Trans. Br. mycol. Soc. **80** (1), 39–66 (1983) *Printed in Great Britain*

THALLIC PHIALIDES

BY D W. MINTER, P. M. KIRK AND B. C. SUTTON
Commonwealth Mycological Institute, Ferry Lane, Kew, Surrey TW9 3AF

The reappraisal initiated recently in these *Transactions* of development in conidial fungi and the language used to describe is continued. The terminology proposed in 'Holoblastic phialides' is applied to a wider range of fungi. Two further developmental stages (conidial maturation and collarette production) and three types of cell-wall building (apical, diffuse and ring) are identified, and the terms used to describe certain conidial chains are revised. Analysis of selected deuteromycetes shows that sympodial, false- or no-chain phialidic, retrogressive, true-chain phialidic and certain types of thallic development are all parts of a continuum. It is concluded that the terms phialidic, blastic and thallic are at present ill defined and cannot be applied to fundamental divisions of conidial fungi, and that if a new system of classification is to be devised for these fungi, it should not rest on such terms.

Radical views on development in some conidial fungi were expressed by Minter, Kirk & Sutton (1982). The present paper continues the reappraisal, using as a foundation the new ideas set out previously. Definitions of the five stages of development which can occur when conidiogenous cells produce conidia, namely conidial ontogeny, conidial delimitation, conidial secession, proliferation and regeneration, are given in Minter *et al.* (1982). Information derived from the transmission electron microscope is distinguished from that derived from the light microscope by the same drawing convention as used by Minter *et al.* (1982).

AIM AND ARRANGEMENT OF THE PRESENT WORK

In deuteromycetes described as having phialides two developmental patterns can be recognized. Conidiogenous cells with one pattern produce conidia in gummy masses or in chains which are not held together by wall material, but result simply from the chance accumulation of one conidium on top of another. Such conidiogenous cells are described as false- or no-chain phialides. Conidiogenous cells with the other pattern produce conidia in chains which are held together by wall material. These are described as true-chain phialides (Minter *et al.*, 1982).

The development of false- or no-chain phialides can be explained in terms of the same five stages as are required to describe development in sympodial and annellidic fungi (i.e. conidial ontogeny, conidial delimitation, conidial secession, proliferation and regeneration). The reason for this is that a continuum exists with known intergrading examples from false- or no-chain phialides, through annellides, to sympodial fungi. These fungi therefore form a group related developmentally, and the unifying factor is that conidiogenous cells of all members, if they are to produce more than one conidium, must proliferate between producing each conidium (Minter *et al.*, 1982). The development of true-chain phialides cannot be explained in such terms alone, however, because they can produce a large number of conidia in succession without intervening proliferation. Minter *et al.* (1982) suggested that additional stages to these five need to be defined if development in true-chain phialides is to be described adequately. They also observed that no intergradation has hitherto been demonstrated between false- or no-chain phialides and true-chain phialides.

This paper attempts to identify these extra stages by assessing additional species. In many cases these have been chosen because they are the subject of previously published research. They are described and discussed in turn, and each new stage of development identified is discussed immediately after the example in which it first became apparent. It will become clear that intergradation exists not only between false- or no-chain phialides and true-chain phialides, but also between these and some fungi in which development has generally been described as thallic.

Examples will be discussed in four parts. To maintain continuity, the first part begins with *Cladobotrym varium* Nees which Minter *et al.* (1982) showed to be located at one extreme of the sympodial, annellidic and false- or no-chain phialidic continuum. Intergradation will be shown between *C. varium* and certain conidiogenous cells which are not phialides but which produce conidia in true chains. In the second part intergradation

will be shown between these conidiogenous cells and fungi such as *Oidiodendron truncatum* Barron which have generally been described as thallic. In the third part intergradation will be shown between conidiogenous cells producing conidia in true chains and fungi such as *Aspergillus clavatus* Desm., which was cited by Minter *et al.* (1982) as having typical true-chain phialides. Intergradation between thallic fungi and those with true-chain phialides will be demonstrated in the fourth part; this integradation provided the title of this paper. At the end of the four parts a general discussion follows in which the implications of this work, particularly the significance of true and false chains, will be evaluated.

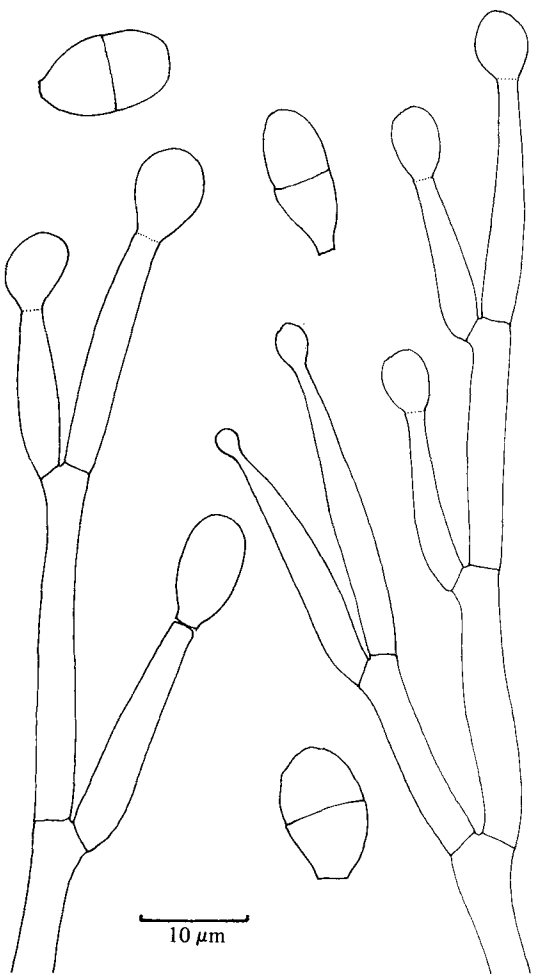

Fig. 1. *Cladobotryum varium.*

PART 1

Cladobotryum varium

Cladobotryum varium (Fig. 1) produces its first conidium holoblastically (conidial ontogeny) and delimits it (conidial delimitation) (Fig. 2). This conidium quickly becomes detached (conidial secession) and the conidiogenous cell proliferates enteroblastically (proliferation) to produce another conidium (conidal ontogeny). The second conidium is delimited by a septum (conidial delimitation) which occurs lower down the axis of the conidiogenous cell than the base of the new inner wall layer produced by the conidiogenous cell during the first proliferation (Fig. 2, arrow). When the second conidium becomes detached (conidial secession) it takes with it all wall layers above the delimiting septum and the conidiogenous cell becomes physically shorter. These stages may then be repeated (succession of holoblastic conidial ontogeny, retrogressive conidial delimitation, conidial secession and enteroblastic proliferation).

Wall building

Early growth of the conidiogenous cell and the first conidium in this and many other deuteromycetes occurs because wall material is produced (Fig. 3) in

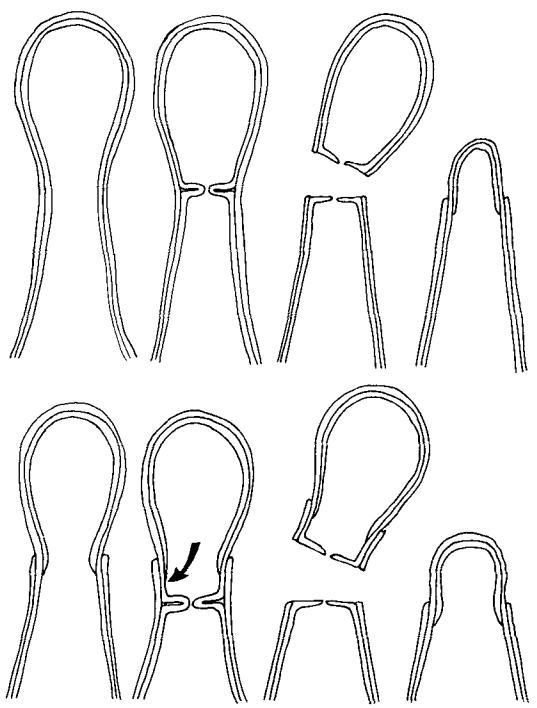

Fig. 2. Interpretation of development in *Cladobotryum varium.*

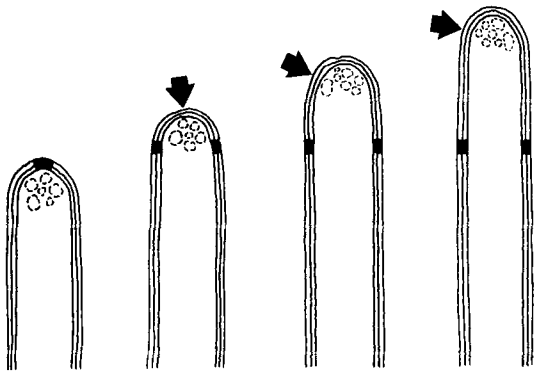

Fig. 3. Production of wall material at the apex of a hypha. Arrows locate secretory organelles. Blackened wall indicates reference point.

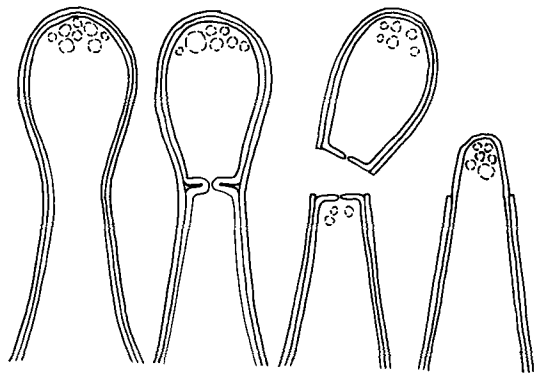

Fig. 4. The secretory organelles of the first wall-building apex are separated from the conidiogenous cell when the first conidium is delimited. A replacement wall-building apex then occurs at the top of the conidiogenous cell.

a small region of the hyphal cell apex which is undergoing modification to form the fertile element (Cole & Samson, 1979). Transmission electron microscopy shows that certain organelles are concentrated in the cytoplasm at the cell apex, adjacent to the walls being laid down. It has been surmised that they have a secretory function in association with wall production (Cole & Samson, 1979). Although these organelles cannot individually be observed with the light microscope, they can sometimes be seen collectively as a refractive body called the 'spitzenkörper' (Cole & Samson, 1979), and the presence of the small apical region where wall is being produced can be inferred by observing growth or because cell walls are thinner and, in dematiaceous hyphomycetes, less pigmented in this area.

This region has been called a meristematic zone (e.g. Cole & Samson, 1979; Kendrick, 1971) by analogy with meristematic zones of higher plants. This is misleading because the meristematic zone of higher plants, as the derivation of the word suggests (Greek: *μερίζειν*, to divide into parts), is a multi-cellular region where growth occurs by cell division. In fungi the term has been adopted appropriately to describe growth by cell division in rhizomorphs of some basidiomycetes, and confusion could result from its use in deuteromycetes to describe a region within a single cell where growth occurs by the laying down of wall material. It therefore seems sensible to avoid the term meristematic altogether when describing cell wall production in individual cells of deuteromycetes, and the words 'wall building' are preferred.

Conidiogenous cells of *C. varium* grow to full size and produce a first conidium by apical wall building (use of the word apex and its derivatives in this context implies that the wall building is strongly localized in that region). When the first conidium is delimited this wall-building apex is lost by the conidiogenous cell (i.e. the apex does not remain in the conidiogenous cell: it may or may not remain in the conidium), and is replaced by a new apex at the top of the conidiogenous cell, which then produces a second conidium when the first secedes (Fig. 4). The replacement wall-building apex in turn is lost when the second conidium is delimited, and a third wall-building apex arises in a sequence which can be repeated. Since *C. varium* is a member of the continuum of fungi with sympodial, annellidic and false- or no-chain phialidic proliferation (Minter *et al.*, 1982), it seems likely that development in those fungi generally follows this pattern of replacement of successive wall-building apices.

Trichothecium roseum

In *Trichothecium roseum* (Pers.) Link (Fig. 5) the first conidium is produced holoblastically by the first wall-building apex (conidial ontogeny) and delimited (conidial delimitation) (Fig. 6). This conidium remains attached, and the conidiogenous cell proliferates enteroblastically (proliferation) to one side below the first conidium by the activity of a new wall-building apex, which takes the line of least resistance. A second conidium is thus produced (conidial ontogeny) and delimited by a septum (conidial delimitation), which however occurs lower down the axis of the conidiogenous cell than the base of the new inner wall layer produced by the conidiogenous cell during the first

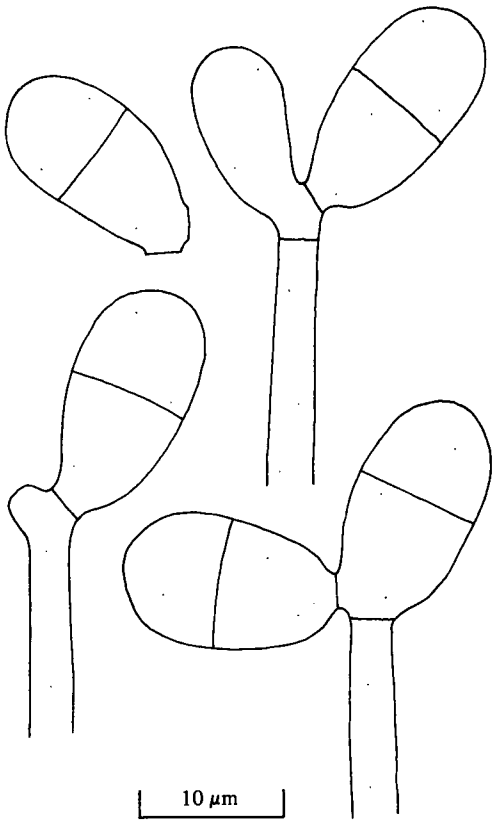

Fig. 5. *Trichothecium roseum.*

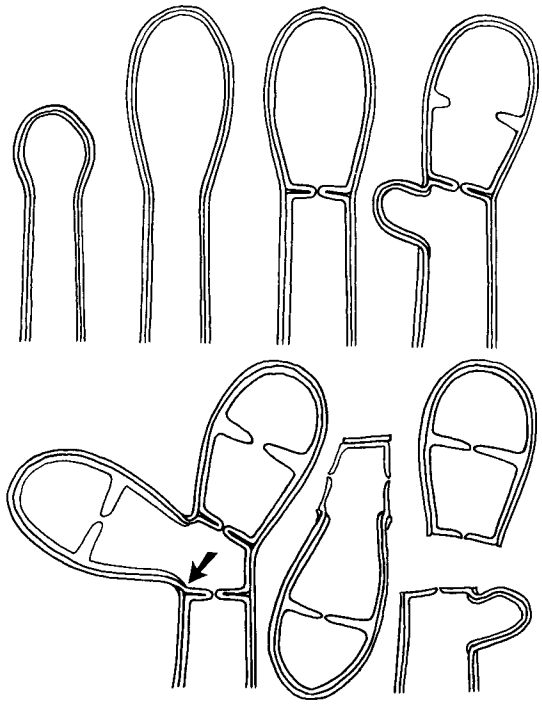

Fig. 6. Interpretation of development in *Trichothecium roseum* (modified from Cole & Samson, 1979).

proliferation (Fig. 6, arrow). These stages may then be repeated (succession of holoblastic conidial ontogeny, retrogressive conidial delimitation and enteroblastic sympodial proliferation) and conidia may become detached (conidial secession) at any time. When conidia become detached, each (like its counterpart in *C. varium*) takes with it all wall layers above the septum delimiting it after it was produced. The conidiogenous cells of *T. roseum* thus, like those of *C. varium*, become physically shorter as a succession of conidia is produced (Cole & Samson, 1979).

