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CONIDIOPHORES, CONIDIA, AND CLASSIFICATION[1]

By S. J. Hughes[2]

Abstract

Characters of conidiophore and conidium development are used for the separation of some common temperate and a few tropical Hyphomycetes into eight Sections. The need for further studies on the precise method of conidium development is stressed because this promises to provide the most stable character for the classification of Fungi Imperfecti as a whole. Conidiophores and conidia of a large number of Hyphomycetes are figured to illustrate the various characters common to each Section.

Introduction

This paper comprises an experiment in classifying some Hyphomycetes into sections based primarily upon the different types of conidiophore and conidium development. The mononematous, synnematous, or tuberculariaceous nature of conidiophores, the form of mature conidia, their dematiaceous or mucedinous nature, their septation, and the presence or absence of slime around them are treated as subsidiary characters.

Saccardo (99) divided the Hyphomycetes into four groups: Mucedineae, Dematieae, Stilbeae (Hyalostilbeae and Phaeostilbeae), and Tubercularieae (Tuberc. mucedineae and Tuberc. dematieae). Sections were then delimited on conidium morphology: Amerosporae, Didymosporae, Phragmosporae, Dictyosporae, Staurosporae (Asterosporae), and Helicosporae. Saccardo (100) made slight modifications of this scheme in 1906.

Most workers on Hyphomycetes are losing confidence in the major division of this group on the basis of Mucedineae/Dematieae, especially when only the conidia and the visible parts of conidiophores are taken into account. It is of interest to note that Saccardo (99) regarded *Verticicladium* Preuss as dematiaceous *Verticillium* Nees. In 1910 A. L. Smith (106) observed dark color in *V. albo-atrum* Reinke & Berth. and she seemed justified, according to the Saccardoan system, in classifying the fungus as *Verticicladium albo-atrum* (Reinke & Berth.) A. L. Smith. This combination has not been taken up and it would be agreed that too great a stress was being laid on color if *Verticillium albo-atrum* were to be separated generically from the only critically distinct *V. dahliae* Kleb., which, however, also develops color in the form of dark sclerotia (Isaac (71)). In any case *Verticillium* and *Verticicladium* have quite distinct types of conidium development (Hughes (51)).

To separate *Ramularia* Unger and *Cercospora* Fres. into the families Mucedineae and Dematieae seems to me to be wrong especially when so many *Ramularia* spp. develop conidiophores from immersed dark colored sclerotia or stromata. Numerous examples occur of the failure of such a division to separate morphologically unrelated fungi and hold together those that have

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a similar morphology. With regard to color, however, it is worth while remembering that large numbers of Hyphomycetes have brightly colored fructifications and mycelium, characters which we have learned to associate with the Hypocreales and some Basidiomycetes; examples are *Apiocrea chrysosperma* (Tul.) Syd. (= *Sepedonium chrysospermum* Fr.) and *Nectria inventa* Pethybr. (= *Acrostalagmus cinnabarinus* Corda). With further knowledge of the perfect states of Hyphomycetes color may prove to be a useful character. A further instance of confusion arising from reliance on color is given below when *Helicomyces scandens* is briefly discussed.

In the division of the Hyphomycetes into four families by Saccardo, stress was laid upon the way conidiophores are grouped or not grouped; briefly, in the Mucedineae and Dematieae they are solitary or at least separate along their length, in the Stilbeae long conidiophores are fused into synnemata, whilst in the Tubercularieae generally short conidiophores are aggregated on stromata usually in the form of tubercles (sporodochia). The conidiophores and conidia in any one of these groups are by no means homologous. The generic name *Phragmocephala* was published by Mason and Hughes (85) in the belief that the species* whose conidiophores are solitary, in tufts on a small stroma or in synnemata, are all congeneric; in Saccardo's scheme they would be separated amongst the Dematieae, Tubercularieae, and Stilbeae, presumably under three different generic names.

The genera *Scopulariopsis*, *Phaeoscopulariopsis*, and *Stysanus* would, under the old scheme, be classified in the Mucedineae, Dematieae, and Stilbeae respectively but the sporogenous cells and conidium development are alike and the three names, if there be need for three, should occupy neighboring positions in any classification.

