

CONIDIAL CHAINS, THEIR NATURE AND SIGNIFICANCE IN THE TAXONOMY OF HYPHOMYCETES*

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CONTINUED interest in conidium ontogeny has not only brought forth much new information on conidium development in many hyphomycetes, but has also stimulated a more critical evaluation of existing concepts and interpretations in the search for better criteria for classification. In this process, certain thoughts and interpretations about conidial chains in hyphomycetes have come up and, since, in my view, they need serious consideration by students of this group, are presented here.

In proposing a classification of the Hyphomyceteae, Saccardo¹ recognized the occurrence of conidial chains as a feature of diagnostic value and this position was maintained in Vol. IV of the *Sylloge*.² Sixty genera which would currently be accepted as hyphomycetes were considered to produce conidia in chains. Saccardo's classification has since been followed by many students. Clements and Shear³ keyed out many more genera, and a count of the genera in which conidial chains were mentioned by them as a diagnostic feature would bring the total to 106. An up-to-date count will take this total still higher.

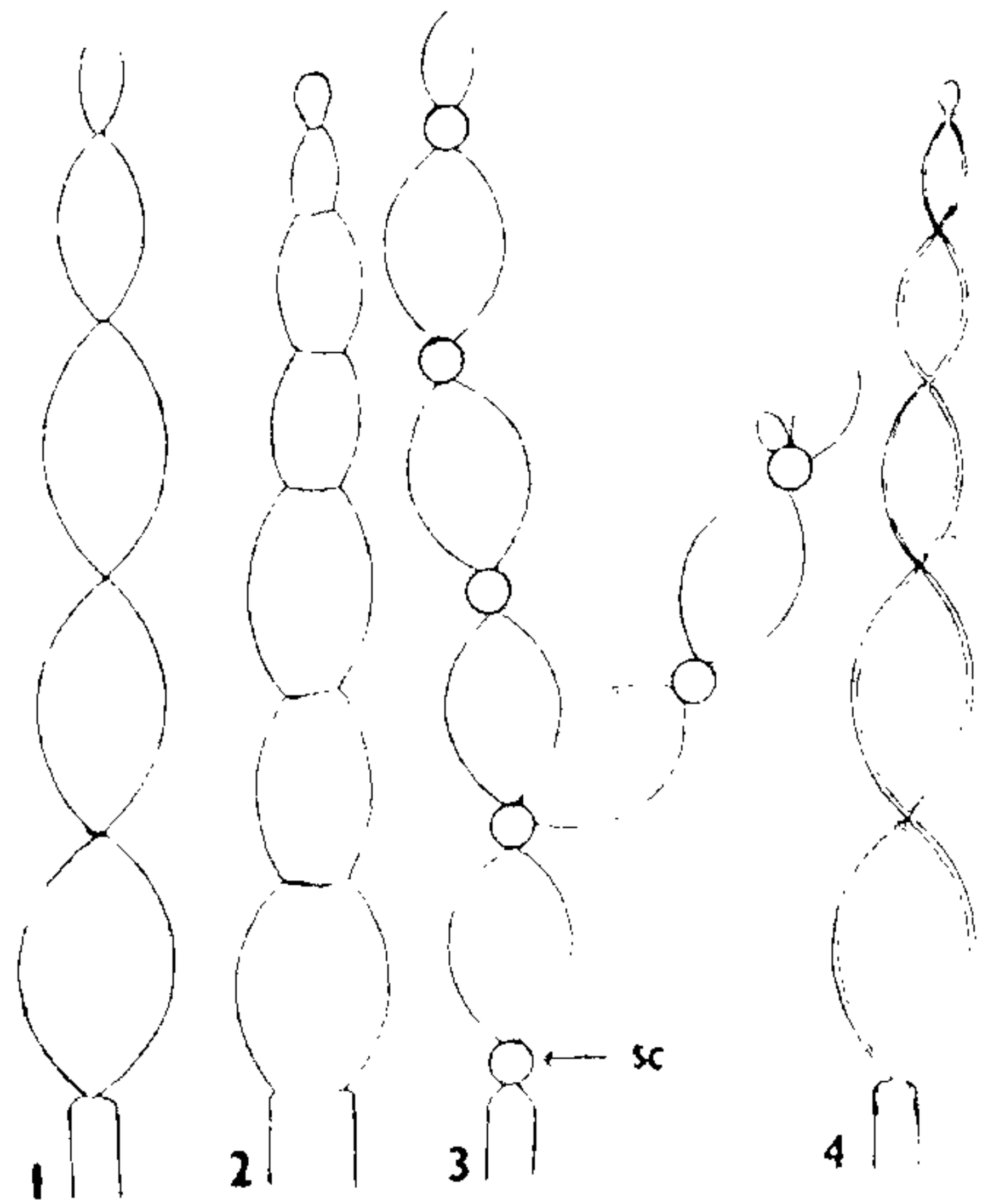
Although many of the older genera are known to us only from their original descriptions or from Saccardo's interpretation of the genera, and much more remains to be done towards the precise understanding of conidium ontogeny based on study of type or authentic material of the type species of several of these genera, our present knowledge indicates that conidial chains may be produced in more than one way. Thus, the conidial chains in *Cladosporium*, *Acrosporium*, *Aspergillus* and *Amblyosporium* are products of differing conidium ontogeny. It is also clear from a study of the literature on the subject that the term "chain" has been used rather loosely and also not always in the same sense by different students. Thus, the conidial "chains" abstracted from the phialides of *Thielaviopsis basicola* (Berk. and Br.) Ferraris and the "chains" of arthrospores of *Geotrichum candidum* Link result from entirely