Trichothecium roseum shares many features with *C. varium*. It differs only because conidial secession is delayed and proliferation as a result is enteroblastic-sympodial, the replacement wall-building apex taking the line of least resistance, whereas in *C. varium* conidial secession is earlier in the sequence and proliferation as a result is enteroblastic-percurrent. This difference is of minor developmental significance (Minter *et al.*, 1982), and is probably not of major taxonomic importance either: *Cladobotryum* Nees and *Trichothecium* Link both contain anamorphs of *Hypomyces* Tul. However, it has a profound effect on the appearance of the fungus. Conidia of *T. roseum* adhere by inner and outer walls in a true chain, while conidia of *C. varium* accumulate in gummy masses. *Trichothecium roseum* can accordingly be regarded either as the sympodial counterpart of *C. varium* (in this sense it is more extreme than *C. varium* in its position in the continuum of sympodial, annellidic and false- or no-chain phialidic fungi) or, because of its unusual combination and sequence of developmental stages, as the first example of another continuum, comprising some of the fungi with conidia in true chains.

Basipetospora rubra

In *Basipetospora rubra* G. Cole & Kendrick (Fig. 7) the first conidium is produced holoblastically by the first wall-building apex (conidial ontogeny), delimited (conidial delimitation) and remains attached (Fig. 8). Just as in *T. roseum*, the first wall-building apex is lost by the conidiogenous cell when the first conidium is delimited. Unlike in *T. roseum*,

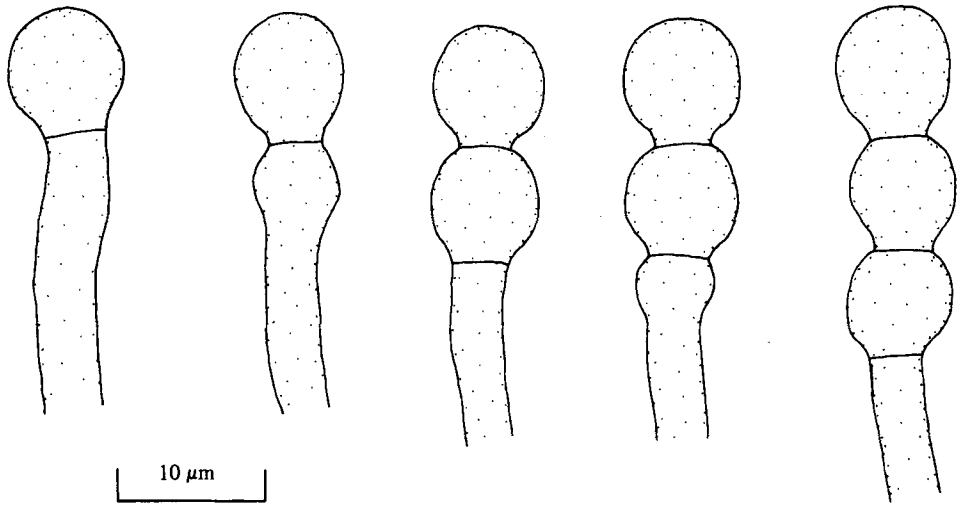

Fig. 7. *Basipetospora rubra.*

however, this lost apex is not replaced, and in the production of the second and all subsequent conidia wall-building apices cannot be observed. Instead, the upper portion of the conidiogenous cell swells on all sides (proliferation) below the septum delimiting the first conidium, and a second conidium is formed which, like the first, remains attached. These stages may then be repeated (alternation of proliferation by swelling of the upper part of the conidiogenous cell to produce a conidium, and retrogressive conidial delimitation) and conidia may become detached at any time (conidial secession). As a result of this combination of developmental stages, the conidiogenous cells of *B. rubra*, like those of *C. varium* and *T. roseum*, become shorter with each conidium produced (Cole & Samson, 1979).

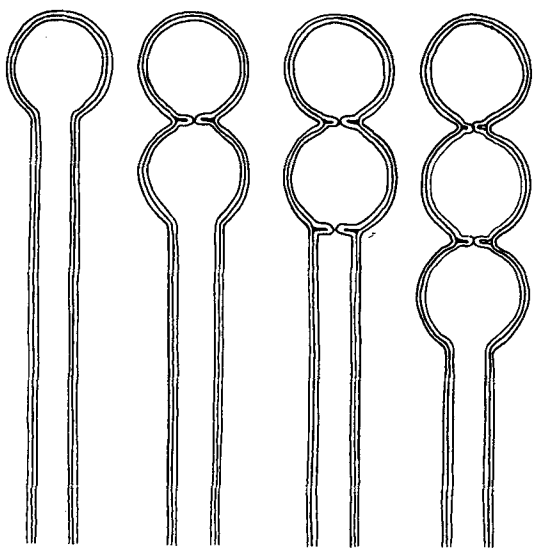

Fig. 8. Interpretation of development in *Basipetospora rubra* (modified from Cole & Samson, 1979).

Until after the first conidium is delimited, the development of *B. rubra* is indistinguishable from that of *T. roseum*, *C. varium* and any of the fungi in the sympodial, annellidic and false- or no-chain phialidic continuum. Even after the first conidium is delimited, there are obvious and strong similarities between *B. rubra* and all of these fungi (but particularly *C. varium* and *T. roseum*). There is also however an important difference: *B. rubra* lacks a replacement wall-building apex. This is evident even under the light microscope, as there is no sympodial growth, no annellidic line across the conidiogenous cell and no periclinal thickening. The proliferation is therefore of a type not involving a wall-building apex, and as such it is different from that in *T. roseum*, *C. varium* and all the fungi cited by Minter *et al.* (1982). It is important to establish the nature of this proliferation and whether or not it enables a significant distinction to be made between *B. rubra* and these other fungi.

Diffuse wall building

In *B. rubra* proliferation occurs not by the replacement of a wall-building apex, but by swelling on all sides of already existing walls. Research has shown that this form of wall building is not associated with high concentrations of cytoplasmic organelles adjacent to the cell apex. Instead they are randomly distributed at a low concentration throughout the cytoplasm (Cole & Samson,1979). This is to be expected given the non-polarized nature of this form of wall building, and is compatible with the surmise that they have a secretory function in association with wall production. It is therefore possible to recognize in the production of second and subsequent conidia of *B. rubra* another type of wall-building activity, different from apical wall building, and described here as 'diffuse'.

Diffuse wall building differs from apical wall building in that there is no region of high-activity wall production localized in the apex of the cell. Instead there is general, lower-activity wall production over a wide area of the cell, giving rise to growth by conversion of existing wall, which is even in all directions. This difference is correlated with and is probably the result of the variation in distribution within the cytoplasm of the relevant organelles.

In *B. rubra* and many other deuteromycetes both types of wall building occur at different times during conidial production. In all of these fungi, for a given length of cell wall, apical wall building always precedes diffuse wall building (thus in *B. rubra* the wall of the conidiogenous cell, originally produced by the first wall-building apex, is converted into the second and subsequent conidia by diffuse wall building). By examining fungi such as *B. rubra* in which the two wall-building types occur at different times, it is possible to deduce what contribution each type makes to the final shape of the conidium.

In *B. rubra* the conidiogenous cell is produced by the activity in isolation of the first wall-building apex and has a cylindrical shape on account of the polarized growth. In the first conidium apical and diffuse wall-building activity are concurrent and their effects cannot separately be evaluated. This conidium is globose. The second and subsequent conidia result from the activity of diffuse wall building upon wall already produced by the wall-building apex. The diffuse wall building causes specific areas of the cylindrical conidiogenous cell to swell, thus forming globose conidia. From this it seems reasonable to infer that apical wall building tends to produce cells cylindrical in shape, while diffuse wall building enables lateral swelling to occur so that spheres and intermediates between spheres and cylinders can be produced. Because both types of wall building have been observed in a wide variety of deuteromycetes, and both have been confirmed at an ultrastructural level in many species, it seems reasonable to generalize that the diverse shapes in many conidia can be explained by postulating different relative levels of activity of the two wall-building types. Cole & Samson (1979) have gathered an impressive array of evidence supporting this generalization.

Fungi may now be considered in which all wall building to produce a given conidium occurs at only one time in the developmental process. Among these fungi are *Tritirachium oryzae* (Vincens) de Hoog (Fig. 9), *Belemnospora epiphylla* P. M. Kirk (Fig. 10) and *Cladobotrym varium* (Fig. 1). If the generalization is true, apical and diffuse wall building occur concurrently, but in different relative proportions in each species because their conidia differ in shape. In *T. oryzae* diffuse wall building plays an important part in determining conidial shape because conidia are almost globose, and thus much wider across their middle than the point at which they are attached to the conidiogenous cell. In *C. varium* diffuse wall building plays a less important part in determining conidial shape because the conidia are elongated ellipsoidal, although they are still about twice as wide across their middle as the point at which they are attached to the conidiogenous cell. In *B. epiphylla* diffuse wall building plays little or no part in determining conidial shape, and the conidia are cylindrical and roughly the same width across their middle as the

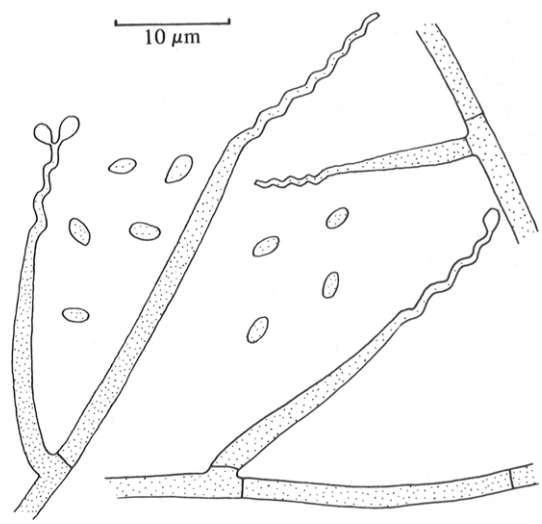

Fig. 9. *Tritirachium oryzae.*

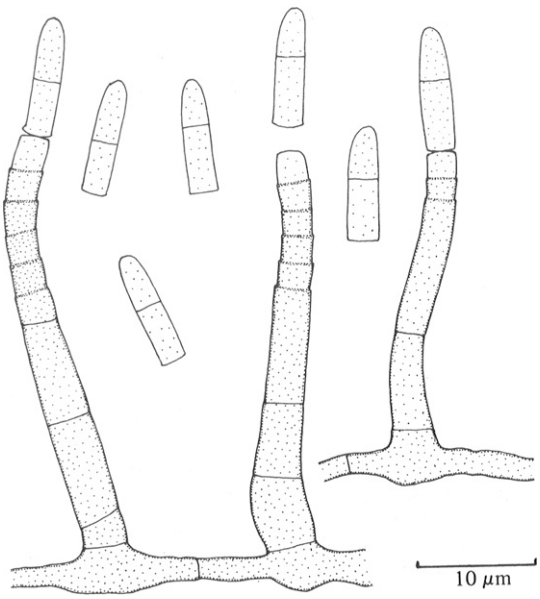

Fig. 10. *Belemnospora epiphylla*.

point at which they are attached to the conidiogenous cell.

It is thus evident that in many deuteromycetes both apical and diffuse wall building are involved in forming conidia, even if these two stages occur concurrently and cannot visually be distinguished except by deduction from the conidial shape (the two types are concurrent in all examples discussed by Minter *et al.* (1982) and in this paper, except for *B. rubra*, which is why until now there has been no need to distinguish the two wall-building types). Apical wall building can precede diffuse wall building (e.g. *Basipetospora rubra*), the two can occur concurrently (e.g. *Tritirachium oryzae*), and apical wall building can produce conidia with little or no contribution from diffuse wall building (e.g. *Belemnospora epiphylla*). There appears however to be no case known where, for a given length of cell wall, diffuse wall building precedes the apical type. This is not surprising, since the conversion of already existing walls appears to be a fundamental feature of diffuse wall building.

Conidial maturation

From the preceding discussion it is evident that the presence of diffuse wall building in *B. rubra* is not highly significant in delimiting it from fungi of the sympodial, annellidic and false- or no-chain phialidic continuum. What is important however is that in *B. rubra* and similar fungi the apical wall building occurs at an earlier and separate stage of development from diffuse wall building. Minter *et al.* (1982) have catalogued some of the confusions which can arise when a stage occurring at one time during the development of a conidial fungus is described in terms applicable only to a different stage occurring at another time. These are exactly the sorts of confusions which could arise if, as has often been done in the past, the diffuse wall-building stage in *B. rubra* is described as conidial ontogeny. Such a description implies that the diffuse wall-building stage is directly comparable with conidial ontogeny in, for example, *Belemnospora epiphylla*, where the term refers to the production of conidia by apical wall building alone.

It is therefore confusing to use the term conidial ontogeny for both apical and diffuse wall-building stages, particularly when the two stages occur at different times. A decision must be made as to which stage the term concerns, and to judge from its general use in the past, maximum clarity will be maintained if conidial ontogeny is used in future to refer only to wall-building stages in which walls are produced where none existed before. Conidial ontogeny can therefore be brought about by apical wall building (although this is not necessarily the only type of wall building which can result in conidial ontogeny), but it cannot be brought about by diffuse wall building. A new term must be found to describe the stage characterized by diffuse wall building, and it is suggested here that a suitable term would be 'conidial maturation'. In this paper conidial maturation is used to refer to the production or modification of conidia by diffuse wall building. Using the light microscope the timing of a conidial maturation stage in a given fungus can be deduced from the shape of the conidium or conidial initial.

Conidial maturation, when it occurs, can be concurrent with or can follow conidial ontogeny. It does not necessarily follow immediately, however, and between conidial ontogeny and conidial maturation intervening stages may occur. In *Basipetospora rubra* the conidial ontogeny of all conidia is incorporated in the initial growth of the conidiogenous cell (this is possible because of retrogressive delimitation), and conidial ontogeny and conidial maturation occur concurrently only in the case of the first conidium. In the second and subsequent conidia the duration of time between conidial ontogeny and conidial maturation is progressively greater, and more stages intervene (Fig. 11).

