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WHAT ARE PHIALIDES ANYWAY?

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The history of the term phialide is outlined. The way the term has been used is analysed and found to be confused. Four problems are identified: nobody in recent years has used the term in its original sense; nobody is agreed on what a typical phialide is; nobody can be certain what anyone else means by the term; the term is promoting the very artificial classification it was introduced to avoid. The reasons for these problems are discussed, and four other terms (aleuriospore, annellide, blastic and thallic) subject to the same difficulties are identified. It is concluded that none of these words can be used as unambiguous, precise scientific terms, but that they can still have a function as vague words describing general symptoms.

This is the third paper in a series providing a radical reappraisal of existing research on deuteromycete taxonomy. The ideas and specialized terms introduced in the first two papers (Minter, Kirk & Sutton, 1982, 1983) are used here. Familiarity with them is assumed. The titles of those papers, *Holoblastic Phialides* and *Thallic Phialides*, beg the question 'What is a phialide anyway?' This paper addresses that question.

ORIGIN OF THE TERM PHIALIDE

The term phialide was invented by Vuillemin (1910*a*), member of a school of French mycologists among whom the use of developmental features in deuteromycete taxonomy can be traced as far back as Costantin (1888). The work in which Vuillemin introduced the term began with the observation that the traditional classification of hyphomycetes provided by Saccardo (1886) was very artificial and that 'it is therefore necessary to look for more reliable characteristics to which those already in use can be subordinated'. It is clear from Vuillemin's words that he was seeking a natural classification of hyphomycetes, and his concept of the phialide must be seen in this context. Vuillemin introduced the term phialide in the following two passages translated by the senior author.

'The branch which serves as the immediate support for conidia often takes the form of a flask with a venter and a neck, reminiscent of a single spored basidium and its sterigma. The word *basidium* ought to be reserved for the organ characteristic of the basidiomycetes, the flask-shaped conidiophore branch will take instead the name *phialide* (*φιάλη*, *phiala*, flask). Apart from cases where it becomes complicated or secondarily reduced, the typical phialide forms conidia exclusively at the top of its neck. Sometimes it exhausts itself in the production of a single conidium, sometimes it produces several successively and in a basipetal direction. These are able to become detached as they are produced, to remain in an agglutinated mass, or to form small chains or strings holding together for a greater or lesser period. The presence of a phialide provides the most reliable taxonomic characteristic after the presence of conidia; among the conidial hyphomycetes it characterizes the group PHIALIDÉS.'

'The order of PHIALIDÉS... is very large. It will gather together a throng of species hitherto dispersed in the most diverse classes and families, and even in heterogeneous genera. *Sporotrichum roseum* Link, *Botrytis bassiana* Bals., the genera *Verticillium*, *Acremonium*, *Penicillium*, *Aspergillus*, etc. form part of it. It will be subdivided according to the arrangement of the spores, their structure; one will have to place in the final position those empirical characteristics hitherto employed exclusively as criteria of the first rank.'

ANALYSIS OF VUILLEMIN'S CONCEPT

In these passages Vuillemin defined the phialide by reference firstly to shape, secondly to development and thirdly to examples. Of the six examples, two are species and the remainder generic names. In assessing what Vuillemin meant by his new term the generic names are of little value, because they do not enable us to trace the individual fungi Vuillemin must have had in his mind when he cited them. *Sporotrichum roseum* would have been familiar to Vuillemin's contemporaries through the illustration in Lindau (1907) (Fig. 1). *Botrytis bassiana* was illustrated by Vuillemin (1912) himself when he redisposed it in his new genus *Beauveria* (Fig. 2).

The illustration of *S. roseum* is poor. It does,

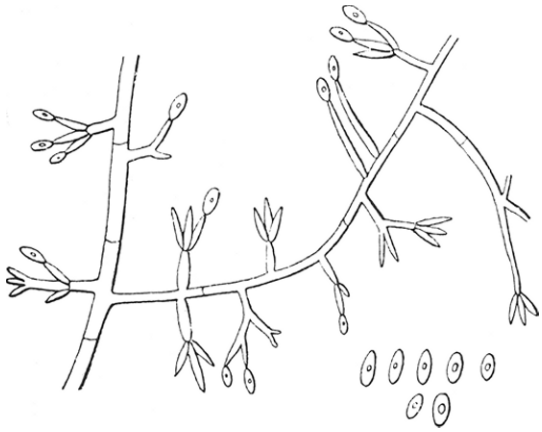

Fig. 1. *Sporotrichum roseum* (from Lindau, 1907).

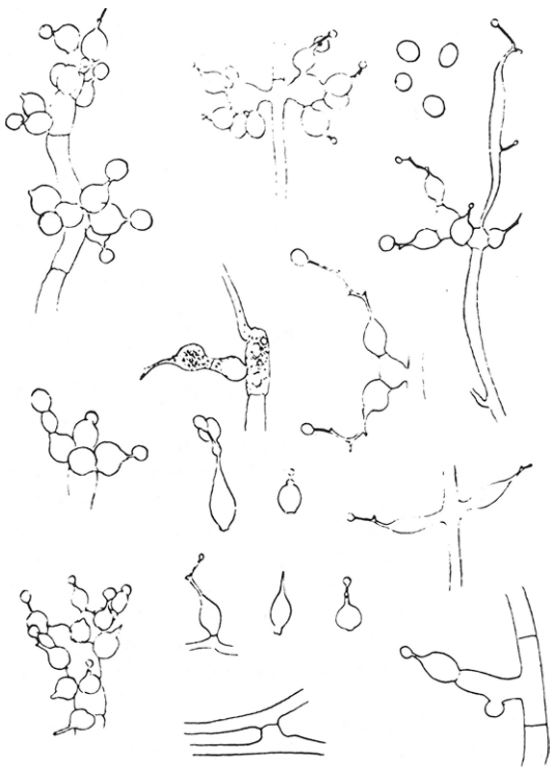

Fig. 2. *Beauveria bassiana* (from Vuillemin, 1912).