different modes of development from what is seen in the four genera just mentioned. It is, therefore, necessary to define a "chain" precisely, and its significance in elucidating relationships and in taxonomy would then become more meaningful than it is now.

THE DEVELOPMENT OF CONIDIAL CHAINS

A proper understanding of the exact manner in which conidial chains develop is essential for appreciation of the importance and significance of this information in the formulation of generic concepts and, indeed, in taxonomy. The different modes of development of conidial chains are briefly described below with known examples and simple schematic diagrams.

Example 1 (Figs. 1-4)



FIGS. 1-4. Schematic diagrams of true chains of conidia to illustrate Example 1. Successive budding in an acropetal sequence. Figs. 1-3, blastospores. Fig. 4, porospores. Not "separating cell" (SC) between conidia in Fig. 3. Budding may involve a narrow zone (Fig. 1) or a relatively wider zone (Fig. 2) of the parent cell-wall.

In the case of the conidial chains in *Cladosporium*, each successive conidium develops as

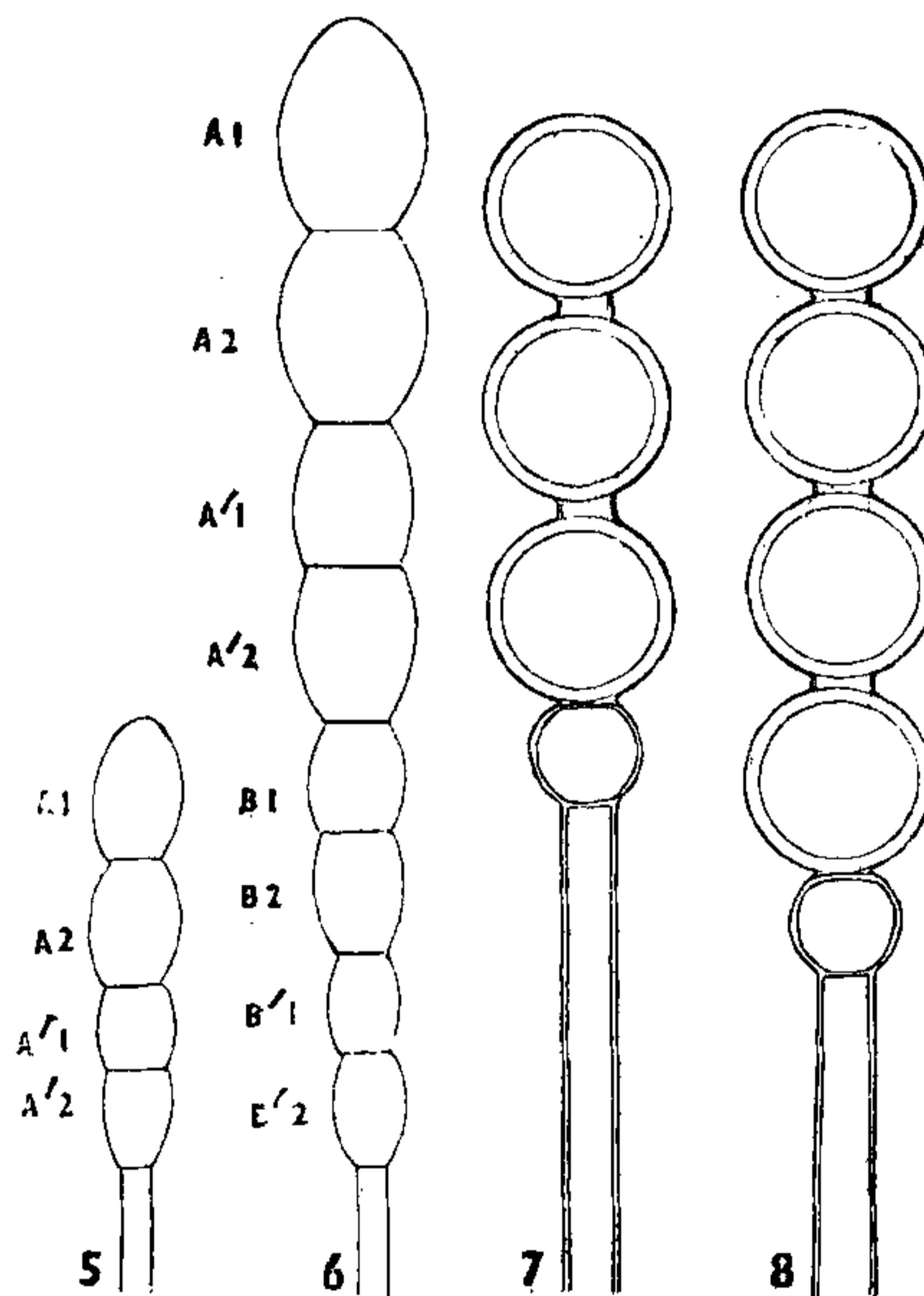
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a bud on the previous conidium in the chain and an acropetally developed chain of conidia is thus produced. The conidium at the distal end of a chain is naturally the most recently formed one and so the youngest. When more than one conidium is budded out from an older conidium, a branched chain is produced. Such acropetal chains of conidia develop in several other genera: e.g., *Septonema*, *Septocylindrium*. Whereas the conidia in these genera are blastospores, in some other genera (e.g., *Alternaria*, *Dendryphon*, *Dendrographium*) the conidia are perospores, but develop in the same acropetal sequence. Fine structure studies on *Alternaria brassicicola* (Schw.) Wiltshire have shown that in the development of acropetal chains of conidia, the inner wall of a conidium is continuous with the outer wall of the next one in the chain¹ and this is presumably the condition in other examples where the conidia in chains are perospores. Despite the discontinuity of the outer wall or wall layer of each conidium in such chains, the units in these chains are linked together by one wall layer or wall common to any two conidia in the chains and so they may be considered true chains.