Two further features of conidial maturation worthy of note can be observed in *B. rubra*. First,

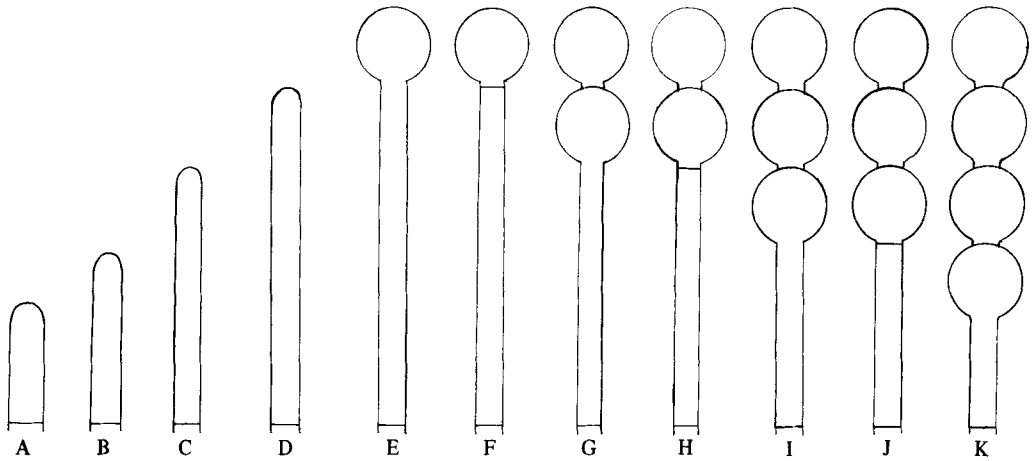

Fig. 11. Development in *Basipetospora rubra* showing how, with each conidium produced, the stages of conidial ontogeny and conidial maturation become increasingly separated in time. A. Conidiogenous cell. B. Conidial ontogeny of the fourth conidium. C. Conidial ontogeny of the third conidium. D. Conidial ontogeny of the second conidium. E. Simultaneous conidial ontogeny and maturation of the first conidium. F. Delimitation of the first conidium. G. Maturation of the second conidium. H. Delimitation of the second conidium. I. Maturation of the third conidium. J. Delimitation of the third conidium. K. Maturation of the fourth conidium.

proliferation and conidial maturation occur concurrently, after conidial ontogeny, on the same area of cell wall, so that it is impossible to distinguish the two stages in terms of the time or place in which they happen. This compares strikingly with development in fungi, where conidial ontogeny and conidial maturation occur concurrently immediately after proliferation (e.g. in false- or no-chain phialides). In these fungi the temporal and spatial distinctions between proliferation and conidial ontogeny, though small, are of crucial importance in understanding the true affinities of the development (Minter *et al.*, 1982) (Fig. 12). Secondly, and linked to the first observation, with diffuse wall building the distinction between holoblastic and enteroblastic proliferation becomes meaningless, as there is no strongly polarized growth to make an identifiable breach in a pre-existing wall barrier.

To summarize, therefore, in fungi where proliferation precedes concurrent conidial ontogeny and conidial maturation (e.g. in false- or no-chain phialides), there is no great value in recognizing as separate conidial ontogeny and conidial maturation, but the distinction between these two and proliferation is essential. By comparison, in fungi where conidial ontogeny precedes concurrent proliferation and conidial maturation (e.g. *Basipetospora rubra*), there is no great value in recognizing proliferation and conidial maturation as separate, but the distinction between these two (particularly conidial maturation, because it has not been recognized before) and conidial ontogeny is essential. There is only one advantage to be gained in recognizing and listing as separate each stage regardless of whether or not it is significant in the particular fungus under observation. Such careful and systematic listing enables the true affinities to be seen between fungi such as *Tritirachium oryzae* and *Basipetospora rubra*. Omission of a stage from the list, simply because it is not obvious, can totally obscure these affinities.

Divergence

Cladobotryum varium, *Trichothecium roseum* and *Basipetospora rubra* show intergradation in developmental characteristics between fungi of the sympodial, annellidic and false- or no-chain phialidic continuum and certain fungi producing conidia in true chains. Both can now be related to a different type of wall-building activity. Although *B. rubra* and similar fungi produce conidia in true chains, they cannot be said to have true-chain phialides for three reasons. The first is that the enteroblastic mode of development is not involved in production of conidia in these fungi. The second

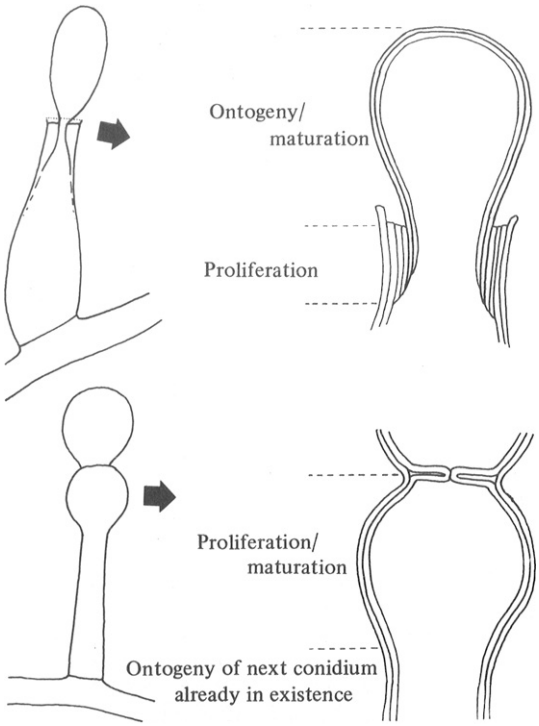

Fig. 12. In false- or no-chain phialides (top) the distinction between proliferation and ontogeny/maturation is important. In fungi like *Basipetospora rubra* (bottom) proliferation and maturation occur simultaneously long after ontogeny has ended.

is that they proliferate between producing each conidium (even though the proliferation is difficult to distinguish from conidial maturation). The third is that the number of conidia which a given conidiogenous cell can produce in these fungi is limited ultimately by the original length of that conidiogenous cell. In many fungi with developmental patterns closely comparable with those of *B. rubra* mechanisms have evolved which circumvent this limitation. They may be divided into two broad categories, perhaps evidence of an evolutionary divergence. The first leads from *Basipetospora variabilis* Matsushima to fungi such as *Oidiodendron truncatum* which in the past have been described as thallic. The second leads from *Basipetospora chlamydosporis* Matsushima eventually to fungi with true-chain phialides like those of *Aspergillus clavatus*.

PART 2

Basipetospora variabilis

No time-lapse or other developmental studies have been carried out on this species, and this account is based on analysis of the original detailed description and illustration by Matsushima (1975). In *Basipetospora variabilis* (Fig. 13) the conidial ontogeny stages of the second and subsequent conidia are incorporated in the initial activity of the first wall-building apex. The first conidium is produced holoblastically by the concurrent activity of the first wall-building apex, and diffuse wall building (concurrent conidial ontogeny and conidial maturation), is delimited (conidial delimitation)

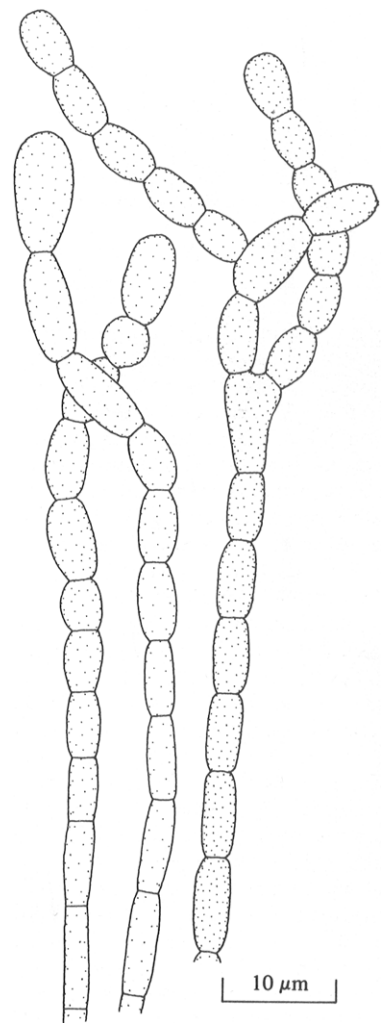

Fig. 13. *Basipetospora variabilis*.

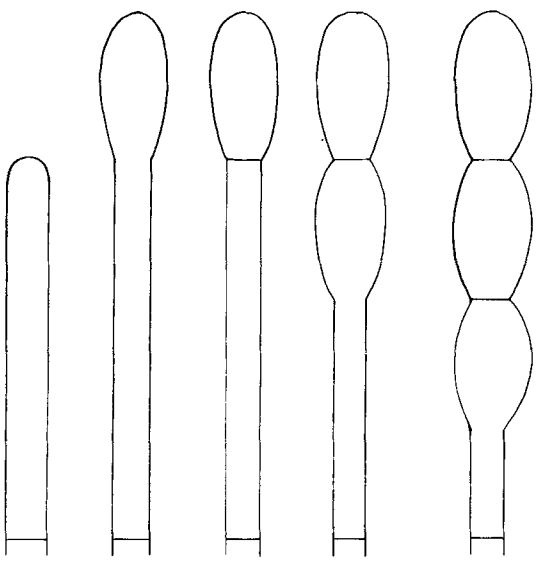

Fig. 14. Hypothetical early development of *Basipetospora variabilis*.

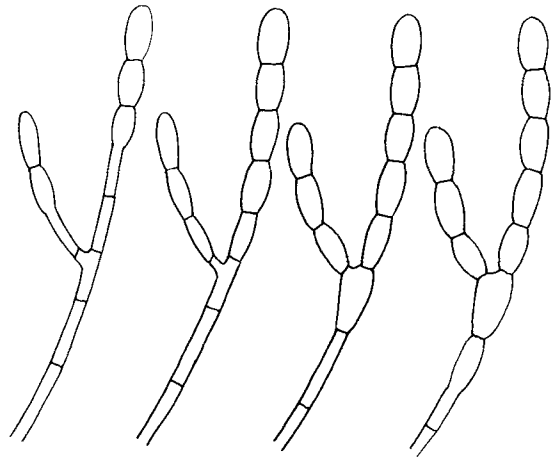

Fig. 15. Hypothetical later development of *Basipetospora variabilis*.

and remains attached (Fig. 14). The first wall-building apex is thus lost into the conidium by the conidiogenous cell, and is not replaced. The conidiogenous cell then proliferates by diffuse wall building below the septum delimiting the first conidium, to produce a second conidium (concurrent proliferation and conidial maturation) which is delimited (conidial delimitation) and remains attached. This sequence of stages can be repeated (alternation of concurrent proliferation/conidial maturation and retrogressive conidial delimitation), and conidia may become detached (conidial secession) at any time.

Thus far development in *B. variabilis* is indistinguishable from that in *B. rubra*. The difference between them becomes apparent only after several conidia have been produced. In *B. variabilis*, unlike in *B. rubra*, the succession of stages to produce new conidia does not stop when the conidiogenous cell is totally converted into conidia: instead it continues by moving retrogressively to the cell below the conidiogenous cell, which becomes a new conidiogenous cell and is in turn gradually converted into conidia. When this cell is totally converted, the succession moves to the cell below in a sequence which can be repeated. In this way, if sufficient conidia are formed, branched chains of conidia will be seen as a result of retrogression to a point beyond the hyphal branching below the original conidiogenous cell (Fig. 15).

In *B. variabilis* therefore the number of conidia produced is not limited by the original length of the conidiogenous cell. The continued retrogression which enables more conidia to be produced can easily be detected with the light microscope simply by comparing the length of a mature chain of conidia with that of a young original conidiogenous cell which has produced only one conidium (the mature chain will be much longer than the young conidiogenous cell), and by looking for branched chains of conidia. As was observed in the comparison of *Cladobotrym varium* and *Trichothecium roseum*, a small difference in development can often have a profound effect on the appearance of a fungus. In the cases of *B. variabilis* and *B. rubra* the small difference is that retrogression continues beyond the original conidiogenous cell in the one, and does not in the other. The profound effect on appearance is that one has branched chains of conidia and the other does not. This however, like the difference in appearance between *C. varium* and *T. roseum*, is not necessarily of great taxonomic significance.

When *B. variabilis* is compared directly with any member of the sympodial, annellidic and false- or no-chain phialidic continuum (e.g. *Belemnospora epiphylla* (Fig. 10) or *Tritirachium oryzae* (Fig. 9)), there are such marked and apparently fundamental differences in development that it is difficult to believe the fungi could be in any way developmentally related. *Belemnospora epiphylla*, for example, produces conidia singly by apical wall building, with percurrent proliferation after each secedes and thus with a growing conidiogenous cell, whereas *Basipetospora variabilis* produces conidia in

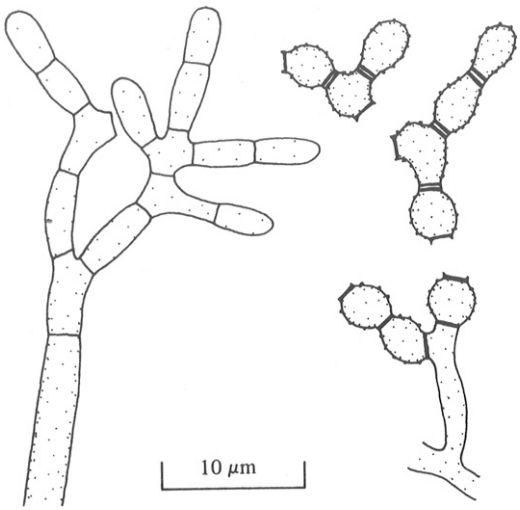

Fig. 16. *Oidiodendron truncatum*.

branched chains by diffuse wall building, with retrogression and hence conidiogenous cells which become smaller. When they are compared indirectly, however, through a series of intergrading examples, as in this paper and Minter *et al.* (1982), it becomes apparent that all are developmentally related. Any two adjacent members of this series have in common almost all developmental features, and differ only slightly in one or two features which, on examination, are clearly not significant in distinguishing these adjacent species developmentally. The apparently fundamental differences observed when *Belemnospora epiphylla* or *Tritirachium oryzae* and *Basipetospora variabilis* are compared are thus clearly only a gradual accumulation of minor differences, and it is evident that continuous intergradation exists between all of these fungi.

