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Roger D. Goos
State University of Iowa

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Classification of the Fungi Imperfecti

By ROGER D. GOOS

In recent years, some dissatisfaction has been expressed concerning the commonly used classification of the Fungi Imperfecti. The discontent with the present system has arisen from the fact that the characteristics used to delimit taxa (i.e. spore color and septation, arrangement of the conidiophores, etc.) often results in the separation of morphologically similar genera, while at the same time placing together what seem to be unrelated genera.

The present system was proposed by Saccardo when the major interest in the Fungi Imperfecti was in their role as plant pathogens. Now these fungi are being studied more intensively than ever before, not only as plant pathogens, but also with reference to the other roles which they play in nature. Members of the imperfect fungi have been found to be among the most common of the soil fungi; they have been found to play a major role in the decomposition of military equipment; they have long been known to play an important role in food spoilage; recently, the biochemical activities of many of these fungi have been recognized as having industrial value.

Many of the characteristics which have been used to distinguish these fungi are evident on natural substrates, such as plant hosts, but are not so evident or may even fail to appear when the fungus is brought into culture. For the mycologist studying soil fungi or isolating fungi from decomposing material, there is little choice but to study the fungus in culture. Thus, while certain morphological features may appear rather consistently on natural substrates, they may be of a transient and changeable nature when a fungus is brought into culture, and it is often difficult to determine the identity of fungi in culture when the original descriptions have been made from material occurring on natural substrates. For example, it is well known that in many cases an acervulus may appear as a sporodochium in culture; a sporodochium may not be produced in culture by genera that typically produce such a structure in nature; the formation of a coremium may be a response to culture conditions and not an unchanging characteristic of a specific species.

Saccardo divided the Fungi Imperfecti into form-orders, then into form-families, and then into spore groups. The orders and families do not represent natural groups or relationships, but serve only to group together forms which are similar in appearance. Saccardo recognized three orders; the Sphaeropsidales, with spores produced in pycnidia; the Melanconiales, with spores borne in an

acervulus; and the Hyphomycetes, with spores and spore-bearing structures not enclosed. Later, a fourth order including forms which produce no spores, the Mycelia Sterilia, was added. Families were delimited on the basis of coloration of the conidia and mycelium, and upon the arrangement of the conidiophores. Sections were then delimited on conidium morphology. Although it is a completely artificial system, it remains the most usable yet devised. As previously pointed out, however, many of its major divisions appear to be based upon characters of secondary taxonomic importance. Mason (1937) has presented one of the most thorough discussions of this problem, giving excellent examples of the transitional nature of the pycnidium, acervulus, and sporodochium.

Examples of the variation of such gross morphological structures may be noted in the genus *Fusarium*. Members of this genus are generally considered to produce sporodochia, but in many cases, such structures are not produced when the organisms are brought into culture. The conidia of this genus are generally multi-septate, but under culture conditions, they may vary from non-septate to 3 or more septate in the same culture. Another genus showing much variation is *Pestalotia*. Saccardo placed this genus in the Melanconiales. In most species of *Pestalotia*, the fructification is described as an acervulus, but Steyaert (1949) has found that the fructification of *P. pezizoides* is a pycnidium-like conceptacle. *P. pezizoides* should therefore be classified in the Sphaeropsidales. Many species of *Pestalotia* form sporodochia in culture, however, and could then be classified in the Tubulariaceae of the Hyphomycetes.

Several examples may be cited of separation of seemingly related genera through the use of coloration as a major delimiting characteristic. *Ramularia* and *Cercospora* are placed in the Moniliaceae and the Dematiaceae respectively, although morphologically they appear related and actually intergrade. Both produce conidia in an identical manner. In the genus *Aspergillus*, dark-spored species are classified in the Moniliaceae, because of their obvious relationship to the lighter spored species, even though the dark color would place them in the Dematiaceae if Saccardo's system were followed consistently. *Haplographium*, except for its dark-colored conidiophores and conidia, closely resembles *Penicillium*. The genus *Coniosporium* in the Dematiaceae corresponds closely to *Chromosporium* in the Moniliaceae.