Example 2 (Figs. 5-8)

In the case of *Acrosporium* (e.g., conidial *Erysiphe*), the conidia are gangliosporae^{5,6} which are cut off in a somewhat basipetal sequence starting from the apex of the conidiogenous hypha and it is noteworthy that, before the first conidium is shed, not only the second conidium initial, but several later conidium initials also are already differentiated below it so that, as pointed out by Hughes⁷, the conidial chain imperceptibly merges with the conidiophore. From the work of Foex⁸, Brodie⁹, Hammett (in Manners¹⁰) and Jordan¹¹ it is clear that the conidiophore arises as a lateral swelling on a hypha and gives rise to a chain of conidia as follows. A papilla appears at the apex of the conidiophore. This divides into two cells (A and A') each of which again divides into two cells (A 1, A 2, and A' 1 and A' 2) forming a chain of four cells. In the meantime, meristematic activity at the tip of the bulbous basal cell produces a further length of the papilla and this is cut off as a further cell (B) which in turn divides again to form a further four cells in the same way (B 1, B 2 and B' 1 and B' 2). This process may continue indefinitely. The cells so cut off become transformed into conidia and do swell to a greater or less extent in the process.

Conidial chains developing and maturing basipetally from conidiophore apices which are meristematic and in which the conidia are produced by the twin processes of swelling and conversion have been reported to occur in a few other hyphomycetes also: e.g., *Coniosporium*, conidial *Hysterium insidens* Schw.⁷, but these need to be studied further. Basipetal chains of gangliosporae have been described for the *Basipetospora* state of *Monascus ruber* v. Tiegh.¹², but with progressive conversion into the basipetal chain of conidia the conidiophore becomes shorter as there is no continued growth of the conidiophore apex such as what is seen in *Acrosporium*. The conidial chain, however, appears to be a true one, as I gathered from the time-lapse sequences shown to us by Drs. Kendrick and Cole at Kananaskis and as can be seen from Fig. 1 A-L in Cole and Kendrick¹².



FIGS. 5-8. Schematic diagrams of true chains of conidia to illustrate Example 2. Gradual basipetal conversion accompanied (Figs. 5-6) or not accompanied (Figs. 7-8) by meristematic growth of conidiophore tip. For explanation, see text.