Although *Belemnospora epiphylla* or *Tritirachium oryzae* and *Basipetospora variabilis* are very different in appearance, belonging as they do to greatly differing parts of a spectrum, it is agreed that the genera to which they belong share at least one important feature in common, namely all are blastic. Blastic is one of two modes of development which, with few dissenting voices (Ingold, 1981*b*), are generally believed to be of fundamental significance in deuteromycete classification (Cole & Samson, 1979; Ellis, 1971, 1976; Kendrick, 1971; Sutton, 1980). The other is thallic. An example of thallic development will now be described and compared with blastic development of *B. variabilis*. This example, *Oidiodendron truncatum* (Fig. 16), has been the subject of a developmental study from which time-lapse pictures have been published (Cole & Samson, 1979; Kendrick, 1971). It is generally agreed to be thallic (Cole & Samson, 1979; Ellis, 1976; Kendrick, 1971) and to be correctly placed in *Oidiodendron*, a genus which all treatments in recent years have regarded as having thallic development (Cole & Samson, 1979; Ellis, 1971, 1976; Kendrick, 1971; Sigler & Carmichael, 1976).

Oidiodendron truncatum

In *O. truncatum* the conidial ontogeny stages of the second and subsequent conidia are incorporated in the initial activity of the first wall-building apex (Fig. 17). The first conidium is produced holoblastically by the activity of the first wall-building

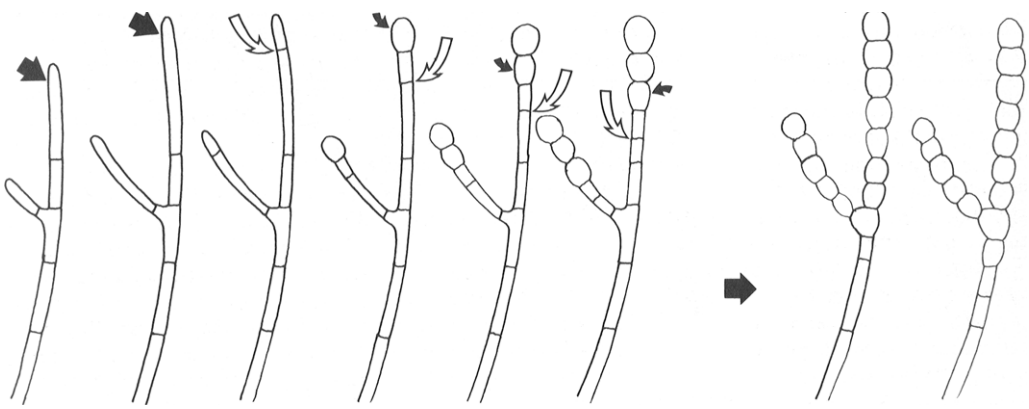

Fig. 17. Development of *Oidiodendron truncatum*. Large arrows point to conidial ontogeny stages. White arrows point to delimitation stages. Small arrows point to maturation stages.

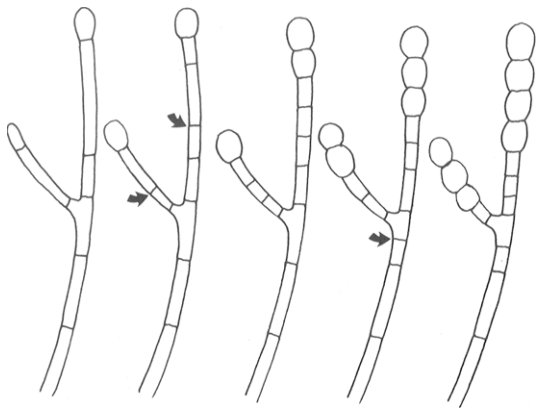

Fig. 18. Development of *Oidiodendron truncatum*. Arrows point to delimitation stages not occurring in exact retrogressive sequence.

apex (conidial ontogeny), is delimited (conidial delimitation) and remains attached. The first wall-building apex is thus lost into the conidium by the conidiogenous cell, and is not replaced. The second conidium is then delimited (conidial delimitation) retrogressively and remains attached, while the first conidium begins to mature slowly (conidial maturation). This sequence of stages can be repeated (retrogressive conidial delimitation followed by retrogressive gradual conidial maturation), and conidia may become detached (conidial secession) at any time following completion of maturation. The succession of stages to produce new conidia does not stop when the conidiogenous cell is totally converted into conidia; instead it continues by moving retrogressively to the cell below the conidiogenous cell, which becomes a new conidiogenous cell and is in turn gradually converted into conidia. When this cell is totally converted, the succession moves to the cell below in a sequence which can be repeated. In this way, if sufficient conidia are formed, branched chains of conidia will be seen as a result of retrogression to a point beyond the hyphal branching below the original conidiogenous cell. Development in *O. truncatum* sometimes deviates from the sequence of stages outlined above in that production of septa which delimit conidia does not always occur in a strict retrogressive sequence (Fig. 18).

In the foregoing account, no new term has been introduced and much of the wording is very similar to that used to describe the conjectured development in *B. variabilis* and even the well-studied development of *B. rubra*. Thus thallic development in *O. truncatum* can be described in a way broadly similar to blastic development in *B. variabilis*. Indeed in many respects development in the two species is the same. Both produce conidia in branched chains as a result of diffuse wall building acting upon walls already built by a wall-building apex. In both the youngest conidium is at the base, and is produced as a result of a sequence involving retrogressive delimitation and conidial maturation, with no replacement wall-building apices. In both, after the original conidiogenous cell is totally converted into conidia, the cell below and then the cell below that in turn become conidiogenous cells and are converted into conidia in a sequence which can be repeated. Therefore there are many more similarities in development between *O. truncatum* and *B. variabilis* than there are between *B. variabilis* and, for example, *Belemnospora epiphylla*.

It is however also important to observe what differences exist between the developments of *O. truncatum* and *B. variabilis*. First, conidial delimitation does not occur in a perfectly regular retrogressive sequence in *O. truncatum*. Secondly, in *O. truncatum* conidial delimitation occurs earlier, so that conidia are usually delimited before the onset of diffuse wall building and always well before diffuse wall building has finished (examination of the time-lapse photomicrographs published by Kendrick (1971) shows some enlargement before delimitation of the pro-penultimate conidium of the right-hand branch). Thirdly and related to the

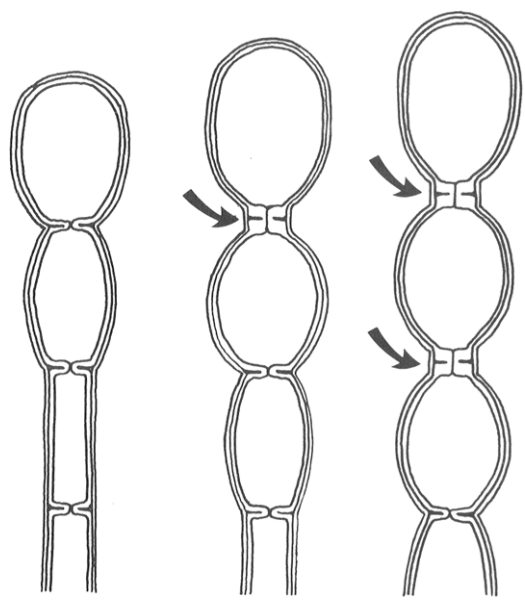

Fig. 19. Marked thickening of delimiting septa in *Oidiodendron truncatum*.

second difference, because delimitation is earlier, second and subsequent conidia are usually produced without the conidiogenous cell proliferating. Fourthly, and not mentioned in the foregoing description, the delimiting septa of *O. truncatum* become markedly thickened as the conidium matures (Fig. 19).

Of these differences, the third need not receive much discussion as it is clearly dependent upon the second, and it has already been suggested in this paper that in some deuteromycetes with retrogressive development the distinction between proliferation and conidial maturation is not greatly significant. It is difficult to comment on the significance of the first difference, because this sort of information is available for only a small number of deuteromycetes, and little is known about such variation. There appear to have been no serious suggestions that the order in which conidia are delimited should be the basis for the fundamental division of deuteromycetes into blastic and thallic. The same can be said about the fourth difference: secondary thickening of septal walls during conidial maturation is well known in many strong chain phialides (e.g. in *Aspergillus* Mich. ex Fr.) and these have always in the past been regarded as blastic. The only difference remaining to be discussed is the second.

In essence, the second difference is that the sequence of developmental stages is altered, so that conidial delimitation occurs earlier when compared to conidial maturation. In the series of intergrading examples considered in this paper and Minter *et al.* (1982), alterations in the sequence of developmental stages have been observed between several adjacent examples. Conidial secession in *Acrogenospora sphaerocephala* (Berk. & Br.) M. B. Ellis is delayed in comparison with *Stigmina angusiana* M. B. Ellis (Minter *et al.*, 1982), and conidial maturation occurs later in *Basipetospora rubra* than in *Trichothecium roseum*. When these examples were examined, it was concluded that the alterations in sequence were of minor significance: it was certainly evident that no fundamental distinction in developmental classification could be based on them. Although the following statement questions the basis for recognizing thallic development as distinct from blastic, there is no intention of entering into a detailed discussion of this subject in the present paper. There appears to be no cogent reason why the alteration in sequence of conidial delimitation between *B. variabilis* and *O. truncatum* should be considered of more significance than any of the other alterations in sequence already encountered, especially in view of the fact that the two species share a great majority of other developmental features. It is therefore concluded that a continuous intergradation exists between thallic fungi such as *O. truncatum* and members of the sympodial, annellidic and false- or no-chain phialidic continuum.

PART 3

Basipetospora chlamydosporis

As with *B. variabilis*, no time-lapse or other developmental study of *B. chlamydosporis* (Fig. 20) is available, and the following account is based on analysis of the original detailed description and illustration by Matsushima (1975). The deductions from this analysis rely greatly on Matsushima's use of the word 'meristem', and may appear at first sight to have little justification. These deductions are, however, backed by further evidence which

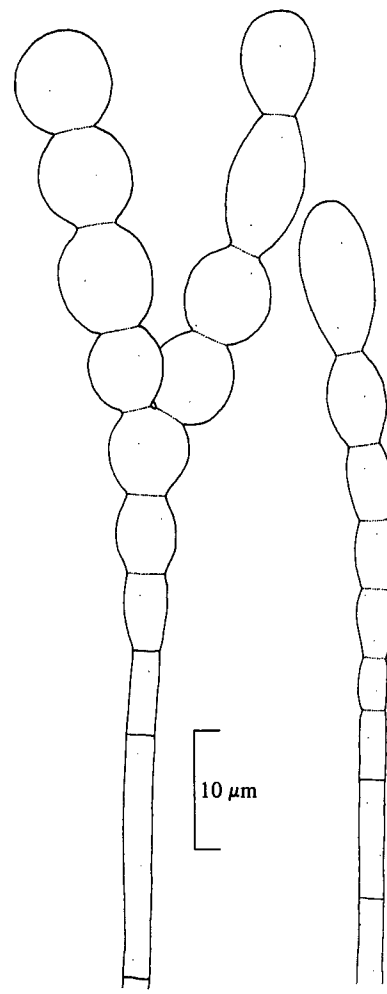

Fig. 20. *Basipetospora chlamydosporis*.

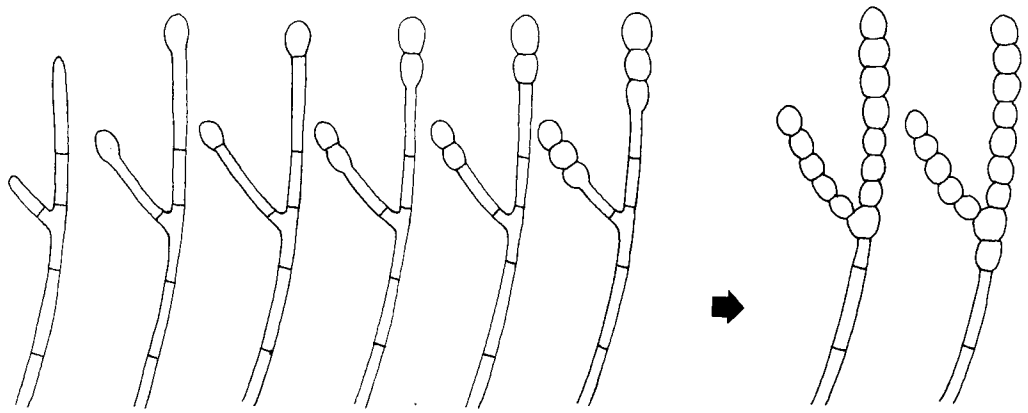

Fig. 21. Hypothetical early development of *Basipetospora chlamydosporis*.

will become apparent when other fungi are analysed later in the text.

In *B. chlamydosporis* the conidial ontogeny stages of the second and some subsequent conidia are incorporated in the initial activity of the first wall-building apex. The first conidium is produced holoblastically by the concurrent activity of the first wall-building apex and diffuse wall building (concurrent conidial ontogeny and conidial maturation), is delimited (conidial delimitation) and remains attached (Fig. 21). The first wall-building apex is thus lost into the conidium by the conidiogenous cell, and is not replaced. The conidiogenous cell proliferates by diffuse wall building below the septum delimiting the first conidium, to produce a second conidium (concurrent proliferation and conidial maturation) which is delimited (conidial delimitation) and remains attached. This sequence of stages can be repeated (alternation of concurrent proliferation/conidial maturation and retrogressive conidial delimitation), and conidia may become detached (conidial secession) at any time. The succession of stages to produce new conidia does not stop when the conidiogenous cell is totally converted into conidia: instead it continues by moving retrogressively to the cell below the conidiogenous cell, which becomes a new conidiogenous cell and is in turn gradually converted into conidia. When this cell is totally converted, the succession moves to the cell below in a sequence which can be repeated. In this way, if sufficient conidia are formed, branched chains of conidia will be seen as a result of retrogression to a point beyond the hyphal branching below the original conidiogenous cell.

Thus far development is indistinguishable from that of *B. variabilis*, and the two species are therefore very similar in appearance, but at this point an important difference can be observed: whereas in *B. variabilis* retrogression continues indefinitely, resulting in more and more of the original hyphae being converted into conidia, in *B. chlamydosporis* after a while the original hyphae cease to be converted into conidia, and retrogression appears to halt. At this point a new wall-building zone comes into being beneath the last conidium to be produced and delimited by retrogression. This wall-building zone produces new wall material

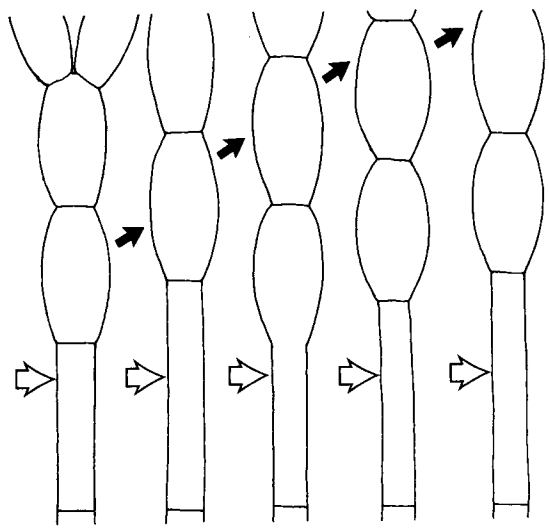

Fig. 22. Hypothetical later development of *Basipetospora chlamydosporis*. Black arrows indicate movement of reference conidium. White arrows indicate position of new wall-building zone.

continuously at its upper end, and it is this wall material rather than the walls of already existing hyphae which forms the walls of all subsequent conidia. A steady state therefore comes about in which the continuous upward conidial ontogeny balances the continuous downward maturation and delimitation, with the result that the conidiogenous cell in which the new wall building zone has arisen ceases to become shorter, but the chain of conidia increases in length (Fig. 22).