A number of proposals for classification of the imperfects have been made in addition to that of Saccardo, but for one reason or another none of these has been widely used. Constantin (1888) proposed an arrangement for certain of the Hyphomycetes which has never been accepted, possibly because of its limited scope. A proposal for a rearrangement of the imperfects was made by Von

Höhnel in 1921. This system did not differ greatly in its essentials from that of Saccardo, and at the same time was more difficult to use. It was, perhaps, best evaluated by Petrak (1925). "Dass v. Höhnels System die natürlichen, verwandschaftlichen Verhältnisse der Gattung nicht besser, teilweise sogar eher noch schlechter zum Ausdrucke bringt als das alte System Saccardos, ist für mich eine feststehende Tatsache. Es hat aber, mit Saccardos System verglichen, nach den grossen Nachteil, dass es auch praktisch so gut wie wertlos ist. Denn während sich der Anfänger in Saccardoschen Systeme immer noch mit einer gewissen Sicherheit zurechtfinden kann, wird er nach v. Höhnels System in den allermeisten Fällen ganz irgehen und von einem Fehler in den anderen verfallen müssen."

Vuillemin, probably more than any other mycologist, has stimulated interest in a rearrangement of the Fungi Imperfecti, and has pointed out the difficulties connected with describing the different spore forms of this group with the single term, conidium. He has proposed a classification based upon spore forms, which he recognized as being of two basic types: thallospores, which are formed directly from pre-existing elements of the thallus, and conidia vera, which are produced as newly formed elements. The classification of Vuillemin is summarized by Langeron and Vanbreuseghem (1952), and representative genera cited, as follows:

A. Thallosporés.

1. Arthrosporés: *Geotrichum*, *Trichosporon*, *Hormodendrum*.
2. Blastosporés: *Candida*, *Torula*, *Geotrichoides*.
3. Aleurioporés: *Aleurisma*, *Trichophyton*, *Nigrospora*.

B. Conidiospores (conidia vera).

1. Sporotrichés (conidia borne on undifferentiated hyphae) *Sporotrichum*, *Trichosporium*, *Acrotheca*.
2. Sporophorés (conidia on definite conidiophores): *Monosporium*, *Scedosporium*.
3. Phialidés (conidia produced from phialides): *Aspergillus*, *Trichoderma*, *Phialophora*, *Penicillium*.

Vuillemin's definitions of spore types have been reviewed and emended by Mason (1933) and by Langeron and Vanbreuseghem (1952). The latter authors have summarized them as follows:

A. Thallospores—Essentially non-caducous spores, formed at the expense of the thallus by transformation of certain elements.

1. Arthrospores—formed by disarticulation of the mycelium.
2. Blastospores—originating by budding of a pre-existing element of the mycelium.
3. Chlamyospores—a general spore type, found in all groups of fungi, formed by a rounding up of a portion of the mycelium, and characterized by a thickened wall and dense cyto-

plasm.

4. Dictyospores—multicellular spores with cross and longitudinal septation.
5. Aleuriospores—small terminal chlamydospores, resembling true conidia, but nearly always terminal, non-caducous, and inserted on a surface equal to the branch or filament that bears them.

B. Conidiospores (*conidia vera*)—external spores, terminal or lateral and essentially caducous, which originate upon the thallus as newly formed elements.

1. Radula spores—small conidia, borne upon small sterigmata, which originate from the surface of the filament. The term was introduced by Mason (1933), and the spore type has been rather fully discussed by Nannfeldt (1934).
2. Terminus spores—this term was introduced by Mason (1933) to designate the unique spores which form on the extremity of a phialide, of which they terminate the growth. Further growth can take place only by the formation of a new growing point below the apex.
3. Phialospores (*meristem spores*)—conidia abstricted from the mouth of a more or less bottle-shaped phialide. The apex of the conidiophore remains active, producing successive conidia.

Until Moreau (1953) adopted this system in his arrangement of the imperfects, it had not been used, to my knowledge, in any complete arrangement of the Fungi Imperfecti. Moreau included the orders Melanconiales and Sphaeropsidales of the Saccardo system as families under the order Sporophorales, while the genera of the Saccardoan Hyphomycetes are found in all of the orders. Subdivisions below families are made on the grouping of the sporebearing structures, the form of the spores, their septation and color. Characteristics of the mycelium are used only to separate genera. It should be noted that Vuillemin did not include fungi of the Saccardoan orders Melanconiales and Sphaeropsidales in his considerations of spore types, but confined his considerations of spore types to the Hyphomycetes. Thus, Moreau's arrangement represents an extension of Vuillemin's interpretations.

