

# CONIDIUM ONTOGENY\*

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**D**URING the past twenty-five years and more I have been fortunate to have been able to devote myself to the study of Hyphomycetes and have been especially concerned with conidium ontogeny and classification. It seems appropriate, therefore, that conidium ontogeny should be the subject of this address.

Although no apology is needed for the academic pursuit of Hyphomycetology for its own sake, I have always derived added satisfaction from the thought that such pursuit has other relevance too. Current interest in Hyphomycetes flows from such relevance. These fungi incite serious diseases of our major crops and inflict heavy losses. They cause irksome dermal as well as chronic systemic mycoses in man and animals. In stored grain and feed they produce toxins which have been shown to be carcinogenic to animals, and might also be a hazard to human health. Severe damage to textiles, tentage, paper and stored food and fruit, especially in the humid tropics, can be ascribed to them. On the other hand, they can be used to our advantage to effect chemical transformations, for example, of steroids which are important in medicine, in the production of antibiotics and numerous other metabolites or fermentation products. Both governmental and private agencies are, therefore, interested in fostering research on these fungi in the hope that, if not now, in the future, the results of such research must prove useful.

In many ways, the Hyphomycetes are a fascinating group of organisms and the fact that the majority of them do not reproduce sexually and produce elaborate or complex perfect fructifications does not make them less interesting for that reason. They have other (parasexual) means for interchange of cytoplasm or nuclei contributing to heterogeneity amongst their population which makes their pedigree not always easy to determine. Over 7,000 species in about 900 genera are known to science, thriving on a variety of substrata: soil, dung and other animal excreta, litter, insects,

feathers of birds, wood and bark, and even in running streams and in the sea. Many new ones are constantly being discovered especially in the tropics and we have ourselves described several new genera and species from India during the past several years. They can decompose a variety of substrates since they can produce the enzymes needed to break down these substrates. They may also give out numerous metabolites, seemingly a casual accompaniment of their growth!

They reproduce asexually by producing conidia. Conidia show a remarkable variety of shape, size and septation. Many of them remain perfectly hyaline; others are dark-coloured, mostly brown or some shade of it. The conidiophores on which conidia are produced may be simple or variously branched, and often may be aggregated into cushion-like groups called sporodochia or columnar structures called synnemata. These are features which can be readily seen when these fungi are examined under the ordinary microscope and were the ones used by the great Italian mycologist P. A. Saccardo in 1880 in developing a classification of these fungi.

The Saccardoan classification is still in use, not because it is the best that can be had, but chiefly because no alternative system incorporating all genera of Hyphomycetes has yet been fully or adequately evolved. During the years 1910-11, the French mycologist Vuillemin observed how conidia may be produced in different ways and suggested that conidium types may be distinguished on the basis of their ontogeny, rather than merely by their shape, septation, etc. It was he who first pointed out that conidium types based on their ontogeny could be useful in classification and also proposed a classification on this basis. Since then, conidium ontogeny has engaged the attention of several active students, notably E. W. Mason, S. J. Hughes, K. Tubaki, M. B. Ellis, E. S. Luttrell, S. Nilsson, G. L. Barron and W. B. Kendrick. I have summarised elsewhere past work on the subject<sup>1,2</sup>. The most recent addition to the literature on the subject will be found in the Proceedings<sup>3</sup> of an International Conference on Criteria and Terminology in the Classification of Fungi Imperfecti held at Kananaskis, Canada, in 1969. This Conference endorsed the idea that the Saccardoan system must eventually be replaced by

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a system based on conidium ontogeny. As I have said elsewhere<sup>1</sup>: "The passive acquiescence in the Saccardo system is borne partly of satisfaction with things as they are, and partly of fear of experiment. Its evasion is always the evasion of the need for a positive attitude and concealment, if possible, of all that creates the need for a change." Naturally, I am pleased to find general agreement amongst hyphomycetologists in favour of the new approach which was so well and forcefully brought out by Hughes<sup>4</sup> in 1953.