however, show that conidiogenous cells of this example are consistent with certainly the morphological and probably also the developmental criteria provided by Vuillemin for the phialide. The illustration of *B. bassiana* is, by comparison, excellent. It shows that conidiogenous cells of this fungus have the right shape for a phialide in

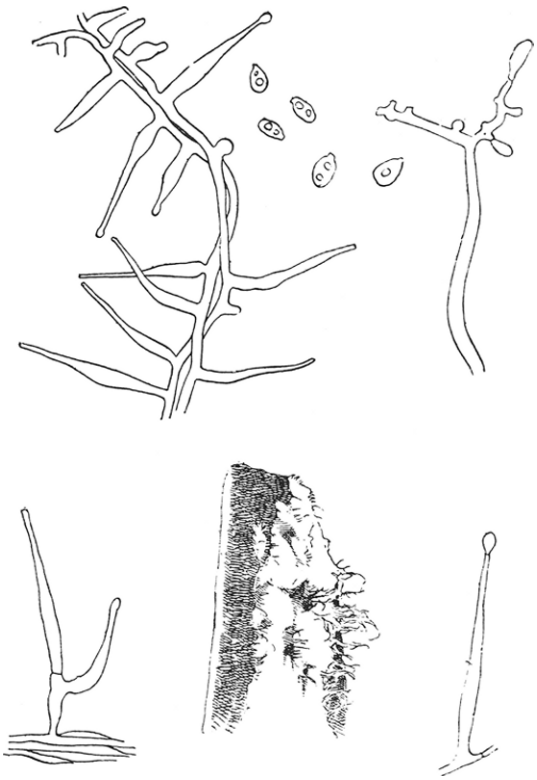

Fig. 3. *Acremonium potronii* (from Vuillemin, 1910*b*).

Vuillemin's sense, but develop by sympodial proliferation and therefore do not produce conidia 'in a basipetal direction.' The development in *B. bassiana* is thus not as described by Vuillemin for a typical phialide. Since this illustration is Vuillemin's own and appeared in the same paper (1912) as a description of the conidiogenous cells of this fungus as phialides, there is considerable evidence that Vuillemin was aware of this anomaly and, nevertheless, regarded the conidiogenous cells of *B. bassiana* as phialides.

In another paper produced shortly after the first, Vuillemin (1910*b*) discussed the fungus *Acremonium potronii* Vuill. (Fig. 3). He noted that conidiogenous cells of this species were flask-shaped and produced conidia in a manner appropriate for phialides; but he observed that in many cases no septum was formed at the base of the flask-shaped portion, and for this reason concluded that conidiogenous cells of *A. potronii* were not phialides. He therefore excluded the fungus from his order Phialidés. In the same paper, Vuillemin unambiguously designated the species *Spicaria aphodii* Vuill. (now called *Paecilomyces fumosoroseus* (Wize)

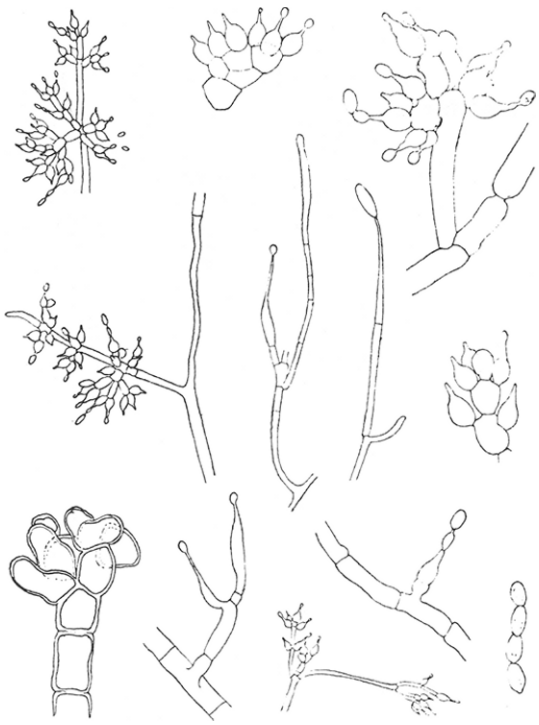

Fig. 4. *Spicaria aphodii* (from Vuillemin, 1910*b*).

Brown & Smith) as type of his order Phialidés, and provided a careful description and illustration of this fungus (Fig. 4). To judge from this illustration, the conidiogenous cells of *S. aphodii* agree with his original definition of a phialide.

Vuillemin's use of examples enables two deductions to be made concerning his concept of the phialide. Firstly, his inclusion of *B. bassiana* in the order Phialidés shows that, in recognizing a phialide, he did not regard mode of development of the conidiogenous cell as necessarily more significant than its shape. Secondly, and conversely, his exclusion of *A. potronii* shows that he did not regard the shape of a conidiogenous cell as necessarily more important than its mode of development.

At first sight, therefore, Vuillemin's use of his own criteria appears inconsistent and arbitrary: in one example shape is important, in another development. It must be remembered, however, that he was not concerned primarily with the consistency of his criteria. He was attempting to produce a natural classification and believed his order Phialidés constituted a naturally related group of fungi. His principal interest was therefore to identify members of that group by the characteristic organ they produced.