Mason (1937) presents one of the most lucid and analytical discussions of the need for better classification in the imperfect fungi. For the applied mycologist, he says, "the most pressing need is for a classification of fungi in their imperfect condition, which makes the distinctions, so to speak, that the fungi themselves make. . . . For them (the applied mycologists) the proper business of taxonomy is the consistent application of generic and specific names." The method of attack, he says, should be directed at the means of conidia dispersal. "Conidia are created for dispersal. If

dispersal fails, the species disappears and ceases to be an object of any interest to applied mycology. Our fundamental attack should surely be directed at those morphological characters that display themselves at the moment of conidial dispersal." Two methods of spore dispersal are distinguished by Mason in the imperfect fungi: dispersal by wind or mechanical means, in which case the conidia are dry at the time of dispersal, or dispersal by water, in which event the conidia are produced in slime. On the basis of the manner in which the spore is presented for dispersal, he proposed division of all of the Fungi Imperfecti into two groups based upon slime spores, which "become separated by histolysis from the hypha which bears them," and dry spores, which do "not become separated by histolysis from the hypha that bears them." The scheme was not elaborated beyond this point.

Mason's major divisions were used by Wakefield and Bisby (1941) in their listing of British Hyphomycetes, but have not been employed in any other taxonomic work, to my knowledge. It may be pointed out that this arrangement is as artificial in many respects as Saccardo's system. For example, the genera *Memnoniella* and *Stachybotrys*, which appear to be closely related, are separated by this division. This is also true of the genera *Penicillium* and *Gliocladium*. Furthermore, it appears that often the presence or absence of slime is a physiological response to environmental conditions, and in many genera there are gradations from one state to the other. As Bisby (1953) states, "nature presents us with the expected intermediates". While gradation between taxonomic categories is to be expected, it does not seem logical to base a major division upon a character which seems so obviously transitional.

In this connection, the work of Ingold (1942) should be mentioned. In his work with aquatic Hyphomycetes, he found that certain types of conidia are normally produced and dispersed only when the fungus is submerged in water. Where is this spore type to have a place in a classification based upon wet and dry spores? Ingold suggested that a third biological spore type must be recognized.

The most recent attempt at reclassification of the Hyphomycetes has been that of Hughes (1953). Hughes believes "that there are only a limited number of methods whereby conidia can develop from other cells and that morphologically related imperfect states will only be brought together when the precise methods of conidium origin take first place in the delimitation of the major groupings." On the basis of conidia and conidiophore ontogeny, Hughes has divided the Hyphomycetes into eight sections (with a ninth possibly required for the "isthmospores" of *Trichothyrium*). Other sections may be required as more genera are studied. No keys are presented,

nor are the sections named.

Whether Hughes' system will prove practical remains to be seen. Its true value will not be known until it has been applied to more species, but certainly some of the ideas presented are worthy of serious consideration. It is, for the most part, an extension of the ideas of Vuillemin, and seems to show morphological relationships in the Hyphomycetes better than any of the other systems proposed to date. One of the interesting questions which will be answered only by further study of this group is whether or not Hughes' arrangement and interpretations can be applied to all genera of the Hyphomycetes.

Although basing a scheme of classification on conidial ontogeny, as Hughes has done, appears to be the most useful approach to a rational rearrangement of these fungi, it has the serious disadvantage that such features may be difficult to determine without culture studies. It appears that in the majority of cases, Hughes based his interpretations upon cultural observations. From a practical viewpoint, this is not always possible or expedient. The use of such a scheme under these conditions may involve difficulties. It is, of course, possible to base a classification upon such characters, and rely upon a more artificial system as a means of rapid identification.

