

The History of Conidial Fungi

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I. INTRODUCTION

I used to think that history was a field which permitted little leeway to its practitioners, since what's done is done and cannot be altered. How naive I was, how unmycologically green! I now know that history is continually being rewritten, that historical personages such as Canada's own Louis Riel can be transmogrified from arch-villain to hero, and that "fact" may come to be regarded as fiction and mere speculation assume the solid flesh of authenticity. Many of these manipulations are politically motivated; some are dictated by changes in the moral tone of society. And although I believe in the perfectibility of neither humans nor mycology, and although the words "enlightenment" and "progress" are subject to many interpretations (remember "newspeak" in George Orwell's

1984), I do believe that mycology has reached a level of sophistication from which we can make some fairly realistic judgments of our forebears.

It would be easy to linger indefinitely among the poppy fields of conidiophores and conidiomata, forgetting (as most specialists occasionally do) that there are other organisms out there and that they too have historical relevance. In order thoroughly to clear the air, and my conscience, I must advise you that there exists an excellent *Introduction to the History of Mycology*, written by the peripatetic scholar Geoffrey Ainsworth and published in 1976 by Cambridge University Press. A perusal of this book should help you place my more specialized and limited account in perspective. If you do not have time to read a whole book, then at least scan the brief survey by the same author that appears in *The Fungi*, Vol. 1, pages 3–20 (1965).

It would also be easy to fall into the trap of believing that the only worthwhile mycological research is that being pursued right now and that the past presents an almost unrelieved panorama of hare-brained hypotheses, off-track observations, erroneous experimental design, and incorrect interpretations.

Of course, mycology has its equivalents of the flat earth and phlogiston hypotheses, and wildly inaccurate phylogenies abound in the literature. Too often, we forget that mycology, as an ongoing cultural artifact, has attained its current level of sophistication largely through the proposal, followed by the testing and rejection of, inadequate hypotheses. Of course, we have an excuse for neglecting the past; so much literature issues from the mouth of the scientific volcano that it is all we can do (we say, casting our eyes piteously to the heavens) to avoid being engulfed.

Yet there is much to be learned from a consideration of the ideas of our forebears, who were just as intelligent as we are, and who, albeit from a narrower data base, were sometimes extremely intuitive. Many scientists labor today to achieve a form of personal immortality; yet if they will not grant this to the pioneers, surely they themselves will ultimately be denied the palm. If some of my readers do not emerge from this chapter with a new respect for some of the historical figures of mycology, I shall not have done my job well.

Those who seek accounts of such historical landmarks as the discovery of penicillin and aflatoxin, and subsequent developments, will find what they seek elsewhere in these volumes. I have contented myself with a consideration of the central, synthesizing discipline of systematics.

II. HISTORY

It is now clear that many of the anamorphs we know today have changed little since the Tertiary period (Pirozynski and Weresub, 1979) and possibly since much earlier times. This means that they considerably antedate human intelli-

gence and must therefore have been noted as molds spoiling fruit and other foods, and sometimes as causing annoying skin diseases such as ringworm and athlete's foot, by the earliest human beings. Their true nature as independent living organisms has been divined and experimentally established beyond doubt only comparatively recently.

Of course, interest in the fungi began with the sporomata of agarics and other macrofungi, and for centuries fungi were simply classified as poisonous or non-poisonous. Needless to say, this kind of dichotomy did not concern itself with the microfungi (at least, not until very recently, when the word "aflatoxin" entered the language), and the elaboration of a rational classification encompassing all true fungi had to await the elucidation of their microscopic anatomy. The microscope was invented in the middle of the seventeenth century, and at once the world of the microfungi, which includes virtually all conidial fungi, was revealed.

A. Before 1800

In 1665 Hooke published the first illustrations of microfungi, including anamorphic *Mucor*. A few years later Leeuwenhoek provided more information, and in 1680 he observed anamorphic *Saccharomyces cerevisiae* undergoing multiplication by budding. But these were scattered and unsystematic observations.

My average second-year undergraduate student, provided with a concisely written, profusely illustrated textbook and looking at a well-stained slide preparation of a hyphomycete through a twentieth-century microscope, looks me in the eye and says, "Is this anything?" One hardly needs to wonder what he or she would have done in the early 1700s, surrounded by a sea of almost total ignorance and indifference. Yet Micheli, in his *Nova Plantarum Genera* (1729), beautifully illustrated and described the microscopic anamorphs *Aspergillus* and *Botrytis*. I venture to suggest that in his situation most of us would have been nonstarters.