In *Exosporium tiliae*, *Helminthosporium velutinum*, and *Helminthosporium stilbaceum* (Hughes (59)) the method of development of the helminthosporioid conidia is identical. The first named, however, is found amongst the Tubercularieae, and the second amongst the Dematieae although this species and a number of congeneric ones sometimes develop groups of conidiophores on small stromata; the third species would presumably be classified in the Stilbeae although here the conidiophores are only closely pressed together and not fused along their length.

v. Höhnel (42) published his genus *Helicostilbe* for the single species *H. helicina* v. Höhnel. According to Linder (77) this is *Helicomyces scandens* Morgan; Linder showed that in an early stage of development conidiophores are solitary on repent hyphae but at maturity synnemata are formed with erect, bristle-like, brown setae. Saccardo (100) classified von Höhnel's genus in the Phaeostilbaceae although Clements and Shear (20) compiled it amongst the Hyalostilbeae.

The absence of septation or the variation in the septation of conidia, with the morphology of mature conidia, has been given too great an importance in classification. It is well known that in some genera, e.g. *Brachysporium* and

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* *The term 'species' is used loosely in this paper.*

Curvularia, septation in the various species is more or less constant; in the graminicolous species assigned erroneously to *Helminthosporium* on the other hand, or in *Sporidesmium* (sensu stricto) the conidia in the different species may show great variation. On the whole it seems that the longer the conidia the more variable is the number of septa. In some genera, in the past, little importance seems to have been paid to variation in the numbers of septa; thus, in *Ramularia*, Saccardo compiled over 400 species whose conidia varied from continuous, up to 1-septate, 2-, 3-, 4-, 5-, 6-, 7-, even up to 8-septate (Hughes (43)). All the species of *Ramularia* which have been studied over a period of time usually show a considerable degree of variation in septation of the conidia composing the chains and this has been shown to be correlated with humidity.

In many fungi whose conidia develop in acropetal chains e.g. *Ramularia* spp. and some *Cladosporium* spp. the first formed conidia are more frequently septate than those formed later. In *Septonema secedens*, however, the conidia in the long chains are invariably 3-septate.

In 1951 Hughes (54) described three species of *Hansfordiella*, two of which produce phragmospores, the third dictyospores; other characteristic features seemed to demand their generic identity.

In *Stigmina platani* (Fuckel) Sacc. the conidia are apparently always phragmospores whereas in the single collection that I have seen of *S. platani-racemosae* (Dearn. & Barth.) Hughes 50% of the conidia are dictyospores; the two species only differ on this score and it seemed wrong to me to include the two in different genera to say nothing of different groupings (Hughes (66)).

The 'Helicosporae' seems to me to be the only Saccardoan grouping based on characters of mature conidia which classifies together species most of which have a similar type of conidium development.

In the primary division of Hyphomycetes into the two groups Xerosporae and Gloiosporae (Wakefield and Bisby (112) and Mason (83)) the presence or absence of slime around the conidia was held to be the distinguishing feature; but here again totally different types of conidia, with regard to their precise mode of development, are classified together and similar types widely separated. According to Ingold (70) a third 'biological spore type must be recognized, namely the aquatic spore produced, liberated and normally dispersed below water'; it was not suggested by this author that the aquatic spore types should comprise a third division of the Hyphomycetes. 'Biological spore type' is the correct appellation for dry, slimy, and aquatic spores; in addition 'biological conidiophore types' could be differentiated and even 'biological mycelium types'. Biological types can be overstressed; in the above instances they bear no relation to the more stable developmental and morphological characters of the reproductive structures. A large number of species do not fit adequately into either Xerosporae or Gloiosporae and may even change their position in either group according to the age of the fruiting structure. Under this scheme *Memnoniella* and *Stachybotrys* are widely separated whereas if the two genera were included under the one name,

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Stachybotrys, no hardship would be suffered. As pointed out by Wakefield and Bisby (112) 'Also, of course, Nature presents us with the expected intermediate forms'. Mason (83) had already pointed out 'there is such an obvious transition between genera characterised by slimy phialospores to other genera characterised by dry phialospores'; I fail to understand, therefore, why 'moist spores verus dry spores' was made the 'primary differentiating character' in the List of British Hyphomycetes (Wakefield and Bisby (112)).

If the above mentioned characters are not regarded as important for the differentiation of major groupings of Hyphomycetes what then remains? The answer appears to me to be found at the apex (or the base!) of the conidiophore or sporogenous cell, or where the conidium initial is being produced. I believe that there are only a limited number of methods whereby conidia can develop from other cells and that morphologically related imperfect states will only be brought together when the precise methods of conidium origin take first place in the delimitation of the major groupings.