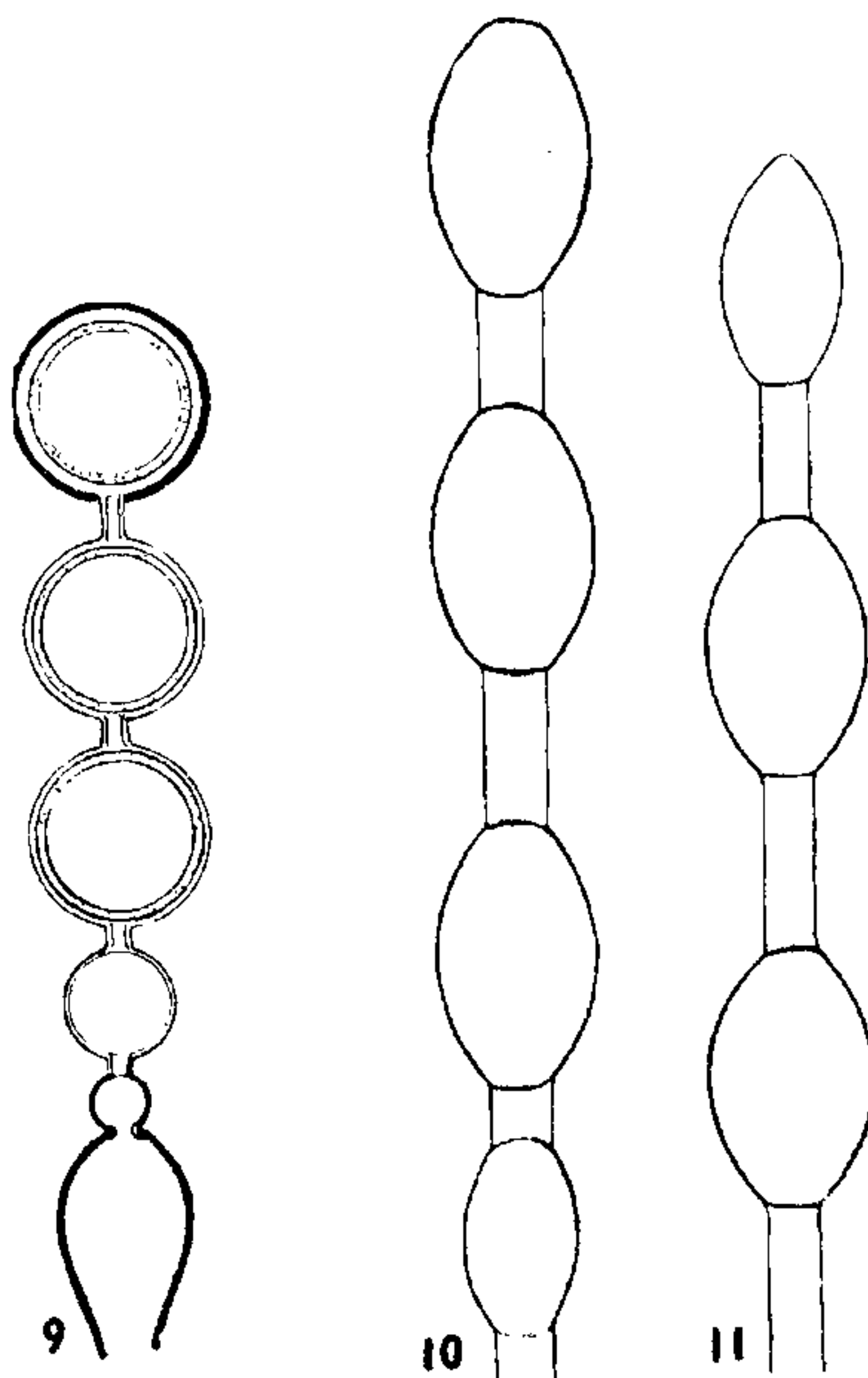
Conidium ontogeny in *Trichothecium roseum* (Pers.) Link ex Fries was considered by Kendrick and Cole¹³ to follow basically the same pattern as that described by them in

Basipetospora. Several students have reported on conidium ontogeny in this fungus and particular mention may be made here of the work of Ingold¹⁴, Nicot and Leduc¹⁵, and Meyer¹⁶. Quite rightly, Meyer interpreted the so-called conidial chain as "une fausse chaine" (a false chain). It is, therefore, surprising to read Kendrick and Cole's comment on Meyer's interpretation: "The only phrase to which we take objection is the reference to a "false chain". Why the kind of spore chain formed by *T. roseum* should be any less genuine than those developing in other ways is not clear to us, since we regard any coherent linear sequence of conidia as a chain". The answer is that any linear sequence of conidia need not be a chain—indeed, all linear sequences are not, and this in fact is the main theme of this paper. If each of the conidia formed in succession is cut off and shed before the next one develops below it, their walls cannot be continuous and so no true chains can result. Only a linear series in which the conidia have a basipetal arrangement can emerge as a result of this mode of ontogeny. It is necessary to distinguish such linear series which are the equivalent of "false chains" in the terminology of Meyer, from "true chains" in which the wall between conidia in a chain is a continuum. Indeed, the development of conidia in *Trichothecium roseum* seems quite different from that reported for the *Basipetospora* state of *Monascus ruber*. The wall of the successive conidia in the latter (i.e., *Basipetospora*) is continuous, but this is not the case in *Trichothecium roseum*. In *T. roseum* the first formed conidium is a gangliosporer; the second and later conidia can also be interpreted as gangliosporers, as part of the conidiogenous hypha is incorporated in the body of the conidium. Quite obviously, there are no true chains of conidia in *Trichothecium roseum*. On the other hand, if each of the conidia in the basipetal sequence in *T. roseum* did not get severed and retained its organic connection with the previous and the later conidia, there would have been continuity of the wall between these conidia and one would then have interpreted this as a true chain, but we know that this does not seem to occur. In essence, then, we should distinguish between a basipetal succession of conidia which may result in a (true) chain and a basipetal succession in which no (true) chain is produced, but only a linear series or a false chain in which there is no continuity of the wall between the successive conidia.