### Terminology

New knowledge and new interpretations of conidium ontogeny are inevitably tied up with terminology: this presents problems, and solutions have to be found. Clothing old terms with new meaning in line with new thinking and interpretations, however well intended, may often lead us into a path beset with perennial difficulties; this is particularly true of some old terms which have been in use for a long time, and it may not be easy to find general acceptance from mycologists for such a proposal. In other cases, indifference to the proper use of a term in its original sense has often lent a halo of ambiguity to the term, and then the term has first fallen into misuse, and then into disuse, for no fault of the author! A good example of this is the term "aleuriospore", proposed by Vuillemin, later misused by several students until finally the term gave no satisfaction to at least some of the participants of the Canadian Conference.

### Blastospores

The term "blastospore" (= blastoconidium) has been in wide use for a long time. A blastospore is a product of a process of "budding", and what can be seen of this under the ordinary light microscope is a narrow zone of the wall of a conidiogenous cell or conidiophore blowing out a bud that enlarges and becomes a conidium. Budding in the classical sense is that found in yeasts. The budding process in yeasts has been described variously<sup>5</sup>. In some there is continuity of wall/wall layers between parent cell and bud; in others this is not the case, and there may be continuity only of one or more wall layers, but not all layers of a usually stratified parent cell wall. This generally holds true of the budding process in the few Hyphomycetes that have been investigated by electron microscopy<sup>3,5</sup>.

If, therefore, wall relationships and wall participation in the budding process are considered, it is obvious that this process may or may not involve all wall layers of the parent cell; sometimes the

wall that buds out is a newly formed one and internal. All the same, the process is one of budding or, if we may use the adjective, *blastic*. To retain the term *blastic* to connote budding would be no departure from original usage. The advantage in using the term in its original sense is that, under the ordinary light microscope, the budding process is easily observed, but adequate information about participation of wall layers in the budding process cannot be had easily. Sometimes it is even difficult to decide if the budding takes place through a pore or not. This difficulty is illustrated by the case of *Stemphylium botryosum*: in this, the conidium had for long been considered to bud out through a pore<sup>4</sup>, but we now have evidence from electron microscopy that this is not so<sup>3</sup>. The converse of this can also happen. For instance, conidial origin by budding through pores is not known in moniliaceous Hyphomycetes: this may be because the pore may be seen only with difficulty under the ordinary light microscope in the case of these hyaline fungi. Since this condition is more widely known in dematiaceous Hyphomycetes, it may also be true that pores may be much more easily discernible in the case of dark-coloured fungi. In view of these difficulties, it would be wise to retain the term *blastic* in its original sense and when further information on continuity of wall layers in the budding process becomes available, these can be indicated by appropriate terms which can be coined to describe features of continuity or discontinuity of wall layers between conidiophore and conidium during the budding process and to indicate the extent or nature of participation of wall/wall layers of the conidiogenous cell in conidium ontogeny.

### Wall Relationships in Conidium Ontogeny

From our present knowledge of participation of wall/wall layers in conidium ontogeny<sup>5</sup>, the following possibilities are known:

1. All wall layers of a conidiogenous cell or conidiophore may contribute to the conidium wall, with or without extension growth, so that there is continuity of all wall layers between conidium and its parent cell. The integrity of the wall (as a whole) of the conidiogenous cell is not disrupted or broken during conidiogenesis. The term *totitunicogenous* [etym. L. *totus* (whole) + *tunica* (coat) + *genus* (origin)] will aptly describe this condition, this mode of ontogeny and conidia so produced.

*Examples*: *Chromelosporium* state of *Peziza ostracoderma*; *Stemphylium botryosum*; *Bactridium*; *Basipetospora*; *Acrosporium*; *Geotrichum*; the first conidium of *Scopulariopsis brevicaulis*,

2. All wall layers of a conidiogenous cell or conidiophore do not contribute to the conidium wall; only the inner wall/wall layer(s) contribute(s) to the conidium wall, with or without extension growth. The integrity of the cell wall (as a whole) of the conidiophore or conidiogenous cell is disrupted. The continuity of the wall/wall layers between the conidiogenous cell/conidiophore and the conidium is limited to the wall layer(s) contributing to the wall of the conidium. The term **penititunicogenous** [etym. L. *penitus* (inner) + *tunica* (coat) + *genus* (origin)] will adequately describe this condition, this mode of ontogeny and the conidia so produced.