In the sections differentiated below, I have almost restricted myself to the commoner Hyphomycetes which I have collected on wood and bark in Britain; but a number of species from tropical Africa and North America have been included here and there in order to illustrate certain points. A few Coelomycetes have also been brought into the discussion.

The work of Vuillemin has been fully discussed by Mason (82, 83) who also proposed terms for types of 'conidia'. In Sections I to VIII (pp. 582-645) and in the very brief summary below, the term conidium is used throughout, except in Section IV in which phialospores develop from phialides (used in a restricted sense). Following the main text some of the terms of Vuillemin and Mason are discussed (pp. 647-650) and applied to the 'conidia' of the various sections where applicable. Langeron (76) used the terminology of Vuillemin and Mason but occasionally in so wide a sense that I believe some of the terms thus employed lost their usefulness.

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Summary of Sections I to VIII

Growth of Conidiophore Initial or of Conidiophore During Sporulation Restricted to Apical Region

SECTION IA

Mycelium generally narrow. Conidia usually developing in acropetal succession as blown-out ends at the apex of simple or branched conidiophores which do not then increase in length. The basal conidia of chains aggregated around the apical region of a conidiophore may be morphologically different from the others and in one instance are modified into permanent metulae bearing a terminal conidium and a number of subterminal conidia.

SECTION IB

Mycelium generally wide. Conidia developing in acropetal succession as blown-out ends on simple or branched conidiophores; sometimes the lateral branches are modified entirely into a number of conidia or into solitary conidia and in these instances the conidia are borne on conspicuous denticles. The solitary conidia or short, simple, or branched chains of conidia may be aggregated on well differentiated swollen cells and arise more or less simultaneously on them. In examples with intercalary or lateral swollen and fertile cells bearing simultaneously produced conidia, the main stalk may proliferate to develop further intercalary fertile cells or bear further lateral fertile branches.

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SECTION II

Conidia arising as blown-out ends of apex of simple or branched conidiophores and the ends of successively produced new growing points developing to one side of the previous conidium. The conidiophore, therefore, either increases in length or becomes swollen as a result of conidium production. Acropetal chains of conidia may develop on the primary conidia.

SECTION III

Conidia usually thick-walled, arising solitarily as blown-out ends of apex of simple or branched conidiophores; a plurality of conidia may be produced, each new conidium developing as a blown-out end of successive proliferations *through* the scars of previous conidia so that the conidiophores in such cases become annellate.

SECTION IV

Conidia (phialospores) developing in rapidly maturing basipetal series from the apex of a conidiophore (phialide) which may or may not possess an evident collarette.

SECTION V

Conidia developing in gradually maturing basipetal series and originating by the meristematic growth of the apical region of the conidiophore in such a way that the chain of conidia merges imperceptibly with the conidiophore that gives rise to the chain.

SECTION VI

Conidia usually thick-walled, developing from pores on conidiophores of determinate or indeterminate length; they are solitary or in whorls, and may occur in acropetal chains. The conidiophore may proliferate through the terminal pore to produce a further terminal conidium or the conidiophore may develop a succession of terminal conidia on successive proliferations developing just below the previous conidium.

SECTION VII

Conidia developing by the basipetal fragmentation of conidiophores of determinate length, and which do not possess a meristematic zone.

Growth of Conidiophore Restricted to Basal Region

SECTION VIII

Conidia borne singly at apex, or singly at apex and laterally, often in regular whorls on conidiophores showing basal elongation. Conidia often with longitudinal slit in wall but this character is by no means restricted to this Section.

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Section IA

The mycelium is immersed or superficial, composed generally of narrow hyphae.

The conidiophores are very variable in the different species, their variation being best explained by reference to various examples included in this section. In *Xylohypha nigrescens* (Fr.) Mason (Fig. 1) the conidiophores are short and closely packed together; each usually bears a single, very long, rarely branched acropetal chain of brown amerospores and at maturity a sooty pustule is formed. In **Bispora antennata** (Pers. ex Fr.) Mason comb. nov.* (Fig. 2) the conidiophores are likewise short and crowded together, each producing a single, long, unbranched, acropetal chain of dark brown to almost black didymospores. In *Septonema hormiscium* Sacc. (Fig. 3) the conidiophores are scattered and little different from conidia; the conidiophores bear a single short unbranched acropetal chain of dark brown phragmospores developing at the apex. There is a tendency for acropetal chains of conidia to be unbranched or seldom branched only when the conidiophores are closely aggregated.