Ring wall building

The continuous upward wall production in the final conidiogenous cell of *B. chlamydosporis* is the result of wall-building activity. This activity cannot be described as apical, because there is no cell apex in the region in which it occurs, yet it has obvious similarities with apical wall building in all the examples previously examined: i.e. it produces a new cylindrical wall from a localized region. Because of these similarities, the type of wall building found in *B. chlamydosporis* has rarely been clearly separated in the past from apical wall building. Their differences are however highly significant: the wall building apex produces walls downwards (so that it always remains above the walls it has produced) whereas this wall building zone produces walls upwards (so that it always remains below the walls it has produced). The wall building found in *B. chlamydosporis* is also different from diffuse wall building, because diffuse wall building produces swelling over a wide region by conversion of already existing walls (in any case in *B. chlamydosporis* diffuse wall building can be observed separately causing conidial maturation). The activity in the upper part of the final conidiogenous cell of *B. chlamydosporis* is thus the result of a new and different type of wall building.

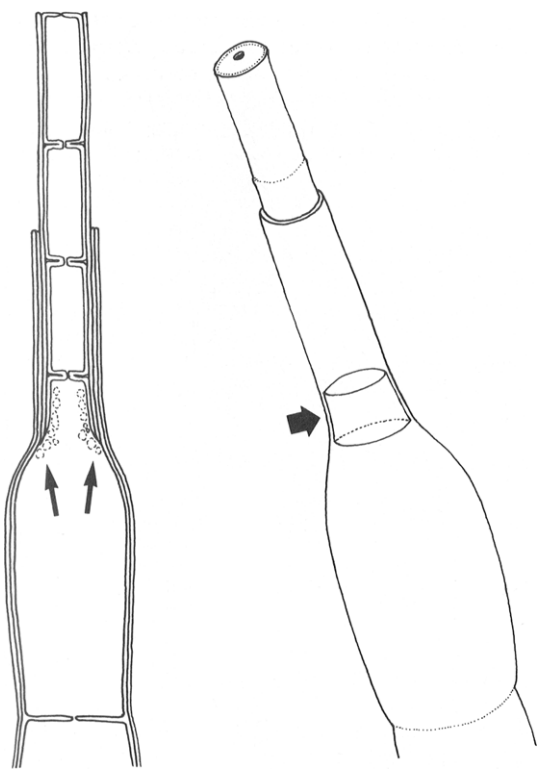

Fig. 23. Distribution of secretory organelles in *Chalara* sp., and semi-diagrammatic illustration of the hypothetical shape of the wall-building ring in *Chalara* sp.

The ultrastructural basis for this wall building cannot be discussed for *B. chlamydosporis* as no transmission electron microscope study is available. It was, however, originally discovered in another hyphomycete, a species of *Chalara* (Cda) Rabenh., and electron microscopy of this species (Hawes & Beckett, 1977*b*) has made it clear that this wall building, like apical and diffuse wall building, can be correlated with variation in concentration of supposed secretory organelles in the cytoplasm. Whereas in diffuse wall building they are distributed randomly and at a low concentration throughout the cytoplasm, and in apical wall building they are concentrated at the cell apex, in the new type of wall building they are concentrated along the sides of the cell (Fig. 23) (Hawes & Beckett, 1977*b*). On account of the shape of this distribution, the new type is described here as 'ring wall building' (the word ring being used here either as an adjective or a noun, and intended to imply that the wall building is highly localized). The ultrastructural explanation of the three different types of wall building makes it very likely that they all intergrade. It should therefore be remembered that each is no more than a convenient highlight in a spectrum.

In ring wall building, as in apical and diffuse wall building, the distribution of the organelles cannot be detected using light microscopy. It is however possible to deduce whether or not ring wall building is in operation from the appearance of a fungus under the light microscope. Just as apical wall building is characterized by sympodial growth, annellidic lines across the conidiogenous cell or periclinal thickening, and diffuse wall building is characterized by deviation in shape from the cylindrical, so the presence of ring wall building can be deduced by observation of true chains which grow in length, with the youngest conidium at the base, from a conidiogenous cell which remains the same size. In the following descriptions and discussions, when ring wall building is mentioned,

its presence has been deduced using this criterion, unless specifically stated otherwise.

In apical wall building, the wall-building apex always remains above the walls it has produced. It therefore moves up into any conidium produced and is lost by the conidiogenous cell. In fungi with conidiogenous cells in which apical wall building is the only means of producing new walls, the production of more than one conidium from a conidiogenous cell is dependent either on continuous retrogression (as in *B. variabilis*) or on a replacement wall-building apex coming into existence after each conidium is produced. Replacement wall-building apices cause not only conidial ontogeny but also proliferation, and this explains why proliferation is unavoidable in the sequence of developmental stages in all fungi of the sympodial, annellidic and false- or no-chain phialidic continuum. By comparison, in ring wall building the wall-building ring always remains below the walls it has produced. The ring does not move up into the conidium and is thus not lost by the conidiogenous cell when a conidium is delimited. Once a conidiogenous cell has been modified to produce a wall-building ring, it can produce a succession of conidia without further proliferation. Recognition of the wall-building ring is thus considered here to be the step of crucial importance towards understanding how true-chain phialides can produce many conidia without intervening proliferations.

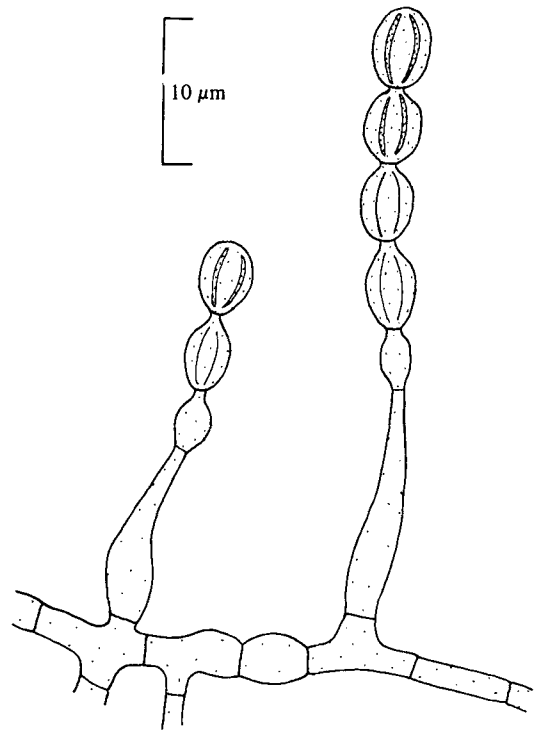

Fig. 24. *Sagenomella striatispora.*

Sagenomella striatispora

This account of development of striated conidia in *S. striatispora* (Onions & Barron) W. Gams (Fig. 24) interprets the detailed developmental studies by light microscopy of Subramanian & Pushkaran (1975). In *S. striatispora* the first conidium is produced holoblastically by the concurrent activity of the first wall-building apex, and diffuse wall building (concurrent conidial ontogeny and conidial maturation), is delimited (conidial delimitation) and remains attached (Fig. 25). The first wall-building apex is thus lost into the conidium by the conidiogenous cell, and is not replaced. The conidiogenous cell immediately produces a wall-building ring below the septum delimiting the first conidium, and the activity of this ring with concurrent (or more likely slightly delayed) diffuse wall building produces the second conidium (conidial ontogeny with slightly delayed conidial maturation) which is delimited (conidial delimitation) and remains attached. This sequence can then be repeated (alternation of conidial ontogeny (by ring wall building)/slightly delayed conidial maturation and retrogressive delimitation) and conidia may become detached (conidial secession) at any time.

The development of *S. striatispora* is obviously very similar to that of *B. chlamydosporis*. Both produce conidia in true chains with the youngest at the bottom. In both the chains begin by the usual holoblastic production of the first conidium, and in both chain production eventually occurs as a result of ring-wall building. The main difference between them is that in *S. striatispora* the wall-building ring comes into operation immediately after the first conidium has been produced, whereas in *B. chlamydosporis*, the appearance of the wall-building ring is delayed until after the original and a variable number of substitute conidiogenous cells have been converted into conidia. Thus, whereas in *B. chlamydosporis* the original conidiogenous cell (i.e. the one from which the first conidium was produced) and the final conidiogenous cell (i.e. the one which has the wall-building ring) are different, in *S. striatispora* the two are the same. The difference in developmental terms between these two species is thus in essence one of the timing of appearance of the wall-building ring.

Several similar differences in timing have already been observed in this paper and the work of Minter

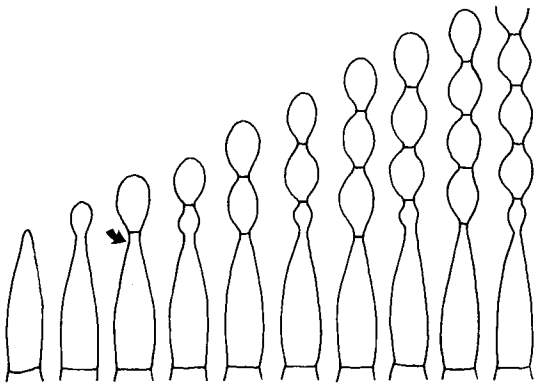

Fig. 25. Development in *Sagenomella striatispora*. Arrow locates wall-building ring.

et al. (1982). None has been considered to be of great taxonomic significance. There appears no reason why the present case should be unlike the others. Indeed, like the others, the present difference in timing, although minor, has a profound effect on the appearance of *S. striatispora* when compared with *B. chlamydosporis*. In *B. chlamydosporis* retrogression has often travelled beyond the hyphal branches below the original conidiogenous cell before the wall-building ring comes into operation, so that branched chains of conidia are frequently observed. In *S. striatispora* by comparison the wall-building ring comes into operation at a very early stage, and once it is supplying upwards continuous new wall material, branched chains cannot develop.

In the second part of this paper the observation was made that deuteromycetes from widely different parts of the spectrum of developmental variation can appear to differ fundamentally when compared directly with each other, and that the true affinities between them can only correctly be assessed when the intergrading examples between them are also taken into consideration. This same observation can be made about *S. striatispora*. When compared with, for example, *Belemnospora epiphylla* (Fig. 10), the differences between the two appear fundamental; but after intergrading examples have been examined, it is evident that these apparently major differences are only a gradual accumulation of a host of minor differences. Thus a continuous intergradation exists between *S. striatispora* and fungi of the sympodial, annellidic and false- or no-chain phialidic continuum.

It is interesting to recall the three ways in which *Basipetospora rubra* (the last fungus to be considered in the first part of this paper) was said to differ from true-chain phialidic species. When *S. striatispora* is examined with these three ways in mind, it will be seen to differ from true-chain phialidic species in only one, being the same in respect of the other two: that is, *S. striatispora* has conidiogenous cells which can produce conidia in numbers not limited by the original size of the conidiogenous cells, and it can produce them without intervening proliferation, but the enteroblastic mode of development is nowhere present. It is clear that development in *S. striatispora* is more similar to the true-chain phialide than is development in *B. rubra*. Development of the true-chain phialide will now be described and compared with development in *S. striatispora*, using as an example *Aspergillus clavatus*.

Aspergillus clavatus

This account of development in *A. clavatus* (Fig. 26) is based on, and interprets, the detailed transmission electron microscope study by Hanlin (1976). In *A. clavatus* the first conidium is produced holoblastically by the activity of the first wall-building apex (conidial ontogeny) which lays down in this conidium and at the top of the conidiogenous cell an extra inner wall (Fig. 27, arrow: this wall is shown as double-layered in accordance with the drawing convention in use here (Minter *et al.*, 1982), but in the transmission electron micrographs on which this drawing is based only one layer can be detected). This new inner wall is not present in the lower part of the conidiogenous cell. The first conidium is then delimited (conidial delimitation). The first wall-building apex ceases to operate, and is not replaced; instead, a wall-building ring occurs below the septum delimiting the first conidium. This wall-building ring lays down wall material on the inner wall arrowed in Fig. 27, causing it to grow upwards and forcing the outer wall between the first conidium and the conidiogenous cell to break, thus producing a collarette (Fig. 27, arrowhead) (part of the stage of secession of the first conidium). The first conidium still remains attached however by the inner wall. Continued wall production by the wall-building ring then produces the walls of the second conidium (conidial ontogeny), which is delimited (conidial delimitation) and remains attached. This sequence of stages can be repeated (alternation of conidial ontogeny by ring-wall building and retrogressive conidial delimitation), conidia gradually mature (retrogressive conidial maturation with associated marked thickening of delimiting septa) and may become detached (conidial secession) at any time after maturation.

Development in *A. clavatus*, as interpreted here,

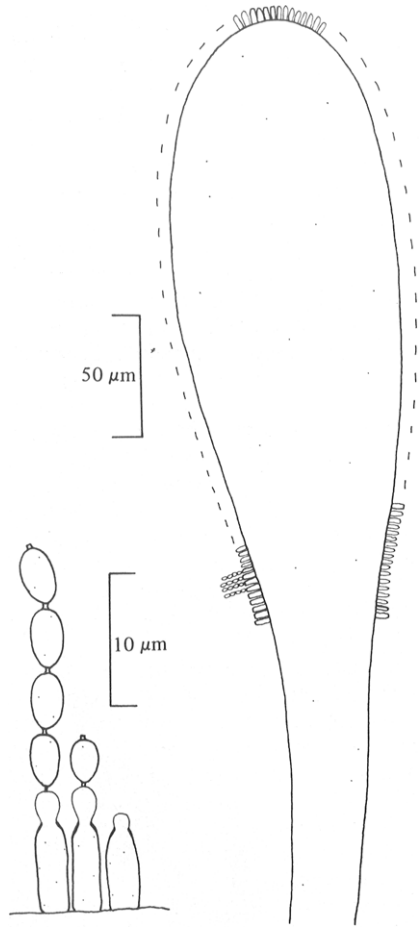

Fig. 26. *Aspergillus clavatus*.