*Examples:* *Alternaria brassicicola*; *Helminthosporium*.

3. All wall layers of a conidiogenous cell or conidiophore do not contribute to the conidium wall; only the outer wall/wall layer(s) contribute(s) to the conidium wall. The integrity of the cell wall (as a whole) of the conidiogenous cell or conidiophore is disrupted. There is continuity of the outer wall/wall layer(s) of the conidiogenous cell/conidiophore and the conidium. The term **exteritunicogenous** [etym. L. *exterius* (outer) + *tunica* (coat) + *genus* (origin)] will aptly describe this condition, this mode of ontogeny and the conidia so produced.

*Examples:* *Penicillium clavigerum*, *P. claviforme*, *P. corymbiferum*.

This term has been necessitated by the recent study of Fletcher<sup>6</sup> on conidium ontogeny in the three *Penicillium* spp. cited above.

4. No wall/wall layer of the conidiogenous cell or conidiophore may contribute to the conidium wall. A new wall/wall layer contributes to the conidium wall, typically involving extension growth. The term **novitunicogenous** [etym. L. *novus* (new) + *tunica* (coat) + *genus* (origin)] will satisfactorily describe this condition, this mode of ontogeny and the conidia so produced.

*Examples:* *Aspergillus*; *Penicillium*; microconidia (? the first one excepted) of *Neurospora crassa*; all conidia, except first one, of *Scopulariopsis brevicaulis*.

5. No wall/wall layer of the conidiogenous cell or conidiophore contributes to the conidium wall. Conidia are produced by protoplasmic cleavage within a conidiogenous cell or conidiophore, followed by formation of a wall *de novo* around the cleaved out protoplasmic unit. Conidium wall, therefore, has no connection with wall of conidiogenous cell or conidiophore. When more than one conidium are produced from a conidiogenous cell, the walls of the successive conidia also have no

continuity with each other. The term **etunicogenous** [etym. L. *e* (without, lacking) + *tunica* (coat) + *genus* (origin)] will aptly describe this condition, this mode of ontogeny and the conidia so produced.

*Examples:* the phialoconidia of *Thielaviopsis basicola*, *Cystodendron*.

It must be stressed that these terms merely pertain to the extent or degree of contribution the parent cell wall makes to the conidium wall and must be used only in this restricted sense. It may also be noted that, in the case of any of these modes of ontogeny, additional wall layer(s) may be laid down *de novo* internal to the primary wall/wall layers within developing conidia, but these are not relevant for the proper use of the above terminology. The distinction between *novitunicogenous* and *etunicogenous* needs to be clearly understood. Formation of a new wall/wall layer is the first step during conidiogenesis in the former, the new wall usually exhibiting extension growth during conidiogenesis. In the case of the latter, on the other hand, protoplasmic cleavage is the first step, followed by development of a wall around the cleaved out protoplasmic unit; no extension growth of this wall apparently takes place during conidium formation.

### Gangliosporos

The term "gangliosporos" (= ganglioconidium) was proposed by me<sup>7</sup> several years ago and refers to a conidium "developed by the transformation of the swollen tip of a hypha into a spore: a conidium initial may or may not be delimited". This definition was based entirely on observations using the ordinary light microscope so that it should be easy to decide whether a conidium belongs to this category. The adjective *gangliar* will aptly describe this mode of ontogeny and the conidia so produced.

*Examples:* *Bactridium*, *Amblyosporium*, *Acrosporium*, *Basipetospora*, *Scopulariopsis*.

By definition, gangliosporos, like blastosporos, are *tunicogenous*; theoretically, they may be either *toti-* or *peniti-* or *novitunicogenous*.