By the production of simple or branched chains a plurality of conidia may be developed on a single conidiophore and this is not accompanied by an increase in length of the conidiophore itself; as in the original conidium so each succeeding one in the acropetal chain is the blown-out end of the previous conidium and throughout such a chain there is direct continuity between the wall of each conidium. In Section IA the conidia of all species develop as blown-out ends; amerospores, didymospores, and phragmospores are found here but as far as I am aware no dictyospores or staurospores develop in chains in acropetal succession.

In *Septonema solidum* Berk. & Curt. (= *Sirodesmium solidum* (Berk. & Curt.) Sacc.) 'conidia' develop from the apical growth of two to five dark brown and closely adpressed hyphae which develop constrictions at intervals at the same level thus giving the appearance of dictyospores in chains. The 'conidia' do not secede readily.

Septonema secedens Corda (Fig. 4), the type species of *Septonema*, is a form-species of great interest and helps to explain the relationship of a number of forms included in Section I; it has the advantage of enabling unbroken preparations to be made readily from young colonies, a single fructification is

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* ≡ *Monilia antennata Pers. in Syn. Meth. Fung. p. 694. Gottingen. 1801.*
≡ *Torula antennata [(Pers.)] Pers. in Mycologia Europaea, 1 : 21. 1822.*
≡ *Torula antennata [(Pers.)] Pers. ex Fr. in Systema Mycologicum, 3 : 501. 1832.*
= *Bispora monilioides Corda in Icones Fungorum, 1 : 9. 1837.*

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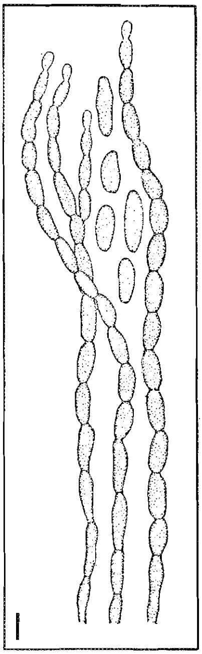

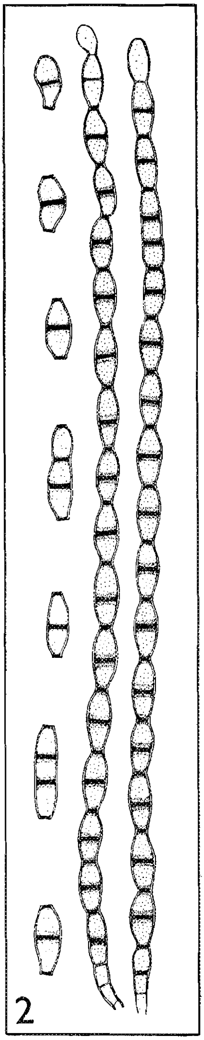

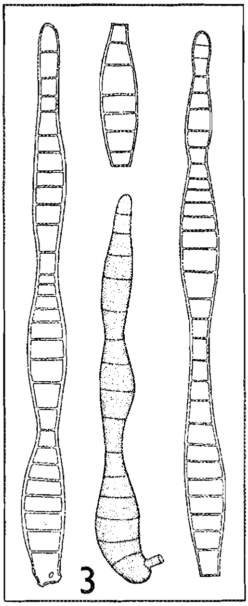

FIG. 1. *Xylohypha nigrescens*, isolated conidiophores with conidial chains, and conidia (I.M.I. 462); × 500.

FIG. 2. *Bispora antennata*, isolated conidiophores with conidial chains, and conidia (I.M.I. 9882); × 500.

FIG. 3. *Septonema hormiscium*, conidiophores and conidia from Hughes (61); × 500.

large and the whole development and sequence of events can easily be followed obtained. The main stalk of the conidiophore, therefore, has resolved itself (Hughes (56)). The conidiophore is formed from an upturned repent hypha or from an erect lateral branch; it is up to 200μ long, 4-5μ wide*, septate, and with the septa 18-25μ apart. Towards the apex of the mature conidiophore, constrictions are found at the septa in increasing depth and with the

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* *All measurements given in this paper were made from preparations in lactic acid, with or without cotton blue.*