Example 3 (Fig. 9)

In the case of *Aspergillus niger* v. Tiegh. a simple basipetal chain of conidia is produced from the tip of the phialide¹⁷. Each conidium is initiated at a 'conidiogenous locus' (a term defined at the Kananaskis meeting: see Kendrick¹⁸) and is pushed up by the next conidium which develops below it. What is very noteworthy about this conidial chain is that the wall around the successive conidia in the chain is a continuum and thus we have a (true) chain¹⁹. New wall material is evidently laid down around the conidium initial at the conidiogenous locus and since this is a continuing process there is theoretically no limit to the number of conidia that can develop: this reminds us of the situation in *Acrosporium* and, in fact, the conidiogenous locus within the phialide of *Aspergillus niger* seems to be the functional equivalent of the 'meristematic tip' of the conidiophore of *Acrosporium*, if one can locate it precisely! Essentially the same pattern of development of conidial chains seen in *Aspergillus niger* is found in several other genera: e.g., *Memnoniella*, *Paecilomyces*, *Phialomyces*.

Example 4 (Figs. 10-11)



FIGS. 9-11. Schematic diagrams of true chains of conidia to illustrate Example 3 (Fig. 9) and Example 4 (Figs. 10-11). For explanation, see text.

The conidial chains in *Amblyosporium* are peculiar and have been described by Pirozynski²⁰. The 'chain' in this case may be composed of two, or up to six, conidia [usually 2 in the type species *A. botrytis* Fres. and up to 6 in *A. spongiosum* (Pers.) Hughes], each separated from the other by a 'disjunctive cell'. The conidia are considered to be arthrospores, but they are products of swelling of the portion of the hypha that surrounds them and in this sense are gangliosporous. Despite the presence of a disjunctive between each conidium, the conidia are indeed linked with each other to form true chains. Disjunctives are also known in other modes of conidium ontogeny which produce true chains, e.g., in the basipetal conidial chains of certain species of *Aspergillus*, *Penicillium* and *Paecilomyces*¹⁹ and also some acropetal conidial chains such as are seen in *Bahusandhika indica* (Subram.) Subram.²¹⁻²². The fact that the wall is a continuum in regard to both conidia and disjunctives strengthens this interpretation, apart from the fact that the occurrence of the disjunctives is regular. The sequence in development of the conidia in *Amblyosporium* may be basipetal, or initially acropetal and then basipetal²⁰. A true chain of conidia which develops in a somewhat basipetal sequence is found in *Oidiodendron truncatum* (Robak) Barron¹⁸.

SOME MISINTERPRETATIONS OF CONIDIAL CHAINS

I wish now to take up examples in which conidial chains are mentioned and usually taken for granted, but do not exist.

(a) *Trichothecium roseum* is one such and has been discussed already (Fig. 12).

(b) In the case of several genera in which the conidiogenous cells show annellations (e.g., *Scopulariopsis*, *Cephalotrichum*, *Trichurus*) the conidia are often considered to form chains; they are also sometimes interpreted as developing in basipetal succession. However, in the genera which are characterised by annellated conidiogenous cells, each percurrent proliferation produces only one conidium and repeated percurrent proliferations result in the secession of a succession of single solitary conidia which may sometimes form a linear series or loose chain. Since each conidium is produced following a new percurrent proliferation, there cannot be continuity of walls between the successive conidia and so this linear series is not a true chain. Yet, if for some reason this normal sequence is disturbed and a conidium is not shed, a conidium may be differentiated below it and, if this is repeated one or more times, a