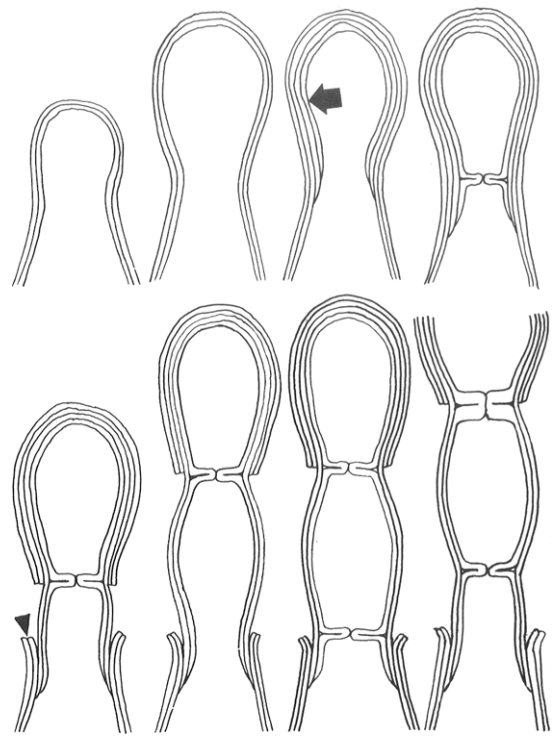

Fig. 27. Development in *Aspergillus clavatus*. Arrow locates new (double-layered) inner wall. Arrowhead locates collarette.

is very similar to development in *S. striatispora*. Both produce their first conidium holoblastically by the activity of the first wall-building apex, and then both switch to produce all subsequent conidia by ring-wall building. Conidia are in true chains with the youngest at the base, produced from conidiogenous cells which remain the same length, and in both the original conidiogenous cell (i.e. the one from which the first conidium was produced) is the same as the final conidiogenous cell (i.e. the one with the wall-building ring). *Sagenomella striatispora* is thus obviously developmentally more similar to *A. clavatus* than to *Belemnospora epiphylla* or any other member of the sympodial, annellidic and false- or no-chain phialidic continuum.

Aspergillus clavatus and *S. striatispora* do, however, differ in some respects. Firstly, conidial maturation is slightly later in *A. clavatus*, and is associated with some thickening of the delimiting septal walls. This difference has already been shown as not significant in other examples and is not considered significant here either. Secondly, in *A. clavatus* a new inner wall is produced inside the first conidium and at the top of the conidiogenous cell, whereas in *S. striatispora* no such wall has been observed. Thirdly, in *A. clavatus* the wall-building ring produces growth of this inner wall only, necessitating partial secession of the first conidium. Furthermore, in *A. clavatus* walls of second and subsequent conidia are produced by the wall-building ring operating on this inner wall only, with the result that there is a discontinuity between the top of the conidiogenous cell wall and the wall of the conidium currently being produced (Fig. 28). In *S. striatispora* however no such discontinuity can be observed with the light microscope (Fig. 28) (Subramanian & Pushkaran, 1975). This provides strong evidence that in *S. striatispora* the second and subseqent conidia are produced by action of the wall-building ring on the original conidiogenous

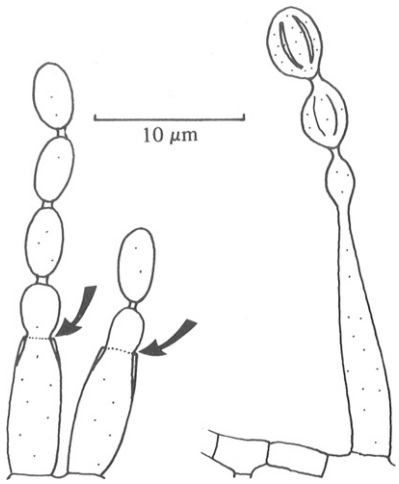

Fig. 28. Comparison of *Aspergillus clavatus* (arrows indicate discontinuity of walls at apices of conidiogenous cells) and *Sagenomella striatispora* (no discontinuity observable).

cell wall, that no new inner wall is produced, and that there is no partial secession of the first conidium before production of the second.

The difference in development between *A. clavatus* and *S. striatispora* thus basically concerns the presence or absence of a new inner wall. When this inner wall is absent there is no partial secession of the first conidium, no collarette and no discontinuity between the conidiogenous cell wall and the wall of the conidial chain: i.e. the enteroblastic mode has no part in the development. When the inner wall is present however there is partial secession of the first conidium, a collarette and discontinuity between the conidiogenous cell wall and the wall of the conidial chain: these are all features indicating the presence of the enteroblastic mode in the development. It follows therefore that the presence or absence of the new inner wall determines whether the enteroblastic mode is or is not present, and hence whether or not the fungus has true-chain phialides.

The presence of a new inner wall in true-chain phialides is, like ring-wall building, a feature which has only recently been discovered. It has been reported with evidence from transmission electron micrographs only in *A. clavatus* (Hanlin, 1976), the *Chalara* anamorph of *Ceratocystis adiposa* (Butl.) C. Moreau (Hawes & Beckett, 1977*b*) and *Thielaviopsis basicola* (Berk. & Br.) Ferraris (Hawes & Beckett, 1977*c*). There are also, however, similar accounts based on light microscopy of development of *Chalara* and *Thielaviopsis basicola* which provide additional evidence strongly suggestive that this type of development is more widespread in species with true-chain phialides (Hawes & Beckett, 1977*a*, *c*; Ingold, 1981*a*); the work of Hawes & Beckett using fluorescent staining techniques also provides further evidence for the existence of ring-wall building. It is very difficult to assess whether the production of this new inner wall is significant either developmentally or taxonomically.

What is certain, however, is that the difference is not necessarily great between development in true-chain phialides and in fungi with conidia in true chains produced holoblastically with the youngest at the top. This has been very clearly demonstrated in *Aspergillus aureolatus* Muntañola-Cvetković & Bata and its *Cladosarum* Yuill & Yuill mutant (Madelin, 1979; Vujičič & Muntañola-Cvetković, 1973) and a wide variety of other true-chain-phialidic species and their mutants in these and similar genera (Clutterbuck, 1969; Raper & Fennell, 1953; Yuill & Yuill, 1938; Zachariah & Metitiri, 1970, 1971). The case of *A. aureolatus* and its *Cladosarum* mutant will be discussed here as an example.

Transmission electron micrographs published by Vujičič & Muntañola-Cvetković (1973) show that in normal growth *A. aureolatus* produces true-chain phialides (Fig. 29). The mutant, however, when grown at 26 °C, produces conidia in true chains with the youngest conidium at the top (Fig. 29). These conidia remain thin-walled unless the temperature is lowered to 18°, when the terminal conidium in each chain becomes thick walled and indistinguishable from conidia of the wild type. Madelin (1979) discussed various possible explanations for these observations, and concluded that the unusual development of the mutant is a result of its failure to produce beneath conidia delimiting septa characteristic of the wild type. While this explanation is accepted as of significance, it is also suggested that the difference in appearance between mutant and wild type can be explained much more satisfactorily in terms of wall building. In the wild type, ring-wall building comes into operation immediately after the first conidium is produced, and diffuse wall building causes conidial maturation. In the mutant, the first wall-building apex remains active and produces an apically elongating conidial chain in which much of the diffuse wall building is suppressed.

If this interpretation is correct, at least some fungi with true-chain phialides can be made to keep their apical wall building operational instead of switching to ring-wall building by mutation of a small number of genes (Madelin, 1979) or even simply by manipulation of temperature. Since the

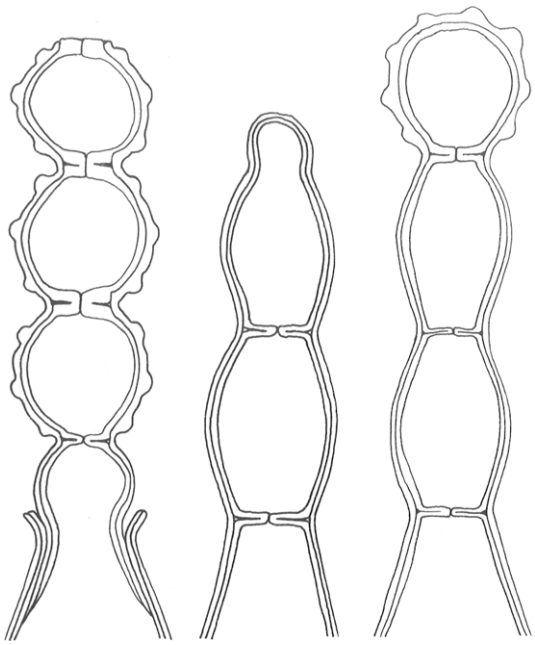

Fig. 29. *Aspergillus aureolatus*. A. Normal development of true-chain phialides. B. Mutant development at 26 °C producing true chains of thin-walled conidia with the youngest spore at the apex. C. Mutant development initially at 26 °C, later at 18 °C: the apical spore of the true chain becomes thick walled, and indistinguishable from conidia of the wild type.

presence of ring-wall building in true-chain phialides has been correlated in this paper with the presence of a new inner wall, it seems highly likely that, if a switch from producing to not producing a wall-building ring can easily be made, a similar switch to not producing a new inner wall could be made with the same facility. Madelin (1979) made the following observation about such switches: 'if fungi in nature occasionally make at least some of the changes between these... modes, the taxonomic significance to be attached to their possession diminishes'. This is strongly supported, and it is believed that the presence of a new inner wall in the true chain phialide is not necessarily any greater a difference developmentally than any other difference already observed between adjacent members of a continuum. When it is remembered that *Sagenomella striatispora* can produce its conidia in true chains by holoblastic ring-wall building (as described above) or by enteroblastic ring-wall building (i.e. as a true-chain phialide) (Subramanian & Pushkaran, 1975), and so can the *Thielaviopsis* anamorph of *Ceratocystis paradoxa* (Dade) C. Moreau (Nag Raj & Kendrick, 1975), this belief becomes considerably substantiated. It is therefore concluded that continuous intergradation exists between development in, for example, *Basipetospora rubra* and species with true-chain phialides. It follows from this and from the conclusion of the second part of this paper that continuous intergradation also exists between fungi with true-chain phialides and species with development which is generally described as thallic. In the fourth part of this paper some other relevant examples will be examined to show how this intergradation is not merely based on the few fungi examined so far.

PART 4

Geotrichum candidum

This account of development in *G. candidum* Link (Fig. 30) is based on the time-lapse study by Cole & Kendrick (1969). In *G. candidum* the conidiogenous cell is produced by the activity of the original wall-building apex (Fig. 31), incorporating the conidial ontogeny stages of all conidia. This wall-building apex then ceases to function and is not replaced, so that at this point the structure has the appearance of a hypha which has ceased to grow. Conidial delimitation then takes place by the formation of septa in an apparently random order. This delimitation is not restricted to the apical conidiogenous cell, but can be observed in all parts of the hypha so that, as in *B. variabilis*, branched chains of conidia occur. There is no conidial

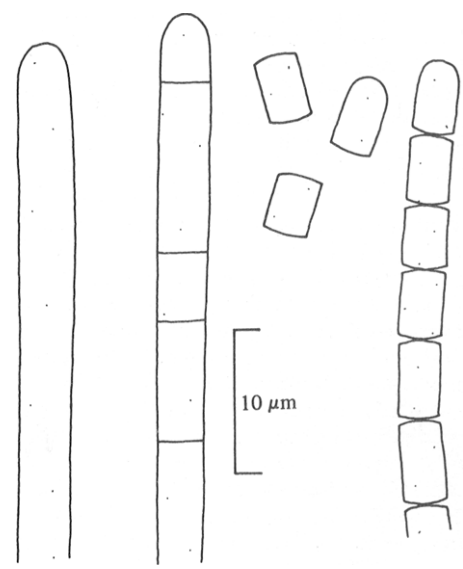

Fig. 30. *Geotrichum candidum*.

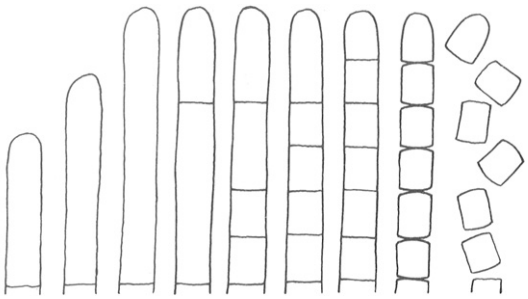

Fig. 31. Development in *Geotrichum candidum*.

maturation, and conidial secession can happen at any time after conidial delimitation.

Production of conidia by *G. candidum* is thus similar to that by *Oidiodendron truncatum* (the thallic species examined in the second part of this paper), except for the absence of conidial maturation and randomness of conidial delimitation. Since all major treatments in recent years have agreed that both of these species have thallic development (Cole & Samson, 1979; Kendrick, 1971; Sigler & Carmichael, 1976), it seems reasonable to conclude that neither of these exceptions is of significance in determining whether or not a fungus has thallic development. As has already been stated, it is not intended in this paper to undertake a detailed discussion of what constitutes the fundamental distinction between blastic and thallic modes of development. It is nevertheless interesting to compare this supposedly thallic development of *G. candidum* with the development of species of *Chalara* (Cda) Rabenh. which recent major treatments have described as phialidic (Cole & Samson, 1979; Nag Raj & Kendrick, 1975).

Chalara

Developmental studies of a variety of species of *Chalara* have been made (Hawes & Beckett, 1977*a*, *b*, *c*; Ingold, 1981*a*; Nag Raj & Kendrick, 1975), and these collectively form the basis of the following account. In species of *Chalara* (Fig. 32) the conidiogenous cell is produced by the activity of the original wall-building apex (Fig. 33). When this wall-building apex ceases to function, a new inner wall (double-layered in accordance with the drawing convention in use (Minter *et al.*, 1982)) is immediately laid down, as in *Aspergillus clavatus*, at the top of the conidiogenous cell. Unlike in *A. clavatus*, however, this inner wall is extensive, being produced not just at the apex, but also retrogressively well down the sides of the conidiogenous cell, until often more than half of the original conidiogenous cell wall is lined by this new inner wall. This new inner wall, although still totally enclosed by the original outer wall of the conidiogenous cell, is destined to be the cell walls of the first conidia (conidial ontogeny); accordingly, as it is laid down, retrogressive conidial delimitation follows, and conidia can be discerned forming within the unbroken original outer wall of the conidiogenous cell. After a while the retrogressive laying down of the new inner wall comes to a halt, and at its lowest part a wall-building ring is formed, which then adds continuously to it in an upward direction (conidial ontogeny). At this point the original outer wall of the conidiogenous cell ruptures almost at the apex, leaving on the uppermost conidium a small cap of wall material sometimes visible with the light microscope. The activity of the wall-building ring causes the chain of conidia (marked off by continuous retrogressive

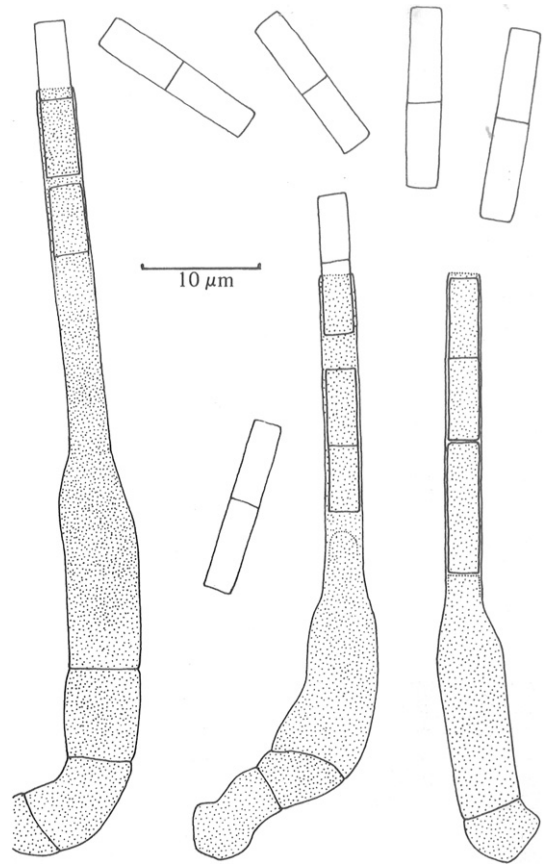

Fig. 32. *Chalara hughesii*.