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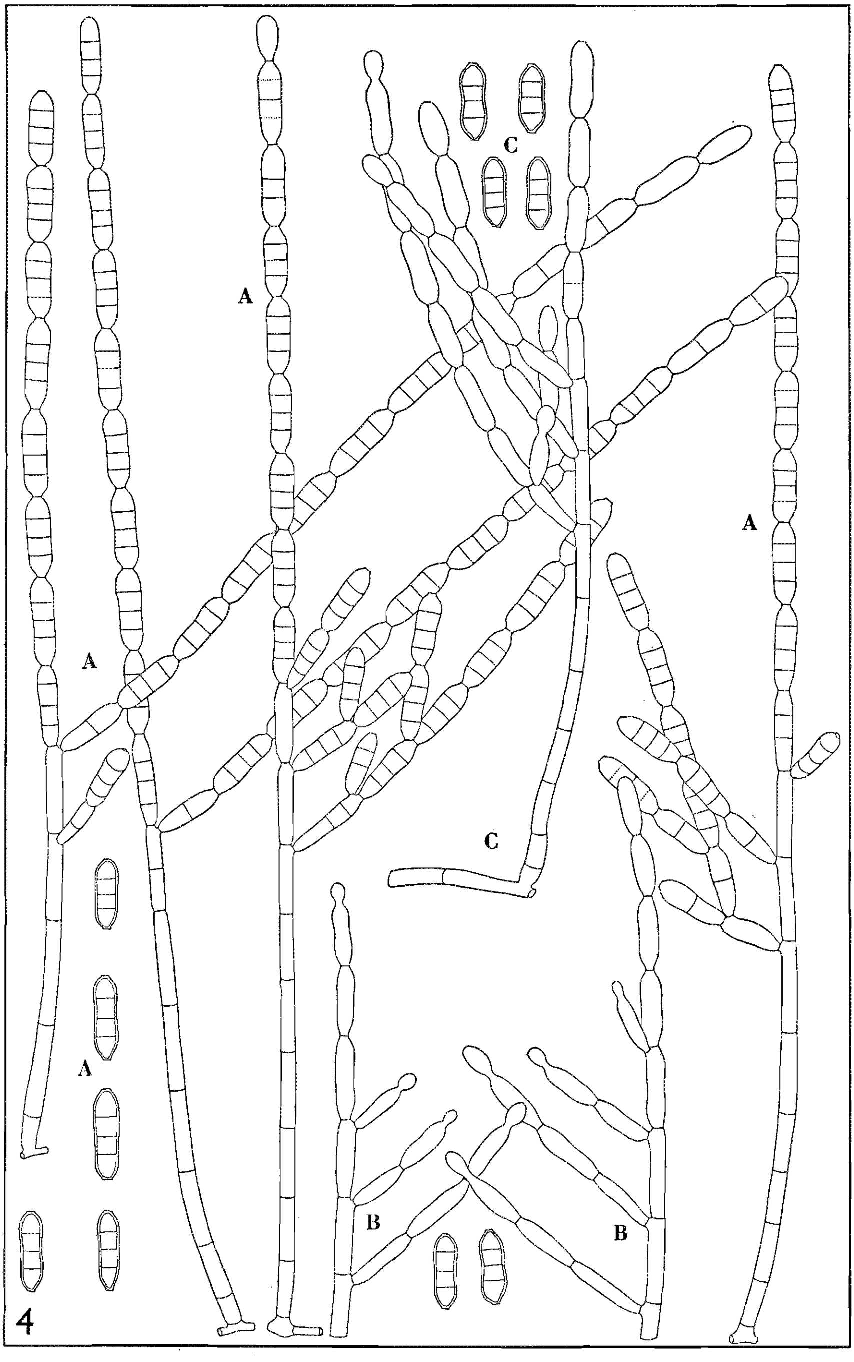

FIG. 4. *Septonema secedens*, conidiophores and conidia from Hughes (56); × 500.

slightly wider cells formed in acropetal succession a long-beaded effect is above, by acropetal growth, into a chain of conidium initials separated by septa at constrictions. Towards the apex of the conidiophore, at different levels, up to four lateral acropetal branches develop; and at the septa of the branches constrictions occur from their first formation, and these may also bear secondary and then even tertiary lateral branches; all the cells of the lateral branches are conidium initials (18-23μ long) and a more or less arborescent (albeit occasionally unilateral) appearance is the result. The mature conidiophore and chains of conidia in *Septonema secedens* is merely a branched aerial hypha, the laterals and the upper part of the main stalk of which have developed as conidial units. Maturity in this fungus is reached with the development of color and of three septa in each initial although the basal conidia of the terminal and lateral chains may be only once or twice septate or even continuous.