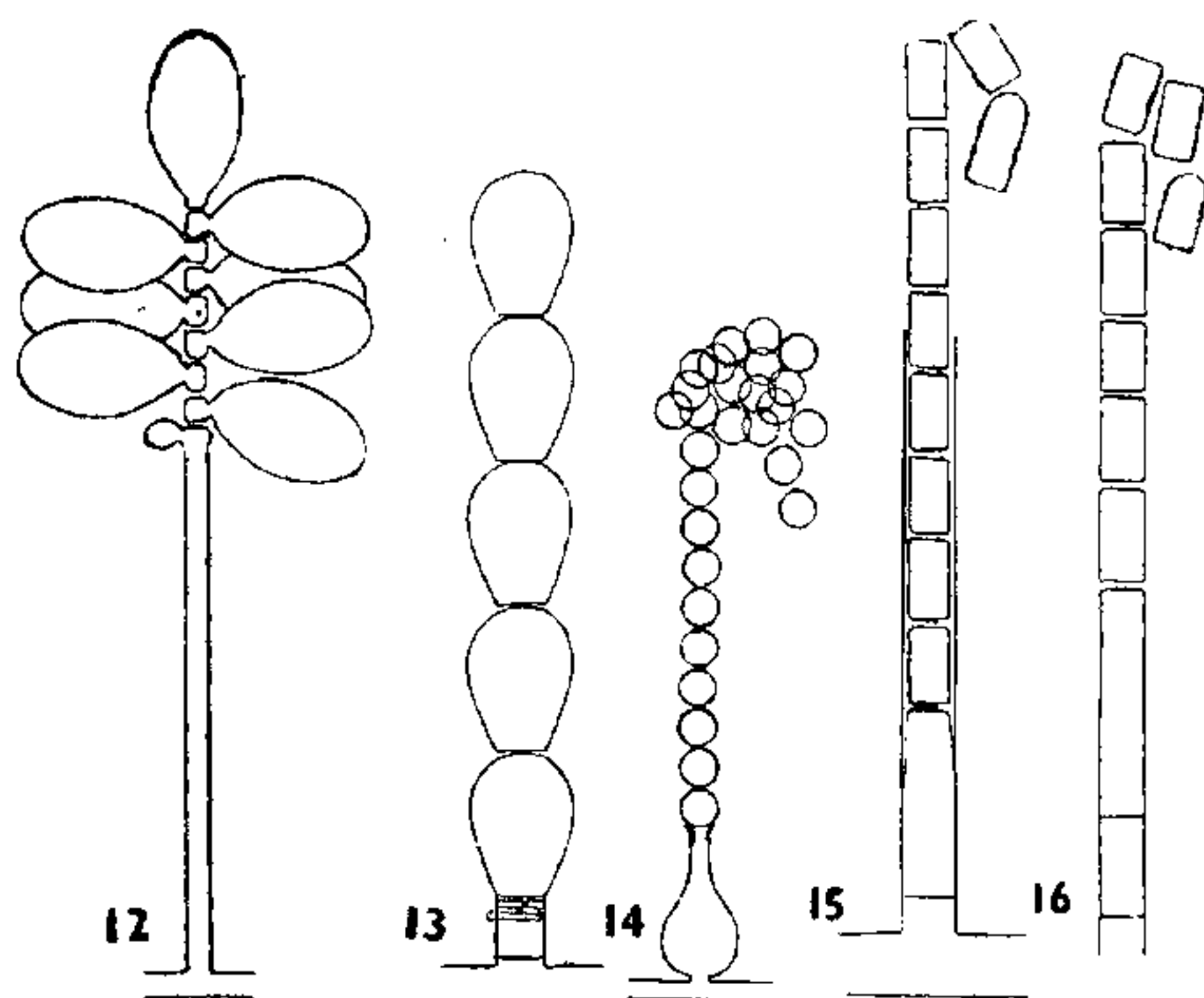
true chain of 2 or more conidia may be formed. The distinction between true and false chains rests on this sequence. In describing conidium ontogeny in *Scopulariopsis brevicaulis* (Sacc.) Bain., Hughes⁷ wrote: "the conidia... persist in long fragile chains but these are not true chains in the sense that those of *Xylohypha nigrescens*... or *Septonema secedens*... are true chains". (Both *Xylohypha* and *Septonema* produce true chains of conidia, the chains being acropetal and developing by budding). In so far as the oldest conidium in this linear series is farthest from the conidiogenous cell, a false chain so formed is a basipetal one, despite the fact that there is a shifting in the conidiogenous locus in the acropetal direction each time proliferation occurs and a conidium is produced (Fig. 13).

That certain phialides which produce similar false chains of conidia without apparent annellations may be essentially similar will be elaborated in a later communication. It is sufficient to emphasize here that the conidial "chains" seen in some phialidic genera in which the conidia may slime down to form slimy masses are in all likelihood not true chains (Fig. 14).

(c) In the development of successive conidia from within phialides of *Thielaviopsis basicola*, protoplasmic cleavage followed by laying down of wall material around the cleaved out protoplasmic mass are considered to be steps in the initiation and maturation of each conidium in the so-called chain¹⁹. In so far as the wall of each successive conidium is formed *de novo*, there cannot be continuity of wall between successive conidia and so no true chains, but only a basipetal succession or an unconnected linear series of conidia¹⁹. This may apply also to several other genera in which such "end-conidia" develop from phialides, e.g., *Chalara*, *Chalaropsis*, *Sporoschisma* (Fig. 15).

(d) The sequence of development of arthrospores in *Geotrichum* was elegantly elucidated by Kendrick and Cole¹⁸ by time-lapse photography and in this case the hyphae just fragment into bits. The current notion that fragmentation in this fungus is basipetal was not supported by the time-lapse sequence. Apparently, a conidium initial is not laid down in advance of secession and, since conidia can be recognised only on secession and the sequence is irregular, true chains do not occur—only a linear series or a false chain can sometimes be seen (Fig. 16).