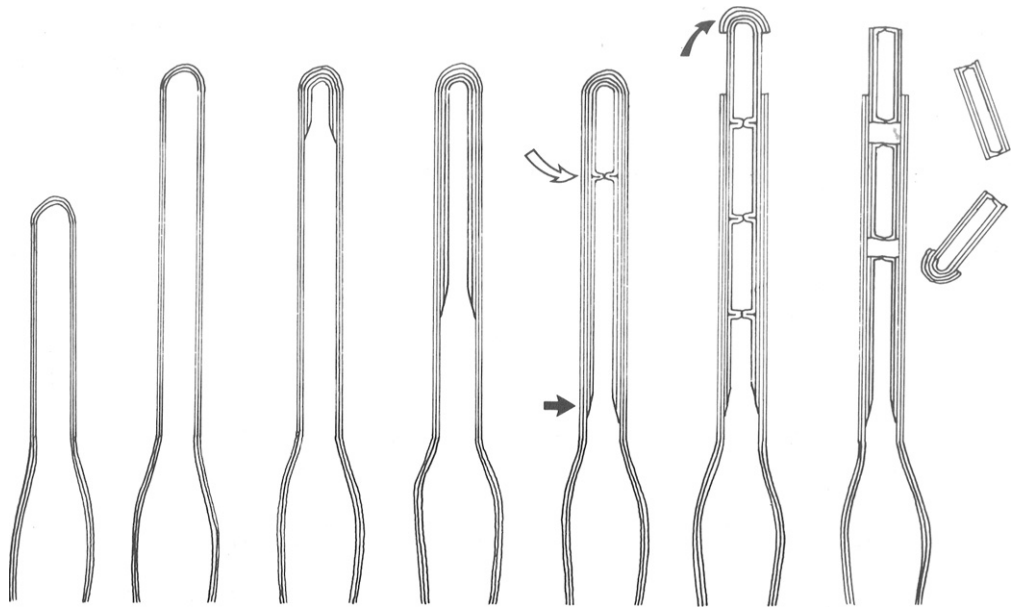

Fig. 33. Development in *Chalara* sp. Straight black arrow locates wall-building ring. White arrow indicates conidial delimitation. Curved black arrow locates cap.

delimitation) to be pushed out of the cylindrical collarette formed by the original outer wall. After leaving the collarette, a small degree of conidial maturation may be observed in some species, but is normally absent, and conidial secession can occur at any time, sometimes even before emergence of the conidium from the collarette.

From the foregoing account development of *Chalara* species is fundamentally similar to that of *A. clavatus*. The main distinctions are that in species of *Chalara* conidial maturation is usually absent, and more inner wall is laid down before the production of a wall-building ring, so that collarettes are much larger: both of these are merely differences of degree. What is interesting, however, is the striking similarity in appearance between conidia of *Chalara* and *G. candidum* and also, apart from the branching in one, between conidial chains of these two taxa (compare fig. 4.25 with fig. 7.8 in Cole & Samson (1979)). The similarity occurs because conidia are formed by the same cocktail of developmental stages: in both a replacement wall-building apex is lacking, conidial maturation is absent, and conidia can only be recognized after the activity of conidial delimitation on a cylindrical region of fertile hypha. This similarity in appearance, of course, no more necessarily indicates that the two taxa are closely related phylogenetically than did the dissimilarity between *Cladobotryum varium* and *Trichothecium roseum* indicate the opposite. What this similarity does indicate, however, is that something is wrong with the present rigid practice of categorizing fungi as either thallic or blastic: because this practice, while purporting to be based on developmental principles, fails to recognize the considerable number of way in which these two taxa are developmentally analogous. *Geotrichum candidum* does, certainly, differ from species of *Chalara* in a number of highly significant developmental features. Examination of the next two relevant examples shows, however, how unsatisfactory it would be to try to use such differences to distinguish the thallic and blastic modes of development.

Wallemia sebi *and* Vouauxiella lichenicola

This account of development in *W. sebi* (Fr.) Arx (Fig. 34) is based on the interpretation by Cole & Samson (1979); the detailed electron microscope studies by Madelin & Dorabjee (1974) are also taken into account. In *W. sebi* the conidiogenous cell is produced by the activity of the first wall-building apex (Fig. 35). The first wall-building apex then ceases to function, and a new inner wall is immediately laid down at the top of the conidio-

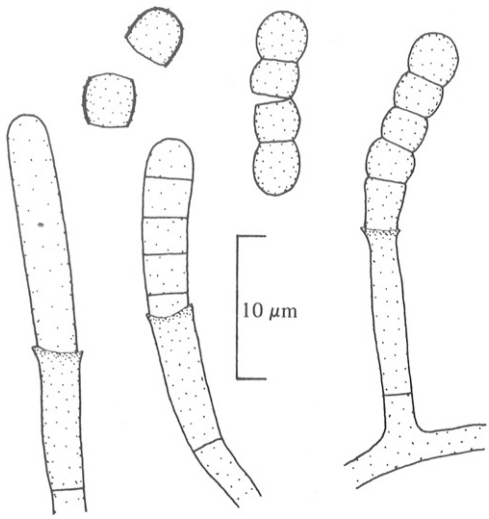

Fig. 34. *Wallemia sebi.*

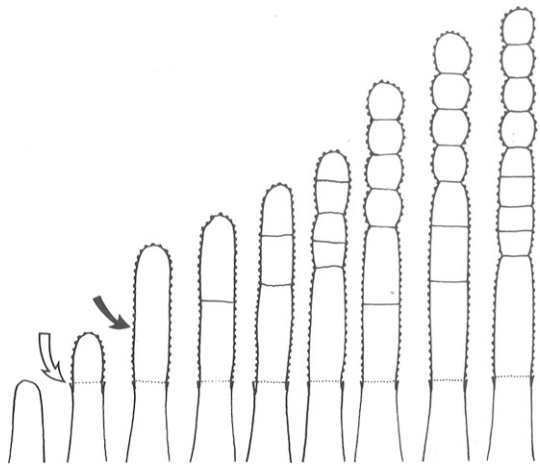

Fig. 35. Development in *Wallemia sebi*. White arrow locates collarette. Black arrow locates wall-building ring.

genous cell by a new wall-building apex. This new inner wall then grows up through the original outer wall, which ruptures, resulting in a collarette. The new inner wall is deduced from the presence of the collarette (the validity of this deduction will be assessed in the discussion) and from the abrupt transition at this point between rough and smooth ornamentation. A small amount of original outer wall material may be carried away as a cap by the upward-growing inner wall. After a short time the new wall-building apex ceases to function and is replaced by a wall-building ring around the inside of this new inner wall a little above the collarette. The activity of this wall-building ring now provides the stage of conidial ontogeny. After new wall material sufficient for several conidia has been produced by the wall-building ring, conidial delimitation begins in a regular but not strictly retrogressive order. During and following conidial delimitation, a small amount of diffuse wall building (conidial maturation) occurs and, after that, conidial secession may occur at any time. When several conidia have been produced in this fashion, the wall-building ring may cease to function, and may be replaced by a new wall-building apex (sympodial or percurrent proliferation). After some growth, the resultant elongated conidiogenous cell usually produces a new inner wall again, and the sequence of developmental stages is repeated, producing more conidia. The development of *V. lichenicola* (Linds.) Petrak & Sydow, to judge from the appearance of its conidiogenous cells and conidia, is an example in the coelomycetes of a similar type of development to that of *W. sebi* (Morgan-Jones, 1971; Sutton, 1980).

Wallemia sebi and *V. lichenicola* have both in the past been classified as thallic (Ellis, 1971; Sutton, 1980), but it has subsequently become obvious to a number of researchers that this is far from satisfactory. At least in the case of *W. sebi* reclassification close to phialidic species such as *Sporoschisma* Berk. & Br. (a genus similar in development to *Chalara*) has been proposed (Madelin & Dorabjee, 1974). The uncertainty surrounding the taxonomic positions of both species clearly exists because each has certain developmental features which resemble those of fungi conventionally regarded as thallic, and others which resemble those of fungi conventionally regarded as phialidic. Thus, like the thallic species *Oidiodendron truncatum*, conidial maturation is mostly delayed until after conidial delimitation, which itself follows conidial ontogeny irregularly and only after an interval; similarly, like the true-chain-phialidic species *Aspergillus clavatus*, they produce a wall-building ring and have at some point in their development the enteroblastic mode. In other words, both *W. sebi* and *V. lichenicola* have a combination of developmental features which makes them intermediate between thallic and true-chain-phialidic species. They are thus fungi with, in the words of the title of this paper, thallic phialides.

DISCUSSION

Conidial chains

The terms 'true' and 'false', used here and by Minter *et al.* (1982) to describe chains of conidia, were originally proposed by Subramanian (1972), who defined them on the basis that in true chains 'the wall around the successive conidia in the chain is a continuum', whereas in false chains it is not. Gams (1978) rejected Subramanian's terminology, but made a similar attempt to distinguish between 'connected' and 'disconnected' chains which he defined by the presence or absence of connectives (i.e. secondary thickening of septal walls during conidial maturation). These two sets of terms, 'true' and 'false', 'connected' and 'disconnected', are now evaluated and compared.

Aspergillus clavatus has chains of conidia which adhere by connectives, with a continuous outer wall between adjacent conidia (Fig. 36). Such chains are obviously 'true' chains in the sense of Subramanian (1972) and, although Gams (1978) did not recognize chain development of this type, it seems reasonable to suppose on the basis of the examples he used that such chains would fall into his 'connected' category. Similarly the fungi examined by Minter *et al.* (1982) which have conidia not adhering by any wall connexions (Fig. 37) clearly fall into Subramanian's 'false' and Gams' 'disconnected' categories. There is therefore a general correspondence between the different ways of classifying chains. It is not however a complete correspondence, as the following example shows.

Gams (1978) illustrated a third type of conidial chain produced by a phialide, shown here using the transmission electron microscope drawing convention in Fig. 38. There is no continuity of the outer wall between adjacent conidia, but there is continuity between the inner wall of the older and the outer wall of the younger of the adjacent conidia. Such development, in this example, also forms a chain in which there are connectives, but they are in the form of an incomplete wall continuity between adjacent conidia. Such a chain is 'connected' in Gams' sense, because his chain categories are defined by the presence or absence of connectives. It is, however, 'false' in Subramanian's sense, because the outer wall is not continuous between two adjacent conidia.

There are thus at least three categories of chains to describe (Figs 36, 37, 38), and since there are only two sets of terms, each containing two words, it is obvious that one set alone will not be enough to describe the three categories, especially since each set covers ground which although similar is not identical. It is believed in this paper that there is good reason to retain both sets at least in concept.

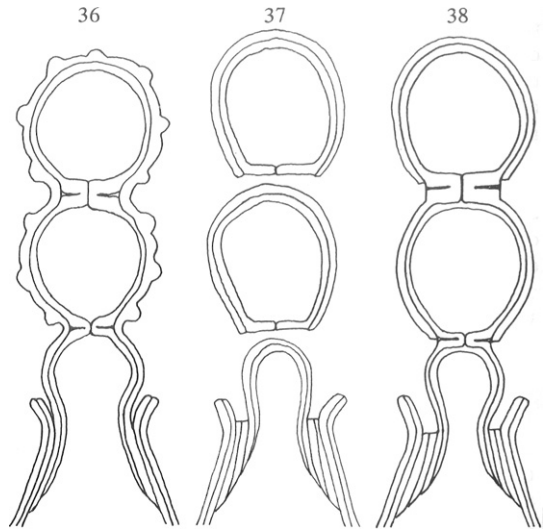

Fig. 36. True chain of conidia with connective joining upper conidia.

Fig. 37. False chain of conidia with no connective.

Fig. 38. False chain of conidia with connective joining upper conidia.

The actual words 'connected' and 'disconnected' are misleading, however: some true chains, e.g. those of *Chalara* species (Fig. 39), have adjacent conidia with firm wall connexions but without connectives, and in these cases the highly specific use of words like 'connected' would be confusing because such words are also used in a very general sense in the English language. It is proposed that these words are replaced with the more descriptive and precise terms 'with connectives' and 'without connectives' respectively.

It is important to note that these terms describe morphological features only. It is therefore impossible to deduce the way in which a chain has developed solely from the combination of terms used to describe the appearance of the finished chain. Thus false chains without connectives (Fig. 37) could be produced by a false- or no-chain phialide (e.g. *Mariannaea elegans* (Cda) Samson) or by an annellidic conidiogenous cell (e.g. in *Scopulariopsis brevicaulis* (Sacc.) Bain.). Similarly true chains without connectives could be produced by ring-wall building (e.g. *Chalara* species), by replacement wall-building apices (e.g. *Trichothecium roseum*) or by simple retrogressive delimitation (e.g. *Basipetospora rubra*). Many more examples could be cited.

By the same token, it is also impossible to deduce the final appearance of a chain solely from the combination of terms used to describe its mode of development. Thus, for example, although a combination of retrogressive delimitation with replacement of wall-building apices can produce a true chain without connectives, e.g. *Trichothecium roseum*, it can equally well produce no chain at all, e.g. *Cladobotrym varium*. A full description of any deuteromycete should therefore contain not only details of its mode of development but also, distinguished from these, an accurate account of its actual physical appearance.