Micheli described no fewer than 900 fungi and must surely be regarded as one of the true founding fathers of mycology. Neither his failure to give magnifications or scales for his illustrations, nor the fact that his classification would not be considered helpful today, can detract from his achievement. The microscopes of the day were plagued with spherical and chromatic aberration, and it is not too surprising that the scientific accuracy of illustrations did not improve much for nearly 200 years. Although the organismic nature of fungi and the role of their spores were not accepted until long after Micheli's death, he was well aware of both concepts—he was simply ahead of his time.

Although Spallanzani (1776) also demonstrated clearly, with anamorphic *Rhizopus*, that it required "seeds" to ensure fungal continuity, it was not until the 1870s that Tyndall and Pasteur finally convinced the world that spontaneous

generation (at least in recent geological times), a long-hallowed idea that had originated with Aristotle, was a fallacy. The self-taught Micheli had been vindicated after a lapse of 150 years, Spallanzani after a mere century.

While this controversy still raged, other mycologists were cautiously constructing the framework of fungal taxonomy.

But they were hardly helped by the otherwise great Linnaeus. A taxonomic genius he most certainly was, but his understanding and treatment of the fungi seems to have been almost a calculated slight. He ignored most of them and placed others in the genus *Chaos* under Vermes (worms), having accepted some deplorably bad observations. He disparaged Micheli's magnificent pioneer work and used only two of the many generic names Micheli had proposed. In addition, he arbitrarily changed the application of some well-known Latin names—for example, what we now call *Amanita caesarea*, the Romans are known to have called *Boletus*. Although Linnaeus did not do anything "illegal," I think such name changes represented unfortunate breaks with tradition—hardly an auspicious start for the principle of priority. Despite his blinkered view of the fungi, Linnaeus's system of naming organisms has done much for mycological communication. I cannot improve on the example given by Ainsworth (1965) in which the complex pre-Linnaean appellation *fungus ramosus niger compressus parvus, apicibus albidis* became, after Linnaeus, simply *Xylaria hypoxylon*.

B. 1801–1851

At the beginning of the nineteenth century, recognition of the true nature and significance of the ascus and the basidium lay in the future, and it is hardly surprising that the classifications of the time grouped what we now know to be very disparate elements. Persoon (1801), for example, divided fungi into two main groups on the basis of whether their fructifications were open or closed. Thus Coelomycetes, Ascomycetes, and even Hyphomycetes made uneasy bed-fellows. His classification is of interest to us here only because its sixth and last order, Nematothecii (Fungi Byssoides), was made up of Hyphomycetes (though other Hyphomycetes were disposed in some of his other groups). Although he neither made extensive use of the microscope nor provided good diagnostic illustrations (of the kind later published by Corda), he did something just as important: He laid down dried material of many microfungi, and his herbarium survives to this day at Leiden. Thus we can discover to what actual fungi his names are attached. As a result, many of his generic names are still in use today.

In 1809 Link used the same kind of primary separations as Persoon and thus grouped many Uredinales with sporodochial Hyphomycetes and some acervular Coelomycetes. Von Martius (1817) worked along similar lines but used different group names. What Link had called Epiphytae and Mucedines, Martius called Coniomycetes and Hyphomycetes. The reader will note that the last name obvi-

ously caught on, since it has now been in use for 160 years. Note also, however, that Martius placed some fungi we would call Hyphomycetes in his Coniomycetes.

Nees von Esenbeck (1817) followed similar lines in his classification, providing yet another name, Protomyci (long disused) for the Epiphytae of Link and the Coniomycetes of Martius.

The next figure to influence the classification of conidial fungi was Fries. His *Systema Mycologicum* (1821–1832), later chosen as the starting point for nomenclature of conidial fungi, actually did not concern itself with such fungi to nearly the same extent as had Persoon's earlier work. The 1821 starting point means that some of Persoon's names, though perfectly understood through reference to his herbarium (see Hughes, 1958), cannot be legally used. Hughes (1959) advanced a number of persuasive arguments for the adoption of 1801 (Persoon's *Synopsis*) as the starting point for Hyphomycetes, but his proposal was rejected. It is probably time for us to try again.