In all these cases the position of the conidia in a linear series may be maintained by their being embedded in slime, but this condition is not obligatory. The conidia may become embedded in slime at the point from where they are abstracted to form a gloeoid mass or else they may slime down from the tip of the linear series or false chain downwards. I am not quite sure if true chains of dry conidia can become secondarily slimy and result in secondarily false chains, and I know of no example where this is known to occur.



FIGS. 12-16. Schematic diagrams of false chains of conidia that are products of different modes of ontogeny. For explanation, see text.

In summary, it can be stated that true chains of conidia may be produced:

1. By successive budding in an acropetal sequence resulting in simple or branched chains. In the development of successive conidia the conidiogenous locus shifts in an acropetal direction. The conidia may be porospores (e.g., *Alternaria*) or blastospores (e.g., *Cladosporium*). The conidia in a chain may be linked by a separating cell (e.g., *Bahusandhika*) or a disjunctive between each conidium (Figs. 1-4).

2. By gradual basipetal conversion accompanied (e.g., *Acrosporium*), or not accompanied (e.g., *Basipetospora*), by meristematic growth of the conidiophore tip, resulting in a basipetal chain which is always simple; in the delimitation of successive conidia some shift(s) in the conidiogenous locus (? basipetal) seem(s) to be involved (e.g., *Acrosporium*). The conidia are gangliospores (Figs. 5-8).

3. By the successive development of an indefinite number of conidium initials one after the other in a basipetal sequence but at a fixed

conidiogenous locus (e.g., *Aspergillus*). The conidia are phialospores (Fig. 9).

4. By a process of swelling, septation and conversion resulting in a chain of conidia, often separated by disjunctive cells. The conidium development may be basipetal, or initially acropetal and then basipetal (e.g., *Amblyosporium*) and the position of the conidiogenous loci varies accordingly. The conidia are gangliospores, but are regarded by some as arthrospores (Figs. 10-11).

In true conidial chains, acropetal or basipetal, one can usually see conidia in different stages of development and maturity, but this is not the case with false chains. Also, in herbarium material, the true chains would normally retain this character, whereas conidia in false chains need not necessarily retain their position in a linear sequence and can easily fall apart.

DRY OR SLIMY CONIDIA AND NATURE OF CONIDIAL CHAIN

It may not be a mere coincidence that, as far as known, in species of genera which are characterised by true chains of conidia, the conidia are all dry. Conversely, in species of the genera characterised by false chains the conidia are slimy so that the "chains" invariably slime down. This explains why some hyphomycetes, especially those producing phialides, have often been described as producing their conidia sometimes in chains, and sometimes in "heads". Thus, there seems to be a clear correlation between the nature of the chain (true or false) and the dry or slimy nature of the conidia: true chains usually having dry conidia, and false chains invariably slimy conidia. I believe this correlation will receive further confirmation from future work and, if it does, would lend strong support to the value of distinguishing between dry-spored and slimy-spored genera of the hyphomycetes, as stressed by Mason²³. Thus, true conidial chains (persistent chains) would not normally slime down, but false chains (fragile chains) would, and recognition of this and the other points raised in this paper should help in the proper circumscription of genera based on studies of type material. Having emphasized, therefore, the importance of studying the ontogeny of conidial chains in classification, it now remains to illustrate this with suitable examples. To this end, the taxonomy of the genus *Gliomastix* will now be briefly reviewed.

AN EXAMPLE—THE GENUS *Gliomastix*

The genus *Gliomastix* was established by Guéguen²⁴ to accommodate *G. chartarum* Guéguen. I have not been able to examine type material of this fungus. According to Guéguen's description the fungus produces (one-celled) slimy conidia in chains from the tips of simple erect conidiophores and the conidia later slime down from the tip of the conidial chains downwards. Mason²⁵ considered the conidiophores to be phialides and his description of the fungus which was based on a study of three isolates seems to agree with the illustrations given by Guéguen so that it seems reasonable to assume that he was dealing with a fungus closely similar to Guéguen's. That the fungus produces conidial chains which may slime down was emphasized by Mason and this has since been accepted as being typical of the genus *Gliomastix*; indeed, Guéguen's illustrations and also the generic name itself are suggestive of this. Mason considered his isolates and Guéguen's to be conspecific with *Torula convoluta* Harz. Mason does not appear to have examined type material of *T. convoluta* in arriving at this conclusion. Hughes²⁶ accepted this synonymy and, in addition, considered *Torula murorum* Corda²⁷ to provide an earlier name for the fungus. Hughes examined the type specimen of *T. murorum*, but type material of *Torula convoluta* and of *Gliomastix chartarum* were apparently not examined. Hughes and Dickinson²⁸, reporting on *Gliomastix* spp. from New Zealand, described *G. novae-zelandiae* Hughes and Dickinson and it is clear from their description and excellent illustrations that the conidia in this species form true chains and, just as might be expected, do not slime down. Similar true chains of conidia are seen also in *Gliomastix luzulae* (Fuckel) Mason ex Hughes²⁶⁻²⁸. Thus, species producing true chains and those producing false chains of conidia both came to be classified together in the genus *Gliomastix*. Dickinson²⁹ adhered to the same concept and classified in *Gliomastix* both species which were characterised by true chains and those that did not produce true chains of conidia.