Traditionally, it has been the concept among mycologists that the Fungi Imperfecti represent something of a waste basket assemblage of fungi, most of which are believed to be the imperfect states of Ascomycetes, and which, it has been assumed, would disappear as taxonomic units as the connection between perfect states became known. Gradually, that attitude has changed. It now seems possible that many of the Fungi Imperfecti may have lost their perfect state, if indeed, they ever possessed one. In addition, in many cases, it is the imperfect state which is commonly encountered or which is the economically important state. As a consequence, even though we should find the perfect state of all imperfect forms, the Fungi Imperfecti would continue to constitute an important group. It is surprising, therefore, to find the following statement in the recent book of Moreau: "On peut espérer que tôt ou tard la plupart des Adéломycetes, tous peut-être, auront reçu une place dans la classification des autres Champignons". Bisby (1953) states, "but the Fungi Imperfecti cannot be eliminated, and they include some of the most important of all fungi", and this seems a more realistic viewpoint of the place of these fungi.

Bender (1931) wrote, "the Fungi Imperfecti are better off the less their classification is tampered with". Also, Bisby (1953) has pointed out that "anyone who proposes another classification has the formidable task of trying to place in it some 2300 generic and

30,000 specific names proposed to date." However, in view of the factors discussed above and the current interest in this group, reclassification appears worth while and justifiable.

The distinction of spore types, based on spore ontogeny, appears to be basic in any attempt at reclassification in this group. In view of this, it may be worth while to review the terminology dealing with spore types. Vuillemin's fundamental division of thallospores and conidiospores (conidia vera) seems to be valid in distinguishing spores of two distinct types of origin and are useful descriptive terms. Similarly, arthospores and blastospores appear to be distinctive spore types.

The term aleuriospore, however, is less clear in its meaning. The definition given by Mason (1933) is that aleuriospores are terminal chlamyospores, "whose position, color, form, structure, and dimensions attain the same consistency as conidia. They differ from conidia vera in that they are not immediately cut off from the mycelium by means of natural dehiscence." The genera *Mycogone*, *Sepedonium*, and *Trichothecium* are cited as examples of fungi producing this spore type. Langeron and Vanbreuseghem (1952) cite *Chlamydomyces*, *Nigrospora*, and *Monotospora* (sensu Corda) as examples of aleuriosporous genera. Ingold (1952), however, considered aleuriospores as being delimited at an early stage of development from the parent hypha by a transverse wall. Ingold's interpretation was followed by Ranzoni (1953), and both authors included as aleuriospores spores which were liberated shortly after their maturity. Clearly, the definition presented by Mason is not the same as that used by Ingold and Ranzoni. The spores of the aquatic Hyphomycetes described by Ingold and Ranzoni as aleuriospores are thin-walled spores, deciduous, and separated early in their ontogeny from the hypha which bears them. This is in contrast with the situation in the genera cited by Mason and by Langeron and Vanbreuseghem, where the conidia are thick-walled and generally non-caducous. Vuillemin (1911) emphasized the chlamyospore-like nature of the aleuriospore. In fact, he regarded them as being midway between chlamyospores and conidia. He further emphasized that aleuriospores are non-caducous, and are shed only by disintegration of the thallus. The spores to which Ingold applied this term bear little resemblance to chlamyospores, and in addition, are shed soon after maturing. Thus, it appears, that either the definition of aleuriospore must be modified so as to include both types of spores, or the spores described by Ingold and Ranzoni designated as another type.

Hughes has discussed spores similar in their mode of development to those described by Ingold and Ranzoni, and placed them in Section III of his arrangement. The spores of this section are desig-

nated by Hughes as chlamydo-spores. The choice of this term, however, seems unfortunate, since it is generally accepted for a different spore type. I believe the meaning of the term aleuriospore could well be extended to include spores of this type. Interpreted in this manner, the term is based upon the mode of ontogeny rather than upon general appearance, and this I believe to be the most useful approach in distinguishing spore types.

Spores produced without the process of nuclear fusion followed by meiosis (such reproduction has been termed akaryallagic by Link, 1929, and Martin, 1940) which are not produced in a sporangium, have commonly been lumped together under the single term conidium. It was this broad usage of the term to which Vuillemin objected, and which prompted him to designate more precise spore types. However, a general term for akaryallagic spores is useful, and since the term conidium has been and continues to be used in this broad sense, it may as well be retained with this meaning. To designate the spores of Vuillemin's Conidiosporales, the term conidiospores can be used. Although this term is undesirable in some ways, it is to be found in the literature and is the basis for the name of one of Vuillemin's major divisions.