Generally speaking, in natural classification, no single criterion can be used consistently and exclusively of others. An example from zoology may make this point clear. Vivipary is a criterion used to identify mammals, but no zoologist would attempt to identify mammals consistently and exclusively on the basis of this criterion. If this happened, the duck-billed platypus would be excluded because it lays eggs, and the aphid, which is an insect, would have to be included. The natural classification proposed by Vuillemin was no exception to this generalization: members of his order Phialidés could, he believed, be recognized by their characteristic organ, the phialide. He did not wish to imply, however, that within this whole order there was no variation in shape or development of that organ. His criteria are therefore not absolute, but merely guidelines.

That this line of thought is correct may be seen from the following comparison of *S. aphodii* and *B. bassiana*. Both species are totally hyaline; both have similar overall dimensions; both produce conidiophores with similar branching patterns; both have conidiogenous cells which are similar in shape, at least in their lower portions; conidiogenous cells of both produce more than one minute aseptate conidium from the apex, and these conidia are attached to the conidiogenous cell by a thin neck; conidial delimitation in both is similar and conidia of both secede probably by schizolysis; both fungi are parasitic on insects and both quite plausibly could have teleomorphs in the same ascomycete order, perhaps the Clavicipitales. The two species differ in that *S. aphodii* produces conidia in true or false chains (it is not clear which from the illustration), whereas those of *B. bassiana* are produced by sympodial proliferation.

The two fungi are therefore similar in so many respects that it is not surprising Vuillemin believed they were related. Many present-day mycologists might agree with him. If the two species are related, it follows that the conidiogenous cells in both are likely to represent the same anatomical organ, even if they do not develop in exactly the same way. One must therefore conclude that Vuillemin's use of his own criteria was not inconsistent, but rather that his concept of the phialide was logically self-consistent and exactly what would be expected from any taxonomist putting together a natural classification.

SUBSEQUENT HISTORY OF THE TERM

Vuillemin's term was adopted by other mycologists, and is in widespread use today. Because so many have used the term, however, the following history is of necessity selective. As a result, for example, there will be no reference to the frequent and problematic use of the term in anamorphs of

groups other than the ascomycetes. Instead this history will be restricted to the examination of certain crucial works on which the use of the term phialide by others greatly depends.

MASON, LANGERON AND VANBREUSEGHEM

The first significant discussion of Vuillemin's term was provided by Mason (1933, 1937). Mason criticized Vuillemin for excluding *A. potronii* from the Phialidés, and expressed the opinion that the presence or absence of a basal septum to the flask-shaped organ was of less taxonomic significance than the events occurring at its apex. In all other respects he accepted Vuillemin's views. Langeron & Vanbreuseghem (1952) produced a textbook account in which Mason's emendation was accepted, but in other respects Vuillemin's views were presented remarkably unchanged, even including, for example, a detailed account of the development of phialides in *B. bassiana*.

HUGHES

The experimental classification of hyphomycetes proposed by Hughes (1953), and inspired and guided by Mason, was a major event in the history of deuteromycete taxonomy. Hughes proposed to classify hyphomycetes into eight sections 'based primarily upon the different types of conidiophore and conidium development'. The fourth of these sections was based on the phialide and comprised fungi described as having 'conidia (phialospores) developing in rapidly maturing basipetal series from the apex of a conidiophore (phialide) which may or may not possess an evident collarette'. At the beginning of this fourth section Hughes defined the phialide in detail with the following words:

'The term phialide is here restricted to those unicellular structures which are usually terminal, but sometimes intercalary as well, on simple or branched conidiophores; they are oval to subcylindrical to flask-shaped or subulate often with a well differentiated basal swelling and a narrower distal neck, with or without a terminal collarette; from the apex of each phialide develops a basipetal succession of phialospores without an increase in the length of the phialide itself. If the phialide does proliferate e.g. in *Catenularia*, then a plurality of conidia develops at each level. Not uncommonly a phialide may possess two or three collarettes in which case the term polyphialide can be applied to it (e.g. *Lasiosphaeria hirsuta*).'

Hughes' concept of the phialide thus differed slightly but significantly from that of Vuillemin. Hughes emphasized shape less and development

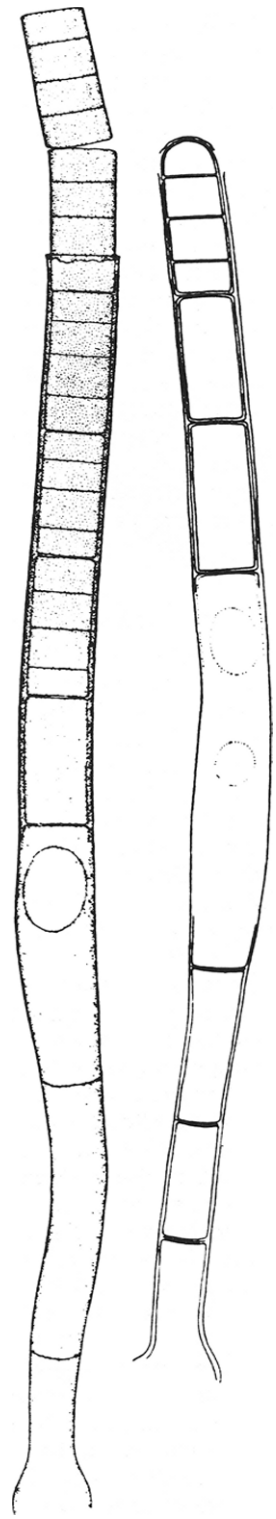

Fig. 5. *Sporoschisma mirabile* (from Hughes, 1953).