Of the examples cited, *Acrosporium* is peculiar in that continued apical "meristematic" activity of the fertile hypha is a characteristic so that an indefinite number of gangliar conidia can be initiated and differentiated in a basipetal sequence and forming true chains<sup>8</sup>. These conidia have been designated variously: meristem arthrospores, meristem aleuriopores, etc., but a better terminology is needed to distinguish this feature from others where this is not found,

Equally interesting are forms such as *Scopulariopsis*, the conidiogenous cells of which were for long considered phialides, but are no longer so designated because they possess characteristic annellations<sup>1</sup>. Accordingly, this mode of ontogeny has been termed *annellidic* and the conidiogenous cell itself called an *annellide* or described as *annellate*<sup>3</sup>. The essential features of this mode of ontogeny are: a conidiogenous cell produces a succession of solitary conidia of which the first is totitunicogenous, and later ones novitunicogenous, the wall of each of the successive conidia being clad in an extension of a new wall which corresponds to the lower half-wall of the double septum that separated the previous conidium from the conidiogenous cell. The double septum is formed during conidium development but prior to conidium liberation. The conidia are produced at progressively higher levels, leaving close and regular annellations that are remains of the successive walls that have contributed to the walls of the successive conidia.

A further point I like to mention here is that the line that separates an annellide from phialides of certain fungi may be dubious. Sutton and Sandhu's observations on fine structure of the annellides of *Cryptosporiopsis* sp. showed that annellations may sometimes be found at a level lower than the first one so that these annellations cannot be seen with the ordinary microscope<sup>5</sup>. In other words, such an annellide in which annellations are concealed below the level of detachment of the first conidium would, for all intents, pass for a phialide, despite the fact that, on the basis of conidium ontogeny, it is basically an annellide. The point I wish to emphasize is that some phialides may really be such annellides. In such cases, the successive annellations form a progressive series each internal to the previous one, and collectively present, in longisection, a layered aspect just below the open end of such a conidiogenous cell. These features are readily seen in electron micrographs of thin sections of the "microconidiophores" (phialides) of *Neurospora crassa*, and I am grateful to Professor G. Turian of the University of Geneva who very kindly showed me some of his excellent electron micrographs which clearly show these features. The successive solitary conidia are abstricted one by one, all at or very nearly the same level. It would be rewarding to ascertain by scanning electron microscopy if there are conidial scars. The conidia thus produced are novitunicogenous, except the first one which is totitunicogenous. Each proliferation produces only one conidium; but yet, because these proliferations are hidden, the conidiogenous cell acquires the semblance of having a "meristem"—

but this situation should not be confused with others where the conidiogenous cell or conidiophore has a true "meristematic" character. The phialides of several genera in which a basipetal succession of solitary conidia are produced and remain agglutinated to form slimy masses or a linear series (pseudo-chains) may eventually come under this category<sup>8</sup>. To summarize, if the annellations which telescope one within the other in a typical annellide are compressed or pushed down to the same level within the annellide, we shall have a phialide of the type of the microconidiophores of *Neurospora crassa*.

It is now possible to consider terminology required to describe the "meristem" characteristics seen in *Acrosporium* and in microconidial *Neurospora crassa*. The following terminology is recommended:

1. The term *synechidic* [etym. Gr. *synechos* (continuous)] is descriptive of the ability of a conidiogenous element to produce an indefinite number of conidia in basipetal succession. The term will also be descriptive of such a mode of ontogeny or conidia which are products of such ontogeny.

*Examples*: *Acrosporium*; *Penicillium*; phialoconidia of *Thielaviopsis basicola*.

2. The term *asynechidic* [etym. Gr. *a* (not) + *synechidic*] means "not synechidic".

*Examples*: *Helminthosporium velutinum*; *Scopulariopsis brevicaulis*.

3. The term *pseudosynechidic* [etym. Gr. *pseudo* (false) + *synechidic*] is descriptive of a mode of ontogeny which in reality is asynechidic, but has the semblance of being synechidic. The term may also be used to describe this condition, conidia produced in this way or a conidiogenous cell that functions like this.

*Example*: microconidial *Neurospora crassa*.

### Arthrospores

The term "arthrospore" (= arthroconidium) has been widely used in the past for "a spore resulting from the breaking up of a hypha into separate cells, e.g., in *Geotrichum*"<sup>9</sup>. The adjective *arthric* will, therefore, aptly describe this mode of ontogeny.