To return to Fries: His *Systema Mycologicum* outlined a highly structured scheme with four main classes. He adopted Martius's Coniomycetes and Hyphomycetes, adding two new names of his own, Gasteromycetes and Hymenomycetes. Note again that, although these names have stuck and have fairly precise modern meanings, Fries placed both Pyrenomycetes and pycnidial Coelomycetes (the latter being brought into the system for the first time) within Gasteromycetes.

Each of Fries's four classes was subdivided into four orders, and each of these in turn into four tribes. Perhaps the most remarkable thing about this scheme, from our viewpoint, is the amazingly naive theory (based in German romantic philosophy) which underlay it; or at least so Fries would have us believe. I cannot resist a brief digression into this theory. A special reproductive force (A), was supposed to give rise to fungi, after which their development could be influenced by air (B), heat (C), and light (D). The four classes of fungi he ascribed to A acting alone, A + B, A + C, and A + D.

In 1825 he revised his classification considerably, now dividing the class Fungi into two subclasses. The Ascomycetes (chalk another one up for Fries), which included what he called Hymenomycetes and Pyrenomycetes, and the Sporomycetes—Gasteromycetes and Coniomycetes. It was all extremely confusing, and I feel constrained to give an undertaking at this point to content myself henceforth with mentioning only forward steps, ignoring the many lateral and regressive moves that bedevil all fungal classifications before those introduced by De Bary in 1866.

In his *Epicrisis Systematis Mycologia* (1836–1838), Fries redeemed the situation with an improved scheme which recognized six classes, perspicaciously separating Discomycetes from Hymenomycetes, and Pyrenomycetes from Gasteromycetes. Fries is noted for his contribution to our knowledge of the Hymenomycetes

rather than the conidial fungi, but the magnitude of his contribution can be seen from the fact that, in *Systema Mycologicum* and its supplement, he described almost 5000 fungi.

About this time some improvements were being made in the design of microscopes, and almost at once the quality of illustrations improved tremendously. Corda's *Icones fungorum hucusque cognitorum*—six volumes published in the years 1837–1854—are still referred to by modern students of Hyphomycetes for their hundreds of idiosyncratic but eminently recognizable drawings. And although he placed a sprinkling of acervular fungi in each of his four orders (1842), he did delineate a new family, Melanconiaceae, within the order Myelomycetes, for some of them, and also put most pycnidial genera in either the Sphaeriacei or Sphaeronemeae of the same order.

Léveillé (1846) used the microscope assiduously and injected a strong element of microanatomy into his scheme of classification. He distributed what we now call Hyphomycetes among three of six major subdivisions, but to his credit he erected the family Sphaeropsidei for some pycnidial fungi.

Bonorden (1851) also removed pycnidial fungi from the Pyrenomycetes, though his segregation was less than perfect, since his Sphaeronemei included *Eurotium* and some other Ascomycetes. The acervular fungi and Hyphomycetes both remained relatively scattered.

C. The Tulasnes, De Bary, Berkeley, and Darwin

And now we come to a dramatic period in the history not only of mycology but of all biology. Two momentous developments occurred within a decade. I will deal with the lesser of the two first. By the middle of the century it had become apparent that some, at least, of the conidial fungi were asexual phases of certain Ascomycetes. This phenomenon was repeatedly demonstrated by the Tulasne brothers in a masterful series of publications, crowned by the three volumes of the *Selecta Fungorum Carpologia* (1861–1865) with their incomparable illustrations. As so often happens in science, the same breakthrough was made at about the same time by De Bary, who in 1854 established that *Aspergillus glaucus* is the anamorph of *Eurotium herbariorum*. Charles Tulasne's magnificent illustrations of teleomorph plus anamorph have never been surpassed, though it must be noted that some of the connections celebrated in his drawings were spurious. This degree of error is hardly surprising when the great Berkeley himself (of whom more later), lacking knowledge of sterile techniques, suggested that yeast cells simply represented an abnormal growth phase of *Penicillium*. Mixed cultures were as common among mycologists in those days as mixed metaphors among politicians today. And even Berkeley's error seems conservative beside the careless rapture of one of his contemporaries, who extravagantly asserted that yeast could give rise not only to *Penicillium* but also to