more, and the aspect of development which received particular attention was that occurring at the apex of the conidiogenous cell. This change in emphasis is not surprising, since Hughes was attempting a far wider reform of the classification of hyphomycetes than had been countenanced by Vuillemin. It also marks an extension of the argument begun by Mason (1933, 1937) when he drew attention away from the basal septum of *A. potronii* to the events occurring at the conidiogenous cell apex. The result of this change in emphasis, however, was that it was no longer possible to classify fungi such as *B. bassiana* as having phialides, in spite of their obvious similarities with other species still classified in that section. Conversely, other fungi such as *Sporoschisma mirabile* Berk. (Fig. 5) were classified as having phialides, in spite of the fact that this species has few similarities with, say, *S. aphodii* (Fig. 4) and was never mentioned by Vuillemin (1910*a*, *b*) in his original works.

TUBAKI, SUBRAMANIAN AND BARRON

Since publication, Hughes' system has undergone considerable scrutiny. Various mycologists have proposed amendments or new but generally similar systems of their own. Notable amongst these were Tubaki (1958, 1963), Subramanian (1962, 1971) and Barron (1968). All of these authors followed Hughes in giving greater weight to developmental features occurring at the apex of the conidiogenous cell than to other developmental features or considerations of shape. Their definitions of the phialide accordingly differ little from those of Hughes.

Interestingly, however, Tubaki (1958) divided his section of fungi with phialides into two subsections. In one the collarette was conspicuous and the conidia, in general, developed deep down within it. In the other the collarette was generally inconspicuous and the conidia, even when young, developed above it. This had the effect of separating genera such as *Sporoschisma* Berk. & Br. (Fig. 5) into the former subsection, and genera such as *Spicaria* (Fig. 4) into the latter. The significance of this was that it constituted early recognition of the fact that fungi with phialides in the sense of Hughes (1953) did not form a homogeneous group.

Subramanian (1962) and Tubaki (1963) each listed a type genus for their respective sections of hyphomycetes with phialides. In the case of Subramanian the section was at family level and the type genus was *Tubercularia* Tode: Fr. In the case of Tubaki the section level was not defined (Tubaki described them as divisions, but could scarcely be using the word in a strict nomenclatural sense since the division is a greater taxonomic rank than the class he was attempting to divide), and the type genus was *Catenularia* Grove, species of which are more similar to *Sporoschisma* species than to *Spicaria* species. Tubaki also deliberately excluded *B. bassiana* from his section with phialides, and even made *Beauveria* (the genus typified by this species) the type genus of his section comprising fungi with holoblastic sympodial proliferation.

KANANASKIS

The first Kananaskis conference (Kendrick, 1971) represents another milestone in the history of deuteromycete taxonomy. One of its main aims, probably the most important, was to try to introduce some consensus over the terminology available to describe hyphomycetes and in particular their modes of development. At this conference the term phialide was the subject of considerable discussion which is fortunately preserved in the proceedings (Kendrick, 1971). The results of this discussion were a 'tentative ontogenetically based system for fungi imperfecti' in which *Penicillium corylophilum* Dierckx was cited as the example of a fungus with phialides, and the following definition:

'Phialide: a conidiogenous cell which produces, from a *fixed* conidiogenous locus, a basipetal succession of *enteroblastic* conidia whose walls arise *de novo* (e.g. *Penicillium*, *Phialophora*, *Chalara*, *Sporoschisma*). A more extended definition of phialide is as follows: a conidiogenous cell in which at least the first conidium initial is produced within an apical extension of the cell, but is liberated sooner or later by the rupture or dissolution of the upper wall of the parent cell. Thereafter, from a fixed conidiogenous locus, a basipetal succession of enteroblastic conidia is produced, each clad in a newly-laid-down wall to which the wall of the conidiogenous cell does not contribute. Any phialide wall distal to the conidiogenous locus is the *collarette*. The length of the phialide does not change during the production of a succession of conidia, though some phialides undergo intermittent vegetative proliferation, either *percurrent* (as in *Catenularia*) or *sympodial* (as in *Codinaea*) between conidiogenous episodes.'

In this definition the phialide is described purely in terms of one restricted aspect of development. This aspect is the series of events occurring at the small fertile locus in the cell where conidia are being produced. No consideration is given to developmental events occurring elsewhere in the cell, nor to shape, or any question of the taxonomic position

of the fungus bearing the cell. According to Kendrick (1971) the phialide is simply a fungal cell which produces conidia in a particular manner.

This definition may be viewed as the culmination of a trend begun by Mason to emphasise the developmental events occurring at the apex of the conidiogenous cell. It has found widespread acceptance and similar definitions may be found in many other recent major works, e.g. Cole & Samson (1979), Ellis (1971, 1976), and Sutton (1980). For convenience such definitions were used in preparing the first two papers in this series (Minter *et al.*, 1982, 1983).

RECENT RESEARCH

Since the first Kananaskis conference much work has been done on the phialide, a lot of it using electron microscopy. There have been two principal results of this research. Firstly, use of the term phialide has now become firmly established in the coelomycetes, on the grounds that development in these fungi is of the same fundamental nature as that in hyphomycetes (Sutton, 1973, 1980). These grounds were first mooted by Mason (1933) and are now generally agreed to be justified. Secondly, it has become clear that the phialide, as defined at Kananaskis, is heterogeneous.