This mode of ontogeny is characterised by conversion and disarticulation of a pre-existing determinate hyphal element, i.e., one whose extension growth has ceased. A conidiogenous cell is not recognizable, but only a conidiogenous hypha, with usually more than one conidiogenous locus. Conidia are produced in random (irregular) linear series (not true chains<sup>8</sup>) from random loci, each locus producing only one conidium. That conidium

initiation begins only after extension growth of the hypha has ceased is very characteristic of this mode of ontogeny and is implied in the definition of arthrospore given above and my intention is merely to make this explicit. From this it becomes clear that conidia of forms such as *Amblyosporium* are not arthric but gangliar since, during development, there is extension growth of the wall.

The term **porrectic** (etym. L. *porrectus* = stretched out, extended) is descriptive of a mode of conidium ontogeny which is characterised by extension growth of the wall.

Examples: *Amblyosporium*; *Penicillium*; *Scopulariopsis*; *microconidia* of *Neurospora crassa*; *Basipetospora*; *Alternaria*; *Chromelosporium* state of *Peziza ostracoderma*.

If such extension growth is absent, the term **exporrectic** (etym. L. *ex* = not + *porrectic*) is recommended.

Examples: *Geotrichum*; phialoconidia of *Thielaviopsis basicola*.

Both terms may be used to describe the conidia which are products of the respective modes of ontogeny.

### The Phialide

The term "phialide" was coined by Vuillemin<sup>10</sup> and his concept of the phialide can be stated as follows: a phialide serves as the immediate support of the conidia, has frequently the form of a flask with a venter and neck, recalling a monosporous basidium and its sterigmata. Excluding cases where it is complicated or reduced secondarily, the typical phialide produces the conidia exclusively at the tip of the neck. Sometimes it produces only one conidium, at other times it produces many, successively and in a basipetal direction. The latter may be shed as soon as formed, remain agglutinated or form a chain or string of beads more or less coherent for a long time. Vuillemin classified forms characterised by phialides in a group which he designated *Phialidées*. As examples of Hyphomycetes characterised by phialides, he cited: *Sporotrichum roseum* Link. *Botrytis bassiana* Bals. [= *Beauveria bassiana* (Bals.-Criv.) Vuill.], and the genera *Verticillium*, *Acremonium*, *Penicillium* and *Aspergillus*. Both from the definition given by Vuillemin and from the examples cited by him, it would appear that the chief distinguishing feature of the phialide is its shape. In a later publication, Vuillemin excluded certain forms such as *Acremonium*, *Cephalosporium* and *Fusarium* from the group *Phialidées*, on the ground that a septum is laid down at the base of the conidiogenous cell and so they are not phialides. The result was that

forms such as *Verticillium* and *Aspergillus* were considered to have phialides, but not *Acremonium*, *Cephalosporium*, etc. From our present knowledge of conidium ontogeny, it would seem that forms differing in conidium ontogeny were placed together in both the original and the second proposal of Vuillemin; indeed, the second proposal further separated forms possibly having similar modes of conidium ontogeny—I mean, on the basis of current knowledge.

In his desire to rescue the term and bring it into usage, or "in order to secure the advance made by Professor Vuillemin", as he would have it, Mason<sup>11</sup> suggested reversion to the original concept of Vuillemin and amendment of the term phialide "to read fusiform truncate, fusiform beaked, or acuminate terminal portion of a hypha, from the apex of which, or within which, thin-walled conidia are abstricted". In further elaboration of this suggestion, Mason recognized two kinds of phialospory:

1. By far the commonest form of the phialide is one from which conidia are abstricted in basipetal succession, so that the tip of the phialide is practically an open growing point. Mason referred to spores so produced as "meristem spores". The term phialospore was used to express "phialomeristem" spores.

2. When only one conidium is produced from a phialide, such a conidium is to be distinguished from typical phialospores as "terminus spores" as each conidium terminates the growth of the phialide.

These two modes of ontogeny clearly differ from each other, but as Mason himself stated, this corresponded to Vuillemin's original concept. Quite obviously, Mason did not favour any concept of the phialide other than the one originally proposed by Vuillemin; more explicitly, Vuillemin's later concept was not acceptable to him.

The interpretation of the phialide given by Langeron and Vanbreuseghem<sup>12</sup> includes the so-called *Oidium* (*Acrosporium*) states of powdery mildews and even *Endophragmia mirabilis*.