Mucor, *Entomophthora*, *Isaria*, and others. Nor was this the worst example: I shall not even outline Hallier's scandalous excursions into pleomorphism—suffice it to say that they were pure science fiction. Perhaps these misguided claims gave the idea of teleomorph-anamorph connections a bad name. Or perhaps it was simply easier to classify teleomorphs without reference to anamorphs, and vice versa. A gulf opened up between the study of sexual and asexual forms which has persisted until today in the minds of many mycologists (see Weresub and Pirozynski, 1979). Of course, the efforts of the Tulasnes, De Bary and, a generation later, Brefeld, were not in vain. After a century we have become very conscious that the elaborate independent classification systems we have built up for teleomorphs and anamorphs must be integrated and have begun to make strenuous efforts in this direction (see Kendrick, 1979). It is clear that we have far to go before this aim will be achieved, as Müller (this volume, Chapter 7) shows only too well, and we can still marvel at how far knowledge of the fungi had already advanced by 1860 from the ancient folklore peddled by Gerarde (1633) to the effect that poisonous fungi acquired their fateful qualities from the exhalations of snakes (a fantasy that originated with Dioscorides in the first century A.D.).

The second, and much the greater, event of the period was Darwin's ringing proclamation of organic evolution in 1859. His massive documentation of the phenomenon gave it instant authority. No branch of biology was unaffected.

Perhaps Berkeley, who published a classification of fungi in 1860, had not had much time to assimilate Darwin's concepts; nevertheless he was the first to consolidate most acervular fungi in the Melanconieae and to group mononematous, synnematous, and sporodochial forms in the Hyphomycetes.

But a few years later came De Bary again, producing in 1866 a classification that was amazingly close in essentials to that widely accepted until very recently (Table I). I must admit that I find De Bary an almost awe-inspiring figure, with an amazingly sure instinct for unlocking fungal secrets. De Bary's classification embodied, as have all subsequent attempts, important elements of phylogenetic speculation. In his revised second edition (1884) De Bary came even closer to modern ideas, regarding rusts as leading into the climax Basidiomycetes and raising questions about the relationships of the Ustilaginales which are still being debated after almost a century. Note also that he did not include conidial fungi as a main-line group. As I have already suggested, it might have been better to leave things that way and to make strenuous efforts to maintain an integrated approach to teleomorph-anamorph systematics.

D. Saccardo

But it was not to be. Fuckel (1869) divided the fungi into two groups, Fungi Perfecti and Fungi Imperfecti, and Saccardo effectively enshrined the dichotomy

TABLE I
De Bary's 1866 Classification
of Fungi

Phycomycetes
Saprolegniae
Peronosporae
Mucorini
Hypodermii
Uredinei
Ustilaginei
Basidiomycetes
Tremellini
Hymenomycetes
Gasteromycetes
Ascomycetes
Protomycetes
Tuberacei
Onygeni
Pyrenomycetes
Discomycetes
Flechten (lichens)
Myxomyceten (slime molds)

in his massive works. Once he had made this decision, it was easy to move further into a convenient marriage of artificiality with convenience. In 1884 he introduced such features as color, shape, and septation of spores to delineate subfamilies and genera. At this point we had the three group names still so widely used: Sphaeropsidae (Sphaeropsidaceae, Sphaeropsidales) for forms with pycnidial conidiomata, Melanconieae (Melanconiaceae, Melanconiales), for those with acervular conidiomata, and Hyphomyceteae (Hyphomycetes) for mononematous, synnematos, and sporodochial forms. His subdivisions of the Hyphomyceteae have been in use until fairly recently. In Volume 4 of his monumental *Sylloge Fungorum* (1886) he divided this group into four families—Mucedineae (mononematous, hyaline, or brightly colored), Dematieae (mononematous, darkly pigmented), Stilbeae (synnematos, light or dark), and Tubercularieae (sporodochia, light or dark). Within the first two families his primary subdivision was based on spore septation (sections Amerosporae, Didymosporae, and so on), and within each of these he recognized subsections Micronemeae and Macronemeae (integrated or morphologically undifferentiated versus discrete or morphologically differentiated conidiogenous structures). In the other two families, the divisions were based first on pigment, then on spore septation or shape.