Evidence for this heterogeneity was provided by many researchers, including Cole & Samson (1979), Hawes & Beckett (1977*a*, *b*, *c*), Shearer & Motta (1973), Subramanian (1979) and in the two earlier papers of this series (Minter *et al.*, 1982, 1983). As a result, the term phialide as defined at Kananaskis is now used to describe such diverse fungi as *Trichoderma saturnisporum* Hammill (Fig. 6) (producing conidia in gummy masses by a system of replacement wall building apices with intervening proliferations), *Chalara hughesii* Nag Raj & Kendrick (Fig. 7) and *Aspergillus clavatus* Desm. (Fig. 8) (producing conidia in true chains by a wall building ring, with and without conspicuous collarettes respectively) and oddities like *Conioscypha varia* Shearer (Fig. 9).

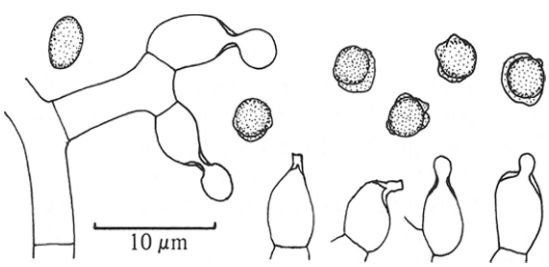

Fig. 6. *Trichoderma saturnisporum.*

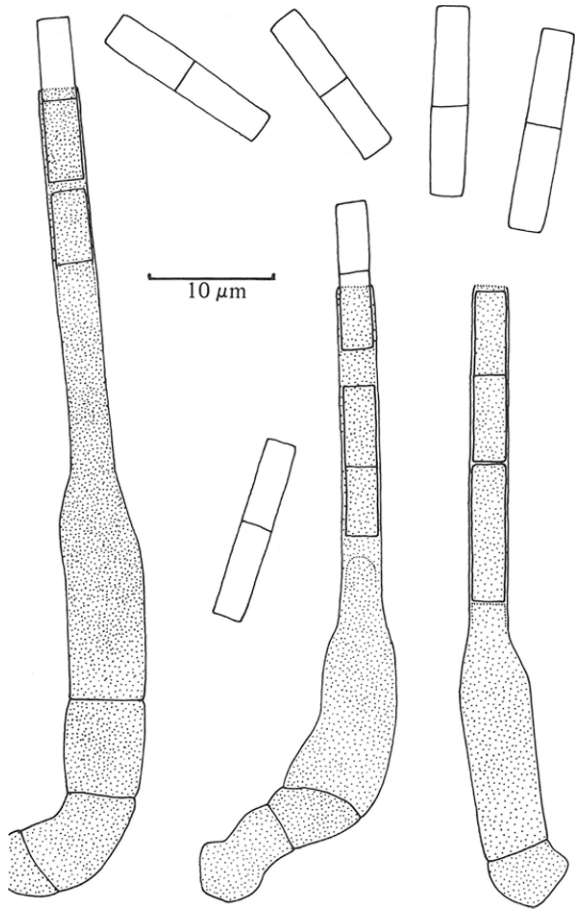

Fig. 7. *Chalara hughesii.*

Another comparatively minor but interesting aspect of recent research has been the appearance of a small but significant number of papers in which the wisdom of defining the phialide purely in terms of the development occurring at its apex has been questioned. The work of Gams (1973) provides a good example of this. In it he discussed the problems presented by fungi such as *Aphanocladium spectabile* W. Gams (Fig. 10) which produces conidiogenous cells indistinguishable from phialides in the sense of Kananaskis (Kendrick, 1971) except in that they each produce only one conidium. Many of these problematic fungi are obviously closely related in every other respect to similar species with conidiogenous cells producing more than one conidium and fitting perfectly the Kananaskis definition of the phialide.

Gams also cites the example provided by the anamorphs of three species of *Hypomyces* Tul. The anamorph of *H. odoratus* Arnold produces conidia

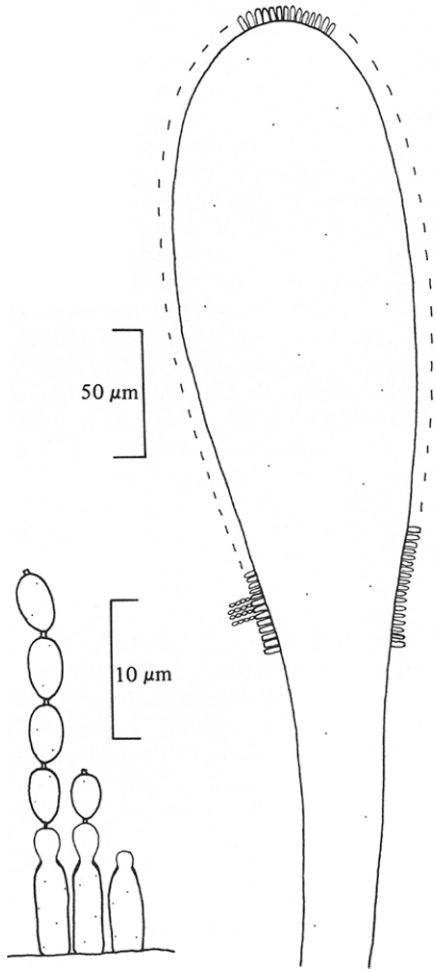

Fig. 8. *Aspergillus clavatus*.