Periclinal thickening

Phialides producing false chains with connectives differ from those producing true chains with connectives because they lack a wall-building ring and there is no outer-wall continuity between adjacent conidia. It is often, however, not possible reliably to tell with the light microscope whether or not outer-wall continuity is present, and so in certain critical cases the problem of determining whether a phialidic conidial chain with connectives is true or false depends on telling whether or not a wall-building ring is present. In theory this can be done by looking for periclinal thickening (Sutton, 1980): its presence indicating a succession of replacement wall-building apices and its absence indicating a wall-building ring. Unfortunately, in practice a certain degree of periclinal thickening can often be observed in fungi such as *A. clavatus*, which are firmly established as having true chains with connectives. It is not known why, but it is possible to speculate. For example, it may perhaps be that conidial production in such fungi has a marked 24 h periodicity, conidia being produced during the day and not during the night. If this were the case, it might well be necessary for the fungus to produce a replacement apex and then immediately a new wall-building ring each day as conidial production recommences. Periclinal thickening would then build up over several days. This sort of phenomenon is unlikely to have been observed, however, by researchers carrying out transmission electron microscope studies, simply because the fungal cultures used in such studies tend (as Madelin (1979) pointed out) to be grown in highly artificial conditions which may make impossible those pauses in development which might have occurred under natural conditions. Until further criteria become available the distinction between true and false chains with connectives (while admittedly of great value) should be applied with caution.

Collarettes

The manner in which collarettes are produced has been explained in Minter *et al.* (1982) and this paper by two different theories. The first explanation, attributed by Minter *et al.* (1982) to Cole & Samson (1979) is illustrated in Fig. 39. According to this theory, the collarette in anatomical terms is part of the outer wall of the first conidium, and this outer wall is left behind, still attached to the conidiogenous cell, when that conidium secedes. If this is correct, then the first conidium, over much of its surface, has as an integument only its original inner wall. The second explanation, used here, is shown in Fig. 40. According to this explanation the collarette is composed of the same inner and outer walls as the conidiogenous cell, and the first conidium has inner and outer walls both of which are totally new and not the same as any wall of the collarette.

The differences between these two explanations may appear at first sight minute and trivial, but careful reflection shows that they lead to profoundly different conclusions. If the first explanation is correct, then the collarette is merely a by-product of conidial ontogeny, and the first conidium to be produced is holoblastic. In developmental terms, therefore, as Minter *et al.* (1982) pointed out, this conidium would not differ from any subsequently produced conidium. If the second explanation is correct, however, the collarette is not merely a by-product of conidial ontogeny. Instead it is the result of wall-building activity actually preceding conidial ontogeny of the first conidium. The first conidium is accordingly produced enteroblastically and thus differs in developmental terms from succeeding conidia which have holoblastic conidial ontogeny.

It is, of course, possible that among the vast array of deuteromycetes examples will be found which

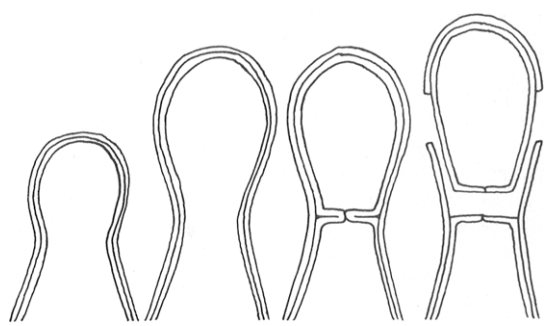

Fig. 39. Collarette production (after Cole & Samson, 1979).

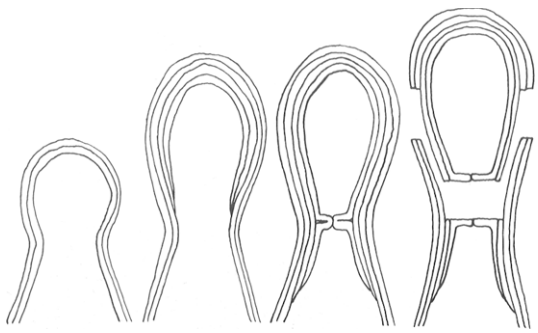

Fig. 40. An alternative explanation of collarette production.

are appropriate for each explanation. Unfortunately, however, both of these explanations purport to be based on the same evidence (contained in transmission electron microscope studies of, for example, *Trichoderma saturnisporum* Hammill (Hammill, 1974) and *A. clavatus* (Hanlin, 1976)); and where both purport to explain development of the same species, based on the same evidence, at least one of them must be wrong. Which one becomes clear when the original publications on which the theories are based are re-examined. Hanlin (1976) stated that, 'as the phialide neared maturity the apex became narrower...the phialide wall was uniformly thin, but became much thicker at the apex due to the formation of a secondary wall layer inside the outer primary wall'. Similarly, Hammill (1974) observed, 'when a phialide produced its first conidium...the first conidial initial was positioned inside of the phialide wall, while the phialide wall outside of it was disintegrating and presumably being sloughed off. The minute collarette of a phialide was that portion of the original phialide wall which remained after completion of the disintegration and sloughing-off processes'. When these descriptions are compared with the two explanations, there can be no doubt that the second theory (Fig. 40) fits the facts more closely than does the first (Fig. 39). It is therefore concluded that collarette production is not merely part of the ontogeny of the first conidium, but must be regarded as a totally independent stage.

Although this conclusion does not affect the truth of the observation that false- or no-chain phialides intergrade with annellides (Minter *et al.*, 1982), it is interesting to note that collarettes tend to be present in the former and absent in the latter. This suggests that there is some evolutionary advantage in having collarettes for those fungi which produce a large number of conidia from the same or almost the same locus. The fact that collarettes are also generally present in true-chain phialides supports this observation, although what this evolutionary advantage is can, at present, only be a subject of speculation. Certainly the apparatus of a wall-building ring or a succession of replacement wall-building apices in a phialide must be rather delicate, and perhaps the collarette is a means of providing such a fragile but important mechanism with some degree of protection.

If collarettes have a protective rôle and are produced as a 'one-off' item before phialidic spore production commences, it is interesting to speculate on how they came about in the first place. Their structure, and particularly the fact that the first conidium is produced by totally new inner walls, is strongly reminiscent of the 'cups' produced by aborted conidia, and the subsequent regeneration observed in *Endophragmiella* Sutton by Hughes (1979). If this similarity is significant, a theory could be advanced that collarettes are the same as 'cups', i.e. in evolutionary terms, collarettes are no more than aborted conidia, and that natural selection in phialidic fungi has generally favoured the abortion of a first conidium and consequential regeneration, because this is an easy way to protect these delicate phialidic mechanisms.

This sort of feature could well have evolved more than once, and so there seems to be no need to regard the presence of a collarette as evidence that phialides are monophyletic. In fact, although it has been suggested on a number of occasions (e.g. Madelin, 1979) that the phialide represents a unique line of evolution, the evidence considered in this paper indicates that this is hardly likely: phialides resulting from a succession of replacement wall-building apices have surely come down a different evolutionary line from those with wall-building rings. Indeed if these two (or more) lines are compared, it is even possible to suggest that one is more recent than the other, since to replace a wall-building apex which has been lost is primitive in comparison to the sophistication of producing the wall-building ring, a mechanism which never needs replacing.

CONCLUSIONS

The arguments presented in the four parts of this paper have made it abundantly clear that intergradation exists developmentally between thallic and blastic fungi in general and, in particular, between true- and false- or no-chain phialidic fungi and between thallic and true-chain-phialidic fungi. Representatives of these groups are therefore in developmental terms merely members of one large continuum. The existence of such a continuum has

long been known (e.g. Kendrick, 1971), but the lack of a suitable vocabulary to describe it has made it difficult for taxonomists to act upon this knowledge. The result has been that deuteromycetes have continued to be classified according to ill-defined groups long after the limitations of these groups have been acknowledged, simply because no viable alternative has been offered.

This paper and its predecessor (Minter *et al.*, 1982) have attempted to generate some of the vocabulary needed if such a viable alternative is to come about. Existing terminology has been rationalized and, where necessary, supplemented with new but easily understood terms. Thus it is now possible to recognize seven developmental stages (conidial ontogeny, conidial maturation, conidial delimitation, conidial secession, proliferation, regeneration and collarette production) where formerly only one, conidial ontogeny, was in common use. The terms 'holoblastic' and 'enteroblastic' have been redefined, and the terminology for describing conidial chains has been put on a rational foundation. Similarly the confusing term 'meristem' has been discarded and in its place three types of wall building have been recognized.

Not all difficulties have been solved, however. If anything, these papers have only revealed more linguistic problems which are holding back deuteromycete systematics. It is now obvious, for example, 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. Similarly, the proposed reforms have not yet been applied to all known types of development in the deuteromycetes, but this must be done to see if there too they really work. In particular, conidia produced in acropetal chains and conidia produced by so-called 'basauxic' conidiophores need to be re-examined carefully.

It is hoped that the ideas put forward here, for all their acknowledged limitations, will stimulate mycologists to realize that current terminology can be improved, and that if this is done, perhaps some viable alternative method of classifying these fungi will be discovered. One day terms like 'phialidic' and 'thallic' may even be viewed in the same way as 'phlegmatic' and 'mercurial', which the chemist now regards as belonging in the out-of-date world of alchemy.

Colleagues at C.M.I. and elsewhere are thanked for their comments, opinions and lively discussions, without which this paper could not have been written. Professor C. V. Subramanian is thanked for hospitality at the Centre for Advanced Studies in Botany, University of Madras, where on a recent visit the senior author prepared some of this manuscript. Most of all, the senior author thanks his wife Helen for her continued patient support, encouragement and perceptive observations.

REFERENCES

CLUTTERBUCK, A. J. (1969). A mutational analysis of conidial development in *Aspergillus nidulans*. *Genetics* **63**, 317–327.

COLE, G. T. & KENDRICK, W. B. (1969). Conidium ontogeny in hyphomycetes. The arthrospores of *Oidiodendron* and *Geotrichum* and the endoarthrospores of *Sporendonema*. *Canadian Journal of Botany* **47**, 1773–1780.

COLE, G. T. & SAMSON, R. A. (1979). *Patterns of Development in Conidial Fungi*. London, San Francisco, Melbourne: Pitman.

ELLIS, M. .B. (1971). *Dematiaceous Hyphomycetes*. Kew: Commonwealth Mycological Institute.

ELLIS, M. B. (1976). *More Dematiaceous Hyphomycetes*. Kew: Commonwealth Mycological Institute.

GAMS, W. (1978). Connected and disconnected chains of phialoconidia and *Sagenomella* gen. nov. segregated from *Acremonium*. *Persoonia* **10**, 97–112.

HAMMILL, T. M. (1974). Electron microscopy of phialides and conidiogenesis in *Trichoderma saturnisporum*. *American Journal of Botany* **61**, 15–24.

HANLIN, R. T. (1976). Phialide and conidium development in *Aspergillus clavatus*. *American Journal of Botany* **63**, 144–155.

HAWES, C. R. & BECKETT, A. (1977*a*). Conidium ontogeny in the *Chalara* state of *Ceratocystis adiposa*. I. Light microscopy. *Transactions of the British Mycological Society* **68**, 259–265.

HAWES, C. R. & BECKETT, A. (1977*b*). Conidium ontogeny in the *Chalara* state of *Ceratocystis adiposa*. II. Electron microscopy. *Transactions of the British Mycological Society* **68**, 267–276.

HAWES, C. R. & BECKETT, A. (1977*c*). Conidium ontogeny in *Thielaviopsis basicola*. *Transactions of the British Mycological Society* **68**, 304–307.

HUGHES, S. J. (1979). Relocation of species of *Endophragmia* auct. with notes on relevant generic names. *New Zealand Journal of Botany* **17**, 139–188.

INGOLD, C. T. (1981*a*). The first-formed phialoconidium of *Thielaviopsis basicola*. *Transactions of the British Mycological Society* **76**, 517–519.

INGOLD, C. T. (1981*b*). The validity of the concept of conidia as either blastic or thallic. *Transactions of the British Mycological Society* **77**, 194–196.

KENDRICK, W. B. (1971). *Taxonomy of Fungi Imperfecti*. Toronto and Buffalo: University of Toronto Press.

MADELIN, M. F. (1979). An appraisal of the taxonomic significance of some different modes of producing blastic conidia. In *The Whole Fungus*, vol. 1 (ed. W. B. Kendrick), pp. 63–80. Ottawa: National Museum of Natural Sciences, National Museums of Canada and the Kananaskis Foundation.

MADELIN, M. F. & DORABJEE, S. (1974). Conidium ontogeny in *Wallemia sebi*. *Transactions of the British Mycological Society* **63**, 121–130.

MATSUSHIMA, T. (1975). *Icones Microfungorum a Matsushima lectorum.* Published by the author, Kobe, Japan.

MINTER, D. W., KIRK, P. M. & SUTTON, B. C. (1982). Holoblastic phialides. *Transactions of the British Mycological Society* **79**, 75–93.

MORGAN-JONES, G. (1971). Conidium ontogeny in Coelomycetes. III. Meristem thalloconidia. *Canadian Journal of Botany* **49**, 1939–1940.

NAG RAJ, T. R. & KENDRICK, W. B. (1975). *A Monograph of* Chalara *and Allied Genera.* Waterloo, Ontario: Wilfred Laurier University Press.

RAPER, K. B. & FENNELL, D. I. (1953). Heterokaryosis in *Aspergillus. Journal of the Elisha Mitchell Scientific Society* **69**, 1–29.

SIGLER, L. & CARMICHAEL, J. W. (1976). Taxonomy of *Malbranchea* and some other hyphomycetes with arthroconidia. *Mycotaxon* **4**, 349–488.

SUBRAMANIAN, C. V. (1972). Conidial chains, their nature and significance in the taxonomy of Hyphomycetes. *Current Science* **41**, 43–49.

SUBRAMANIAN, C. V. & PUSHKARAN, M. (1975). Conidium ontogeny in some monophialidic Hyphomycetes. *Kavaka* **3**, 77–99.

SUTTON, B. C. (1980). *The Coelomycetes.* Kew, Commonwealth Mycological Institute.

VUJICIĆ, R. & MUNTAÑOLA-CVETKOVIĆ, M. (1973). A comparative ultra-structural study on conidium differentiation in the *Cladosarum*-like mutant 22B of *Aspergillus aureolatus. Journal of General Microbiology* **79**, 45–51.

YUILL, E. & YUILL, J. L. (1938). *Cladosarum olivacearum*, a new Hyphomycete. *Transactions of the British Mycological Society* **22**, 194–200.

ZACHARIAH, K. & METITIRI, P. O. (1970). The effect of mutation on cell proliferation and nuclear behaviour in *Penicillium claviforme* Bainier. *Protoplasma* **69**, 331–339.

ZACHARIAH, K. & METITIRI, P. O. (1971). The organization of the penicillus of *Penicillium claviforme* Bainier. In *Taxonomy of Fungi Imperfecti* (ed. W. B. Kendrick), pp. 120–129. Toronto and Buffalo: University of Toronto Press.

(Received for publication 28 January 1982)