E. Potebnia, von Höhnel, and Grove

Potebnia (1910) also subdivided Fungi Imperfecti on their respective kinds of fructification, but rather differently. He joined acervular and sporodochial fungi in the Acervulales, placed genera with incomplete or atypical pycnidia in the Pseudopycnidiales, and typical pycnidial forms in the Pycnidiales. Our recent investigations of conidiomatal structure (Kendrick and Nag Raj, 1979) have given me considerable sympathy for Potebnia's ideas; yet they were not widely accepted. Nor were von Höhnel's (1911) rather similar suggestions. It appears that no one could successfully challenge Saccardo at that time. Grove (1935, 1937) juxtaposed the Sphaeropsidales and Melanconiales in the Coelomycetes, a category equivalent in rank to the Hyphomycetes, and thus bisected the conidial anamorphic fungi. I almost wrote "neatly bisected," but of course we have the doubts first raised by Potebnia (1910) and restated by Kendrick and Nag Raj (1979) and by Müller (this volume, Chapter 7). But whatever has gone on in the upper levels of the taxonomic hierarchy, Saccardoan criteria (color, and shape and septation of conidia) remained supreme at the lower levels and were used essentially unmodified in all published compilations until the 1950s.

The mainstream was dominated by characters of mature morphology. But for nearly 100 yr (almost since Saccardo first elaborated his criteria) dissident elements in the mycological community have found this system strangely unsatisfying. It is admittedly an extremely empirical, artificial system. It can often be seen to bring together alien forms and to separate forms which one has a hunch are really very closely related. Genera such as *Arthrobotrys*, for many years arbitrarily defined by the obligate presence of a single septum in the conidium (no more, no less) could be intuited to be related to other similar nematode-trapping forms disposed in other genera simply and solely because their conidium septation was "wrong." Only recently (Schenck *et al.*, 1977) has a more reasonable initiative been taken. A kind of institutionalized rigidity in the application of this and other Saccardoan criteria, actually quite understandable in the absence of other readily accessible characters, has left us with a legacy of irritating paradoxes and inconsistencies scattered throughout the taxonomy of the conidial fungi. Some of these are now being exposed by the effort to connect anamorphs to their teleomorphs, and Müller (this volume, Chapter 7) cites some notable examples.

The question is of course whether we are willing to settle for a convenient, artificial arrangement of pigeonholes or insist on striving for a system, as yet clearly unattained and probably unattainable in the foreseeable future, which more closely represents biological relationships.

F. Costantin, Vuillemin, and Mason

Costantin (1888) was perhaps the first to attempt this. Note how closely his heresy followed on the heels of the proclamation of Saccardoan orthodoxy.

Costantin tried to use the manner in which hyphomycete conidia were attached to their parent hypha as a taxonomic character, but his work did not greatly influence those who followed him.

Vuillemin (1910a,b) recognized that the term "spores" covered structures of very different origins. He proposed that initially two main kinds be distinguished: conidia vera, or spores liberated by a specific mechanism as soon as they have been formed, and thallospores, which remain an integrated part of the hypha that produces them. Vuillemin recognized three kinds of thallospores: arthrospores, arising from fragmentation of hyphae; blastospores, arising as buds in persistent acropetal chains; and chlamydospores, thick-walled resting spores. In 1911 he added a fourth kind of thallospore, aleuriospores, which were intermediate between chlamydospores (no mechanism for release) and conidia vera (specialized immediate release). Unfortunately, as Carmichael has pointed out (in Kendrick, 1971 p. 61), although Vuillemin understood and clearly described the special built-in lateral wall-dissolution mechanism by which aleuriospores are freed, he confused the issue, and many later workers, by calling these spores indehiscent. Vuillemin subdivided his Conidiosporales—Hyphomycetes produced conidia vera—into three groups: the Sporotrichae, forming conidia on undifferentiated hyphae; the Sporophorae, with differentiated conidiophores; and the Phialidae, forming conidia at the tip of flask-shaped, septum-delimited structures he called phialides.

I have given some detail on Vuillemin's ideas, because they represented such a break with the tradition of mature morphology (despite the fact that he still used the Saccardoan families) and because they foreshadowed much that has gained currency in the last 25 years.