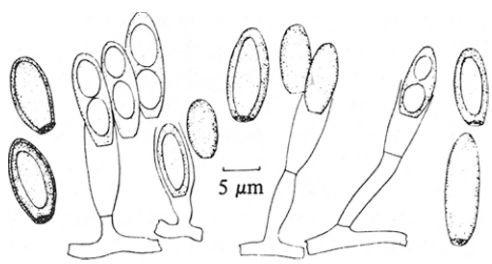

Fig. 9. *Conioscypha varia* (from Ellis, 1976).

in a manner which fits exactly the Kananaskis definition of a phialide. The anamorph of *H. aurantius* (Pers.) Tul. however, produces conidia from conidiogenous cells which become shorter with every spore produced. This species

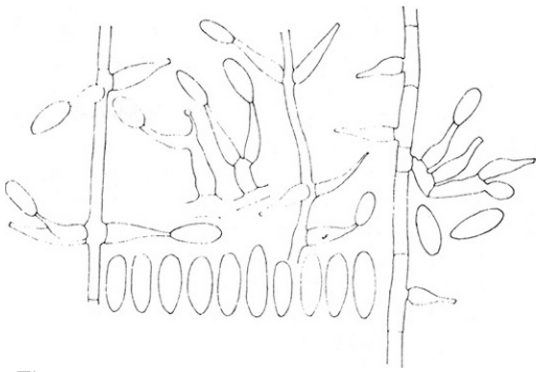

Fig. 10. *Aphanocladium spectabile* (from Gams, 1973).

cannot therefore be described as having phialides in the sense of Kananaskis, because the conidiogenous locus is not fixed. Similarly, the anamorph of *H. rosellus* (Alb. & Schw.: Fr.) Tul. produces conidia from conidiogenous cells which elongate with each conidium formed, and therefore cannot be called phialides for the same reason.

Gams' work demonstrates that use of the term phialide in the sense of Vuillemin (1910*a*, *b*), i.e. as a natural organ produced by a natural group of fungi, has not entirely been overwhelmed by the use of the same term in the highly restricted developmental sense so widespread today, i.e. as a cell developing in a particular way irrespective of the taxonomic affinities of the fungus producing it. The fact that the term phialide still conjures up ideas of shape in the minds of many mycologists is further evidence that the developmentalist's definition of the term on its own is not totally accepted.

DISCUSSION

From the foregoing brief historical outline one thing is clear: with few exceptions, each researcher who has used the term phialide has intended to use it as an unambiguous, precise, scientific term. The following discussion is therefore an assessment of how well this word fulfils the rôle to which everyone has assigned it.

PROBLEMS

There are four big problems with the term phialide. The first is that over the last 30 years, since Hughes (1953), virtually nobody has used the term in the sense originally intended. Over these years the difference between the original sense and current usage has tended to become greater, so that present definitions of the term have little in common with those of Vuillemin.

Although researchers are not obliged to use this term in its original sense, there being no nomenclatural code to cover terminology, their neglect is particularly regrettable because Vuillemin's definition had much to commend it. It was logically self-consistent, and presented in such a way as to encourage the development of a natural classification. Vuillemin's natural order Phialidés was carefully tied to a type species which was fully described and illustrated. Even though typification does not apply to ranks above family level in the International Code of Botanical Nomenclature (Art. 16), this chosen species is surely significant in determining the nature of the phialide.

It is therefore remarkable that in all the research since Vuillemin's time, not one mycologist, it seems, has attempted to re-evaluate the phialide in terms of this species. Of the two other species mentioned as examples of phialides in Vuillemin's (1910*a*) original publication, *Sporotrichum roseum* is still very much an unknown (it has certainly not received the attention it deserves from the developmentalists) and nobody nowadays classifies *B. bassiana* as having phialides at all. It has even been used to typify another group of hyphomycetes categorically stated to be non-phialidic (Tubaki, 1958).

In view of the fact that recent use of the term is so different from its original definition, it might seem politic to discard Vuillemin's views altogether. Even this is not practical, however, because there are sufficient new papers being produced which use the term in Vuillemin's sense, or something very like it, e.g. Gams, 1973, to keep alive this original definition.

The second problem is that nobody is agreed on what is a typical phialide. Vuillemin (1910*b*) cited *Spicaria aphodii*, Subramanian (1962) the genus *Tuberculariа*, Tubaki (1963) *Catenularia* and Kendrick (1971) *Penicillium corylophilum*. Doubtless more examples could be found, and they cannot all be right. Indeed, in view of the heterogeneity which has become apparent in fungi with 'phialides', it is doubtful whether any of the four examples cited above are even closely related.

This problem will become acute if ever a natural system is successfully devised for the deuteromycetes which uses this word. A decision will have to be made as to what genus, species and specimen typify the taxon or taxa containing fungi with phialides. Three attempts at typification were noted in the foregoing historical outline (Vuillemin, 1910*b*; Subramanian, 1962; Tubaki, 1963), none of which is nomenclaturally straightforward. Other similar attempts could probably easily be found in the literature. In addition to these attempts, it might be necessary to take into account some of the instances where a given species is cited as a typical phialide even where no nomenclatural treatment is present, particularly if these instances occur in important works. For example, the citation of *P. corylophilum* as the example for phialides in the 'tentative ontogenetically based system' produced at Kananaskis (Kendrick, 1971) cannot lightly be laid aside in view of the influence this work has had. It would seem that nobody has even begun to sort out the confusions contained in this problem.