In **Septonema harknessii** (Ellis) comb. nov.* the fructification is exactly like that of *S. secedens* but the conidia are much larger and up to 7-septate at maturity. In **Septonema leptaleum** (Ellis) comb. nov.** the conidia are up to 7-septate but narrower than those of *S. harknessii.*

In a young development of *Septonema secedens* (Fig. 4, *B*, *C*) the appearance of the conidiophore and chains is very reminiscent of the *Cladosporium*-type of conidial apparatus (Fig. 5) produced by '*Ceratostomella pluriannulata*' (Lagerberg, Lundberg, and Melin (75)) where all the conidia are amerospores

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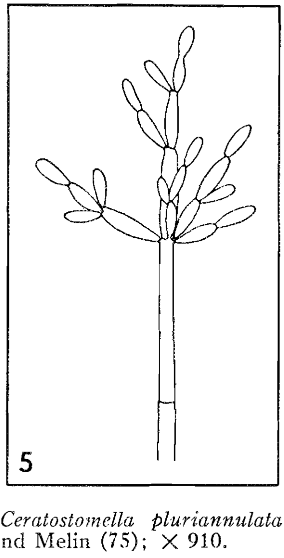


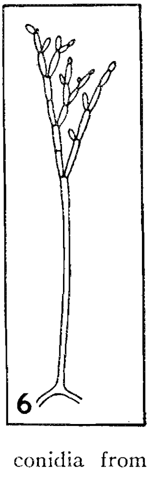


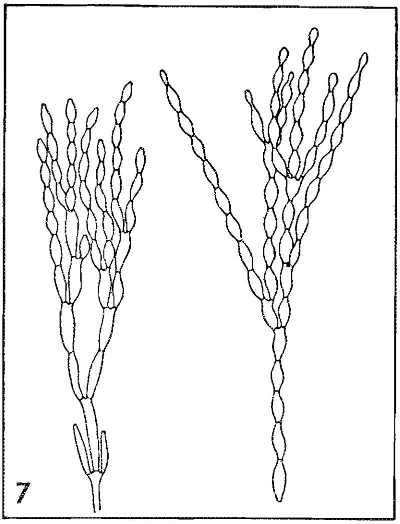
FIG. 5. '*Ceratostomella pluriannulata*', conidiophore and conidia from Lagerberg, Lundberg, and Melin (75); × 910.

FIG. 6. *Cladosporium* sp., conidiophore and conidia from Brett (14); slighty reduced from original.

* ≡*Dendryphion harknessii Ellis in Bull. Torrey Botan. Club, 8 : 27. 1881 (as Deudryphium).*

** ≡ *Dendryphion harknessii var. leptaleum Ellis in Bull. Torrey Botan. Club, 8 : 27. 1881 (as Dendryphium).*

≡ *Dendryphion leptaleum (Ellis) Sacc. in Sylloge Fungorum, 15 : 112. 1901 (as Dendryphium leptaleum Ell.).*



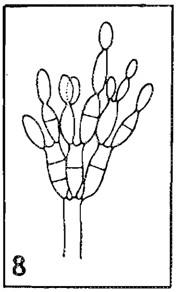


FIG. 7. *Cladosporium harknessii*, portion of conidiophore and two branched chains of conidia (DAOM 28997); × 475.
FIG. 8. *Cladosporium* sp., apex of conidiophore and conidia from Bisby (9); × 450.

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and again where the development of conidial chains is the same. A similar '*Cladosporium*'-type of fructification (Fig. 6), illustrated by Brett (14) was this conidiophore bears unilateral branches as is so often found in *Septonema secedens*.

In **Cladosporium harknessii** (Peck) comb. nov.† (Fig. 7) the fructifications are compact and brownish; the tremendously long, branched, acropetal chains are composed of more or less lemon-shaped amerospores. Towards the base of the chains the conidia are longer, almost cylindrical, and merge gradually with the thin, branched conidiophores below as they do with the shorter conidia above. Peck† stated that this species is 'related to and congeneric with such species as *Oidium aureum*. . . .' !