Vuillemin's papers were published in an obscure journal, but they were also very radical and made little headway at the time. Like Spallanzani and Micheli, he was ahead of his time. His ideas were effectively ignored until Mason (1933), in discussing the then-known anamorphs of the Hypocreales, reworked Vuillemin's definition of the phialide. He extended it to include "the fusiform truncate, fusiform beaked or acuminate terminal portion of a hypha, from the apex of which or from within which thin-walled conidia are abstricted." This definition embraced a number of things we certainly would not call phialides today, but Mason, fortunately, was aware of the heterogeneity of what he had created. What we would call blastic-phialidic conidia, he termed meristem phialospores. What we would call blastic-sympodial conidia, he recognized as terminus phialospores. Although Mason's 1933 paper muddied the waters as far as the term "phialide" was concerned, his recognition of the sympodially proliferating conidiogenous cell represented a real advance. Mason also introduced the term "radulaspor" for conidia arising randomly from a hypha on denticles. Then, because he believed that all anamorphs of the Hypocreales ought to have a phialosporic anamorph of some description, he suggested that radulaspor might

be homologous with phialospores. We do not accept his excessive expansion of the phialidic concept, which clearly arose from a forlorn hope of arriving at one of those underlying generalizations science is always seeking. But we applaud his observations of modes of conidium ontogeny, which were to bear further fruit.

Later, Mason (1937) shifted his attention to the manner in which spores are dispersed and stressed the difference between the slimy-spored (mainly water- and insect-dispersed) and dry-spored (mainly wind-dispersed) forms. He revised his earlier claim that all hypocrealean anamorphs produced phialospores, now suggesting that pleomorphic forms had one dry-spored and one slimy-spored state and that, if the slimy spores were abstracted from free conidiophores, then these or their apical cells would be phialides.

G. Wakefield and Bisby, Ingold, and Langeron

Although conceding the existence of transitional series (not to mention such dry-slimy twins as *Stachybotrys* and *Memmoniella*), Wakefield and Bisby (1941) in their list of British Hyphomycetes, adopted the two divisions, christening them Xerosporae and Gloiosporae (but still subdividing each on spore morphology, after Saccardo).

I admit that such features as waxy, hydrophobic conidia and conidia embedded in mucilage have considerable importance, but I believe that they represent ecologically imposed differences that have evolved again and again, often between phylogenetically closely related taxa. We also now know that fungal slimes are of various kinds, some merely hydrophilic, some actually surface-active (Bandoni, 1975).

Ingold (1942) discussed a third "biological" spore type, the "aquatic" spore, produced and dispersed underwater. This is an interesting group containing many beautiful examples of parallel or convergent evolution, as shown by Webster and Descals (1979), but it is numerically small (less than 200 species), hence of only minor importance in the general classification.

Langeron (1945), in his often admirable *Précis de mycologie*, tried to apply the terminology of Saccardo, Vuillemin, Mason, and Wakefield and Bisby, but his interpretation of terms such as "phialide" was unacceptably broad, and his work has not been influential.

H. Hughes

Working at the Commonwealth Mycological Institute in the late 1940s, under the tutelage of E. W. Mason, was a young Welsh mycologist, S. J. Hughes. Absorbing Mason's (and Vuillemin's) ideas, Hughes was soon to build on them and develop a stimulating new hypothesis. As one of a series of important papers

on hyphomycete taxonomy, Hughes (1951) published a discussion of some phialidic conidial fungi and came up with what is essentially the current developmental definition of the phialide and its unique conidiogenesis. This paper was just a taste of what was to come. In 1953, he produced a remarkable contribution in which he suggested that there are "only a limited number of methods whereby conidia can develop from other cells." He proceeded to describe no fewer than eight such methods and ascribed prime taxonomic importance to them. I refer my readers to his classic paper, but also feel constrained to outline the eight sections he proposed, though using more current terminology to describe them.

Section I: blastic-synchronous (e.g., *Botrytis*) or blastic-acropetal (e.g., *Cladosporium*)

Section II: blastic-sympodial (e.g., *Nodulisporium*)

Section III: blastic-annellidic (e.g., *Scopulariopsis*)

Section IV: blastic-phialidic (e.g., *Penicillium*, *Phialophora*)

Section V: thallic-meristem (e.g., *Oidium*)

Section VI: blastic-tretic (porospores, e.g., *Alternaria*)

Section VII: thallic-arthric (e.g., *Oidiodendron*, *Geotrichum*)

Section VIII: basauxic (e.g., *Arthrinium*)

Hughes neither formally named his groups nor attempted an overall classification of conidial fungi using these developmental criteria. Yet he made it clear that he thought these features might well represent more natural bases than those on which the Saccardoan scheme had been erected. He also suggested that, although most of his examples were drawn from the Hyphomycetes, the same developmental criteria could be applied throughout the Coelomycetes as well.

