain groups, but to me these observa-

tions strongly suggest that our dream of a fully-connected fungal flora may never be realized.

Biochemistry. Bartnicki-Garcia (4) has demonstrated that different fungal groups have differing wall compositions and that there are other biochemical markers, whose basis may be well established, as in the various enzyme aggregations involved in tryptophane synthesis as discussed by Hütter and DeMoos (8), or obscure, as in many of the chemical color tests outlined by Skalicky and Jechova (15). But most of these data apply only at higher levels of classification, and are of little use for segregating genera or species.

DNA base composition and hybridization studies, despite highly optimistic early claims, have been disappointing. The reasons for this are now being elucidated, as L. H. Throckmorton shows in Chapter 13 of this book. We cannot look to the biochemists for solutions to our taxonomic problems.

New characters. Conidium ontogeny arrived in 1953—a quarter of a century ago. It is clearly time for further innovation.

Ecology. In recent years some mycologists have shown that many conidia fungi exhibit considerable phenotypic plasticity in culture when subjected to changes in temperature, pH, radiation, carbon source, etc. These observations are sometimes used to criticize the existing classification, since it appears that species (and even genera) can be transmuted by appropriate manipulations. Yet the species in question often appear to be very stable and distinct in their natural habitats. My suspicion is that many species have very narrow ecological ranges, and that if the limits of those ranges are transgressed, other organisms will displace them. In culture, we remove the competition factor and can gain a false impression of flexibility.

CONCLUSIONS

I interpret the foregoing to mean that in order to define many of our taxa properly, we must consider not simply the morphology of a sexual or asexual state, nor morphology supplemented by development, nor even those augmented by knowledge of the entire life history, but all of the above, placed in an environmental context that specifies the ecological demands made by each species. This context may have been millions of years in the making, and will not easily reveal all of its secrets. Nevertheless one shorthand form incorporating much of this ecological information already exists for many fungi, and is made use of in taxonomy. I refer to host or substrate range. It is significant that in M. B. Ellis's second book *Morphology of Dematiaceous Hyphomycetes* (6), the key to species of *Cladosporium* concerns itself almost entirely with host or substrate, rather than with other available characters. I am not promoting a return to the old days when 40

species of *Ramularia* were recognized on 400 different hosts; I am merely advocating a closer look at the factors that determine where, when, and on what a fungus will grow.

Fungal ecology and biogeography are in their infancy. We can say little about the ecological necessities of most fungi. Perhaps we need better communications. Much of the information we need could be supplied by applied mycologists. I will close by inviting these colleagues to include as much ecological information as possible with every fungus they submit for identification; in this way we could work together in building the twin, interconnected edifices of fungal ecology and taxonomy.

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