The third difficulty is that present day use of the term encompasses such a wide variety of fungi that when one researcher uses the term there is no guarantee that he will be understood by others. One reason for this is that the definition of a phialide has changed gradually over the years, largely without being noticed, and the classifications resulting from these subtly different definitions are encountered whenever one has to refer to the literature. Another reason is that even the most rigorous definitions yet devised by the developmentalists have failed to circumscribe the term sufficiently for it to refer solely to a homogeneous group of fungi.

In a sense their failure is not surprising. The developmentalists' definitions, although in direct line of evolution from Vuillemin's, have changed so much that they must be regarded as fundamentally different. Whereas Vuillemin's definition aimed at a natural classification, and so never stressed one criterion to the exclusion of others, the developmentalists' definitions, e.g. Kendrick, 1971, have concentrated on the developmental sequence occurring at the apex of the conidiogenous cell. This has encouraged mycologists to use this one criterion consistently and to the exclusion of others. Predictably enough, no natural classification has come about. Indeed it must now be obvious that this emphasis has resulted, to paraphrase the zoological example from earlier in this paper, in the aphids of the fungal world being classified as mycological mammals.

The fourth problem is that present-day use of the term results in related fungi being separated. The anamorphs of the three species of *Hypomyces* cited by Gams are a good example of this. If the developmental definition of a phialide were to be rigorously applied, these three hyphomycetes would be placed in different genera. Their appearances and known teleomorphs, however, plainly indicate that such a classification would be ridiculous. Examples of this fourth problem must be familiar to all mycologists working with these groups, and so it is probably not worth while citing more. In fact, so many of these examples exist that it is scarcely surprising that mycologists are losing confidence in the ability of current systems to classify deuteromycetes.

These four problems may be summarized thus: virtually nobody has used the term phialide in its original sense for the past 30 years (problem 1); nobody is agreed on what a typical phialide is (problem 2); nobody can be certain what is meant when anyone else uses the term (problem 3) and the term, as currently used, is promoting the very artificial classification it was designed to avoid (problem 4). Clearly the term phialide is ambiguous. It is certainly not precise, nor is it scientific.

The reasons for these problems are varied, but the following are believed to be significant. The term phialide represents an attempt to sum up in one word a whole sequence of developmental events (conidial ontogeny, conidial maturation, conidial delimitation, conidial secession, proliferation, etc.). The same sequence is present in sufficient fungi to give mycologists the misleading impression that the term phialide has some semblance of meaning. It is now, however, realized that each stage in this sequence can vary independently of the others, so that a wide variety of combinations of stages (developmental cocktails) can exist (Minter *et al.*, 1982, 1983), all of them at present described as phialides.

Worse still, the term is also used to express concepts of shape. Shape in this case is the visible symptom of a developmental cause. It is a commonsensical proposition in biology in general that one symptom can have many causes, e.g. sneezing, a symptom, can result from a cold, pepper, hay-fever, bubonic plague, etc. This proposition is also true for the concept of shape in the phialide: flask-shaped conidiogenous cells with periclinal thickening at their apex need not all come about by the same sequence of developmental stages; they certainly need not be related (Fig. 11). Lastly, the term is also used to express concepts of natural affinity. Clearly this is all too much. A single word serving all of these purposes cannot be expected at the same time to be unambiguous, precise and scientific. It is small wonder that use of the term has proved to be problematic.

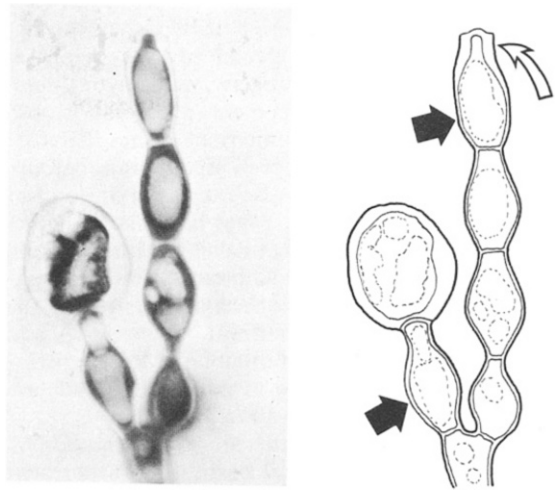

Fig. 11. *Ambrosiella* sp. (IMI 257509). Conidiogenous cells (arrows) can be flask-shaped, with periclinal thickening at their apex (open arrow), making them morphologically indistinguishable from certain 'phialides', but their development is completely different, since each produces at its apex a single, thick-walled 'aleuriospore'.

DIFFERENT TERMS WITH THE SAME PROBLEMS

The term phialide is not unique. Four other terms with the same difficulties will now be identified. It is not intended to spell out in detail for each the reasons why they are problematic. The history of the misuse of the term phialide is a sufficient example that such a discourse for the other terms would not be hard to write.

Aleuriospore is defined in the *Dictionary of the Fungi* (Ainsworth, 1971) as: 'a conidium (frequently thick walled and pigmented but sometimes thin walled and hyaline) developed from the blown-out end of a sporogenous cell or hyphal branch from which it secedes with difficulty... "chlamydospore" sensu Hughes, 1953; gangliospore. Since introduced by Vuillemin in 1911 aleuriospore has been used in various senses, see Mason (1933, 1937) and Barron (1968) for discussions.' With the wisdom of hindsight it is possible to see here all the same problems and causes of these problems as in the case of the phialide. Aleuriospore is an attempt to sum up in one word a sequence of developmental events; it tries to convey a sense of shape and of natural affinity (Vuillemin, 1911). The term has not been used in its original sense in recent years, there is argument as to what a typical aleuriospore is, nobody is sure what anyone else means by the term and, doubtless with such confusion, the term is promoting the artificial classification it was originally set up to avoid!