The term sterigma has been used occasionally for the designation of certain structures in the imperfect fungi. The sterigma is a characteristic structure of the basidiomycetes, and in the interest of precise terminology, should be restricted in its use to fungi of that class. The phialide, which has occasionally been designated as a sterigma, is a unique and characteristic structure, and merits the special name.

In the case of radula spores, which are borne upon minute, but distinct extensions from the conidiophore, the term denticle can be used in place of sterigma in designating the minute extension.

To clarify the meaning of terms used in designating spore types, it appears desirable to list and briefly define the terms which have been used.

Conidium—a general term employed for spores formed without the processes of nuclear fusion followed by reduction not occurring in a sporangium and not formed as chlamydo-spores.

Thallospore—a generic term for spores formed by transformation of existing elements of the thallus. Four types are distinguished. (1) *Arthrospores*—spores formed by fragmentation of hyphal branches. (2) *Blastospores*—spores budded from a parent cell, or directly from the hypha. (3) *Aleuriospores*—spores formed as the blown-out ends of hyphal tips or as lateral protrusions, which are then cut off by a septum. They resemble conidiospores in position, form and dimensions, and are inserted on a surface equal to the hypha which

bears them. (4) *Chlamydo-spores*—spores formed by rounding up of mycelial units, coupled with a thickening of the cytoplasm and wall, so that the mature spore is generally spherical, larger than the hypha which bears it, and dark-colored. They may be formed terminally or laterally, singly or in chains.

Conidiospores (conidia vera)—a generic term for reproductive structures produced as newly formed units, and not originating through a transformation of the existing mycelium. Two types are distinguished. (1) *Radula spores*—small conidia, borne side by side upon small denticles which cover the surface of the conidiophore tips, or which may be produced upon intercalary swellings. (2) *Phialospores*—spores produced from a phialide.

Phialide—an ampulliform non-septate structure, at the tip of which, or within which, thin-walled conidia are abstricted. In most cases, the spores are abstricted in basipetal succession, although in some cases, a single conidium may be produced (i. e. *Acremonium*, *Monosporium*).

The above terminology, which consists of words in more or less general usage, fails to distinguish all distinct spore types. For example, where would one place the spores of *Alternaria*, *Stemphylium*, *Helminthosporium*, or *Spondylocladium*, to cite a few of many possible genera, in the above list of terms? Langeron and Vanbreuseghem (1952) have described the spores of *Alternaria* as dictyospores, which they consider to be one type of thallospore. The conidia of *Alternaria* are borne on distinct conidiophores, and are, therefore, conidiospores and should not be included as thallospores. In general, the term dictyospore fails to designate a spore distinct by its mode of development, and serves only as a useful descriptive term. Whether the conidia of the above named genera, or of any of the genera whose conidia would fail to fit into one of the definitions given, merit a special name will not be discussed here. It is my purpose only to point out that not all spores of the Hyphomycetes are included in the spore types discussed by Vuillemin and Mason.

It remains to be seen whether any workable and practical rearrangement can be made in the imperfect fungi, but it seems highly desirable that the spore types of Vuillemin and Mason be used, in so far as possible, in current descriptions and studies of these fungi. Where possible these fungi should be studied in culture, and developmental studies included in their descriptions. Such information may help to point the way to a more logical and natural arrangement, and a better understanding of these fungi.

The system of Moreau, adapted from that of Vuillemin, is a possibility to be considered. Whether it is a real advance in clas-

sification must yet be decided. It would appear, however, that such gross morphological structures as the sporodochium, acervulus, and pycnidium, coloration of the spore or mycelium, and the septation of the spores, do not provide the most reliable characters for the delimitation of major taxonomic categories. If these are to be considered of secondary importance, what characters can be substituted for them? It seems to me that little remains of practical value except the precise spore type and its mode of development.

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DEPARTMENT OF BOTANY
STATE UNIVERSITY OF IOWA
IOWA CITY, IOWA