Hughes<sup>4</sup> restricted the use of the term phialide to unicellular structures of somewhat variable shape (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 the phialide a basipetal succession of phialospores is produced, without increase in length of the phialide itself. Apart from giving such a restrictive definition, Hughes considered phialide-like conidiogenous cells with annellations (e.g., *Scopulariopsis*) as something unique and

different from phialides. Forms producing terminus spores (e.g., *Beauveria*) were also excluded from his concept of the phialide. *Acrosporium* was also excluded and was placed in a separate group characterised by the production of "meristem arthrospores".

What is currently interpreted as a phialide, in fact, corresponds to Hughes's circumscription of it. Recent evidence, especially derived from studies on ultrastructure of some forms currently considered to show the phialidic mode of ontogeny, however, suggests that, looked at from considerations of wall relationships in conidium ontogeny, even the current concept is not satisfactory, as it reflects heterogeneity in regard to wall relationships in conidium ontogeny.

The following analysis of conidium ontogeny in four selected cases which are currently considered to be phialidic is illustrative of the heterogeneity referred to:

1. *Thielaviopsis basicola*: the phialoconidia are synechidic, etunicogenous, exporrectic, pseudo-catenate, sometimes glomerate, slimy.

2. *Penicillium* spp. (*P. clavigerum*, *P. claviforme*, *P. corymbiferum*): the conidia are synechidic, exteritunicogenous cum novitunicogenous, porrectic, catenate, dry.

3. *Aspergillus niger*: the conidia are synechidic, novitunicogenous, porrectic, catenate, dry.

4. *Neurospora crassa*: the microconidia are pseudosynechidic, tunicogenous (first conidium? totitunicogenous, later conidia novitunicogenous), porrectic, solitary, glomerate, slimy. Note: conidia may be pseudo-catenate in other cases.

The vicissitudes that have befallen "the phialide" from the time it was proposed by Vuillemin over sixty years ago have been briefly reviewed. In the end, nothing seems to me better than to retain it in its original sense. The many students who have tried to redefine the phialide in the past have, in the effort, made significant contributions towards our general understanding of conidium ontogeny, and this in itself is satisfying. On the other hand, it seems hardly justifiable, nor even necessary, to mix up old terms and new concepts in this way, as that will only lead to abuse of terminology which in turn would end up in a lot of confusion.

Although I have discussed primarily cell wall relationships in conidium ontogeny, I like to say that there are other equally fascinating and significant facets of this problem which have not received so far the attention they deserve. Even our knowledge of cell wall relationships is limited, but efforts have been made to elucidate these, chiefly because they are the most obvious ones that compel our attention when

we observe the development of a conidium. What I have said about phialides is still incomplete as I have not dealt with several other Hyphomycetes which have conidiogenous cells currently thought to be phialides primarily on the basis of their shape: critical study may always bring out something not always anticipated. We have yet to learn how conidia attain the shape<sup>3</sup> that is so characteristic for each species. Is conidium shape solely under genetic control, or does "nurture" have an effect? There is then the question about a given fungus producing conidia of differing modes of ontogeny, sometimes on the same conidiophore, such as, for instance, we observed<sup>13,14</sup> in the case of the wheat foot rot fungus (*Drechslera sorokiniana*). Both "nature" and "nurture" may have a say in conidium ontogeny and morphogenesis, and these are areas which are not only fascinating but important. We have evidence from recent work that the normal sequence of events in conidiogenesis, say in a phialide, may sometimes be altered: we do not know how. Karyological aspects of conidium ontogeny are yet another facet of the problem; studies in this area can yield much information that can help in arriving at a more complete picture of conidiogenesis. Karyological data *vis-a-vis* conidium ontogeny are especially needed for Hyphomycetes that produce true chains<sup>8</sup> of conidia, both acropetal and basipetal, and also those in which conidium ontogeny is synechidic.

These and other problems, then, await study. It is, therefore, with an expression of dedication to these tasks, and also an expression of both joy and gratitude for what I consider a recognition that Hyphomycetology has gained today, that I conclude this address. Hyphomycetology in India has come of age.

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