Although the term annellide has not had such a long history as the phialide or aleuriospore, it nevertheless suffers from the same difficulties. As its etymology suggests, it refers to conidiogenous cells around which faint rings can be discerned. These faint rings, in the same way as the flask-shape of the phialide, are the visible result (symptom) of a developmental sequence (cause).

At the time of Hughes' (1953) experimental classification, it was believed that only one developmental sequence produced this symptom (holoblastic conidial ontogeny, schizolytic secession, enteroblastic percurrent proliferation and progressive conidial delimitation). It has therefore been used as though it represented a natural group. The recent studies on *Endophragmiella* Sutton and related genera (Hughes, 1979) have shown, however, that at least one other developmental cocktail can produce this visible symptom (holoblastic conidial ontogeny, rhexolytic secession destroying the conidiogenous cell, percurrent regeneration and progressive conidial delimitation). All the principal causes of confusion in the term phialide are thus also present for the annellide.

The two remaining terms are blastic and thallic. In recent years these have been used to represent the two supposedly fundamental groups of deuteromycetes (Cole & Samson, 1979; Ellis, 1971, 1976; Kendrick, 1971; Sutton, 1980 etc.). The validity of this supposition has, however, recently been questioned by Minter *et al.* (1983) who produced evidence that the thallic category contained many fungi which were the same as certain blastic fungi in every developmental respect but one, i.e. in that conidial maturation was delayed until after conidial delimitation. It must by now be evident, therefore, that these two terms also each represent a visible symptom which can be caused by a variety of different developmental cocktails.

It is also an unpleasant fact that Vuillemin (1910*a*) classified the 'blastic' fungi as a subdivision of the 'thallic' fungi. As has already been observed, the paper in which he made this classification was highly influential and logically thought out. There can be no doubt therefore that both terms have been subject to misuse somewhere along the line. The same problems and confusions thus occur in blastic and thallic as are found in the other terms.

CONCLUSIONS

Five terms at present believed to be of paramount importance in deuteromycete taxonomy have been used until now as though they were unambiguous, precise and scientific. The analysis of these terms offered in this paper has, however, shown that they are all subject to such confusions and problems that it is impossible to continue using them in this way. If they had been subject to the same scrutiny as is applied to binomials by the International Code of Botanical Nomenclature, they would have been rejected years ago because they have 'been used in different senses' and so have 'become a long-persistent source of error' (Art. 69). The sooner, therefore, the practice of using them as though they were unambiguous, precise and scientific is dropped, the better.

Minter *et al.* (1983) observed that 'the terms 'phialidic' and 'thallic' under their present definitions contain inherent confusions and contradictions, and if they are to continue in use in any meaningful sense, they need to be subjected to thorough scrutiny'. The present paper has carried out this thorough examination, and has shown that their observation was justified. The question remains to be answered: can these terms continue to be used in any meaningful sense?

This question can conveniently be turned on its head. If these terms are not unambiguous, precise and scientific, can they be put to any good use in an ambiguous, imprecise and non-scientific way? It is believed that the answer to this question is yes. In describing observations on deuteromycetes, the mycologist needs words at different levels of accuracy. The terminology should therefore reflect this need. If it does not, the researcher will sometimes be obliged to use a general term where a highly specific one is required, or conversely a precise term where he himself is vague about the observation. In the present cases this amounts to a need for precise words to describe the individual developmental stages (the cause) and vague words to describe the resulting symptoms.

In the past terms like phialide have been used both as vague symptom words and as precise terms describing cause. This has led to tautological thinking roughly on the level of 'phialides develop phialidically', a statement which results in zero transfer of information. Now, however, it is realized that although terms like phialide cannot be used at a precise level, they still have a valuable function as general symptom words. The replacement terminology at the precise level already exists (Minter *et al.*, 1982, 1983) in the form of statements describing each stage in the developmental sequence separately. Since all of these stages exist as separate variables it would be foolish to ignore any of them: the replacement terminology takes all of them into account. Although the resulting statements are longer than the old use of a single term, they are unambiguous, precise and scientific, and so surely represent an improvement.

Another advantage of this proposed terminology is that it enables statements to be made which are intermediate between the vagueness of a general symptom, say phialide, and the precision of a full developmental observation. Thus, for example, the phrase 'ring wall-building phialide' identifies that it is not a 'replacement apex phialide', and so conveys more meaning than the word phialide in isolation. But it is not sufficient to distinguish between fungi like *Chalara hughesii* (Fig. 7) and

Aspergillus clavatus (Fig. 8). The proposed terminology thus offers not only precision where it is required, and vagueness if necessary, but also flexibility.

One interesting feature to emerge from the present work is the way in which concepts of form, function and development have all been confused in the terminology. For example the concepts of 'flask-shape' and of development were muddled in the phialide, and the term aleuriospore to many mycologists has included the concept of a survival propagule (function) in addition to concepts of shape and development. The confusions of these three important themes need to be investigated to see whether they too are significant in holding back deuteromycete systematics.

The attention of mycologists is drawn to the similarity between the present terminological reforms and the reforms proposed by Hennebert & Weresub (1977) concerning the terms anamorph, teleomorph and holomorph. Those reforms have already been of considerable benefit to mycology. It is believed that the present proposals could also relieve deuteromycete taxonomy of some of the difficulties which at present encumber it.

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