I. 1968-1978

The next 15 yr (1953-1968) seemed to be a hiatus in ontogenetic studies on conidial fungi. However, Hughes's concepts were being internalized by other mycologists and eventually began to receive the attention they deserved. Barron (1968), Ellis (1971, 1976), Kendrick and Carmichael (1973) and, most recently Carmichael, Kendrick, Connors and Sigler (1980) produced successively more comprehensive compilations of Hyphomycetes and based their groupings in large measure on ontogeny.

In two major reviews, Sutton (1971, 1973) set out to apply developmental criteria to Coelomycetes, and in recent years he and Nag Raj have been steadily enriching the literature with painstaking, beautifully illustrated accounts of coelomycete genera (this volume, Chapter 3).

But the hoped-for, inclusive scheme has never materialized. Some of the reasons for this became clear at the first Kananaskis Conference (see Kendrick, 1971). While time-lapse photomicrographic studies had added another mode of conidiogenesis to the list (blastic-retrogressive: Cole and Kendrick, 1968; Ken-

drick, 1971; e.g., *Basipetospora*, *Trichothecium*), the conference noted that, the more fungi were subjected to ontogenetic analysis, the more atypical and intermediate kinds of conidiogenesis were found. We have since come to believe that there are fewer basic kinds of conidiogenesis than Hughes supposed and that each is capable of more variation than most of us had suspected.

Perhaps I can exemplify this by looking a little more closely at one very common kind of conidiogenous cell that has already come under scrutiny several times in this account, the phialide. Madelin (1966) considered that at least four different phenomena were lumped in Hughes's 1953 definition of the phialide. Questions regarding the homogeneity of the concept were raised repeatedly at the first Kananaskis Conference (see Kendrick, 1971). In 1972, Morgan-Jones, Nag Raj, and Kendrick reported a further variation on the phialidic theme, which they called percurrently proliferating phialides, in some Coelomycetes. After a consideration of the literature these authors were left wondering whether there was a fundamental difference between the phialide and the annellide, or whether a continuous spectrum of intermediates linked the two. At the second Kananaskis Conference (see Kendrick, 1979) it became clear that mycologists were still of two minds about phialides, some suggesting that all extant phialides (at least in ascomycetous anamorphs) shared common ancestry, and others that the phialide has evolved on at least several occasions. Note that, if the latter position turns out to be correct, then phialidic conidium ontogeny as a prime classificatory character will be revealed as essentially artificial.

J. 1979

We have known for many years that some holomorphs incorporate more than one conidial anamorph. The attempt to apply ontogenetic criteria to such fungi led to the conclusion that sibling anamorphs often display different modes of conidium ontogeny. Now we know that the same conidiogenous cell can function in different modes at different times. And at the second Kananaskis Conference, Madelin (1979) advanced a fascinating and plausible explanation of how one method of conidium ontogeny can be transmuted into another by a combination of temporal and edaphic factors. All of which leads me to an inescapable conclusion: Developmental criteria cannot form the basis for a more natural classification of the conidial fungi. This does not mean that the accumulation of developmental data has been a waste of time. On the contrary, it has increased our understanding of these organisms in many ways. But it does mean that extravagant claims can no longer be made for ontogeny. Development now becomes, in perspective, just one more kind of taxonomic information to be added to those we already possess.

As Müller (this volume, Chapter 7) shows so clearly, both morphologically and developmentally based systems sometimes break down in the face of proven connections between anamorph and teleomorph. For example, the anamorphs of

closely related species of *Venturia* exhibit three different kinds of conidium ontogeny. It is hardly likely that these ontogenetic differences in anamorphs could bring about the separation of holomorphs at the generic level or above. [The anamorphs of three species of *Broomella* are disposed in three different anamorph genera in three anamorph families, when they should probably be regarded as congeneric in terms of the holomorphs.]

Fungal systematics is in a state of creative flux. In dealing with conidial fungi we must now consider morphology, development, and connections with teleomorphs. Only by integrating all three kinds of data can be hope to progress toward a more rational system of classification.

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