Not satisfied with this arrangement, I have asked myself the question "What is *Gliomastix*?". Judging by the illustrations given by Guéguen which should serve as the type in the absence of a type specimen, *G. chartarum* must be interpreted as producing a basipetal succession of single conidia, sometimes adhering in loose or fragile chains and quite often also

sliming down. Therefore, *Gliomastix* approximates the genus *Cephalosporium* Corda (or *Acremonium* Link ex Fries, since this is considered the appropriate name, *vide* Gams³⁰), but differs in being dematiaceous. I have examined the type of *Torula murorum* (ex Herb. IMI 37344) and find that the conidia are produced in true chains and these are dry: therefore, I would exclude this from *Gliomastix*. This and other species which produce true chains of dry conidia which are at present disposed in *Gliomastix* have naturally to be classified separately. Indeed, there are also certain monophialidic species of *Paecilomyces* Bainier³¹ which also produce true chains of dry conidia and are the moniliaceous counterparts of the species producing true chains of conidia now disposed in *Gliomastix*. It would be logical to classify all these species together.

From a study of the literature it seemed that the genus *Basitorula* Arnaud³² might be considered as a possible repository for these species. However, Arnaud mentioned two species in one of which (*B. cingulata* Arnaud, nom. nud.) the conidia were in true chains, and in the other [*B. ? cephalosporioides* (v. Beyma) Arnaud comb. nov.] the conidia slimed down. Further, the generic name *Basitorula* needs to be validated. As no other generic name seems available, a new name is being proposed to take in some species producing true chains of conidia and currently placed in *Gliomastix*, and also some of the monophialidic species of *Paecilomyces*.

The generic name *Sagrahamala* is derived from Sanskrit: सग्रह (sagraha) = persistent, and माला (mala) = chain, suggestive of the persistent (true) chains of conidia.

Sagrahamala gen. nov.

Hyphomycete producens catenas simplices, basipetales, veras conidiorum. Cellulae conidiogenae (phialides) simplices, erectae vel flexuosae. Conidia unicellularia, sicca, a catenis secedentia, non elabentia.

Hyphomycete producing simple basipetal true chains of conidia. Conidiogenous cells (phialides) simple, erect or flexuous. Conidia one-celled, dry, seceding from chains, not sliming down.

Type species:

S. luzulae (Fuckel) comb. nov.

= *Torula luzulae* Fuckel, 1870, *Symb. Mycol.*, p. 348.

= *Gliomastix luzulae* (Fuckel) Mason ex Hughes, 1958, *Can. J. Bot.*, 36: 769.

Other species :

- S. murorum* (Corda) comb. nov.
= *Torula murorum* Corda, 1838, *Icon. Fung.*, 2: 9.
= *Gliomastix murorum* (Corda) Hughes, 1958, *Can. J. Bot.*, 36: 769.
- S. musicola* (Speg.) comb. nov.
= *Coniosporium musicola* Speg., 1910, *An. Mus. nac. Hist. nat. B: Aires*, 20: 430:
= *Gliomastix musicola* (Speg.) Dickinson, 1968, *Mycol. Pap.*, 115: 8.
- S. polychroma* (v. Beyma) comb. nov.
= *Oospora polychroma* v. Beyma, 1928, *Verh. K. Akad. Wet. (b)*, 26: 5.
= *Gliomastix murorum* (Corda) Hughes v. *polychroma* (v. Beyma) Dickinson, 1968, *Mycol. Pap.*, 115: 11.
- S. novae-zelandiae* (Hughes and Dickinson) comb. nov.
= *Gliomastix novae-zelandiae* Hughes and Dickinson, 1968, *N.Z. Jl. Bot.*, 6: 108.
- S. variabilis* (Barron) comb. nov.
= *Paecilomyces variabilis* Barron, 1961, *Can. J. Bot.*, 39: 1576.
= *Paecilomyces roseolus* G. Smith, 1962, *Trans. Br. mycol. Soc.*, 45: 388.
- S. humicola* (Onions and Barron) comb. nov.
= *Paecilomyces humicola* Onions and Barron, 1967, *Mycol. Pap.*; 107, 20.
- S. striatispora* (Onions and Barron) comb. nov.
= *Paecilomyces striatisporus* Onions and Barron 1967, *Mycol. Pap.*, 107: 19.
- S. bacillispora* (Onions and Barron) comb. nov.
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