In one of Bisby's (9) illustrations of a Canadian isolation of *Cladosporium* sp. (Fig. 8) the lower conidia in the branched system are variously septate but they secede as readily as the others and function as conidia. These lower conidia in the chain have been called 'ramoconidia' by Mr. Mason (oral communications) and although the term is not restrictive its does imply that the lower or first formed conidia are somewhat different from the smaller upper ones formed later. Differences in the component conidia of acropetal chains are not at all uncommon especially in *Ramularia* spp. (e.g. *R. onobrychidis* Allesch. (Hughes (43)) and *Septonema pallidum* (Grove) Hughes (61).

Dendryphion griseum Berk. & Br. seems to be somewhat half way between *Cladosporium* and *Septonema*. In this fungus (Fig. 9) the conidiophore is of determinate length and one to three branched chains of conidia are produced on short denticles at the apex. The conidia are continuous to 3-septate whereas in *Septonema* the conidia are mostly three or more septate at maturity. And this seems to me to be the only real difference between the two genera

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† ≡ *Monilia harknessii Peck in N.Y. State Museum Rept., 34 : 49. 1883 [as 1881].*

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although it must be admitted that *S. secedens* and *S. harknessii* do not remind one much of a *Cladosporium*. *Dendryphion griseum* in any case is not a *Dendryphion* and I consider it to be best classified as **Cladosporium griseum** (Berk. & Br.) comb. nov.*

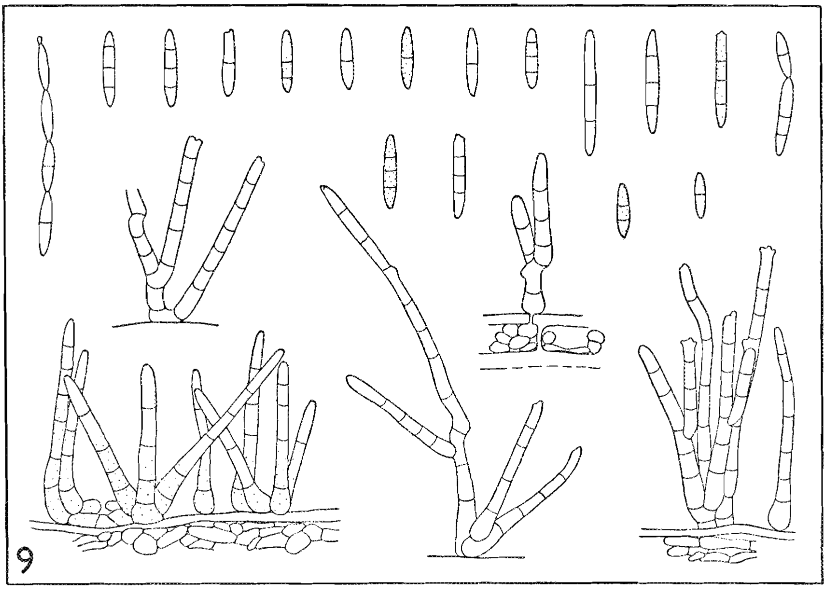

FIG. 9. *Cladosporium griseum*, mycelium, conidiophores, and conidia (I.M.I. 4333); × 500.

De Vries (30) has discussed conidium development in *Cladosporium* spp.; his figure of *C. avellaneum* de Vries forma *avellaneum* de Vries is reproduced here as Fig. 10. In *C. cladosporioides* (Fres.) de Vries he figured the conidiophores as not increasing in length whereas in *Heterosporium variabile* Cooke (which he called *Cladosporium variabile* (Cooke) de Vries) the main stalk of the conidiophore was shown to increase in length by the development of a succession of lateral subterminal growing points and terminal conidia produced in turn at each new growing point after varying degrees of elongation; chains of conidia produced on the primary conidia, however, develop in the manner of *Cladosporium* proper. (A similar type of conidiophore elongation and production of *Cladosporium*-like chains is found on the primary conidia of *Ramularia* spp. e.g. *R. onobrychidis* Allesch.). This character of the increase in length of the main stalk of the conidiophore in some species, or of sporogenous cells in other species, I consider to be of paramount importance in the classification of Fungi Imperfecti as set out here. (This type of development is dealt with in Section II and will include such fungi as *Helminthosporium* auct (e.g. *H. apiculatum*), *Heterosporium*, *Dactylosporium*, *Atractina*, and *Tritirachium* to mention only a few.)

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* ≡ *Dendryphion griseum Berk. & Br. in Ann. Mag. Nat. Hist. II, 7 : 177. 1851* [*as Dendryphium*].

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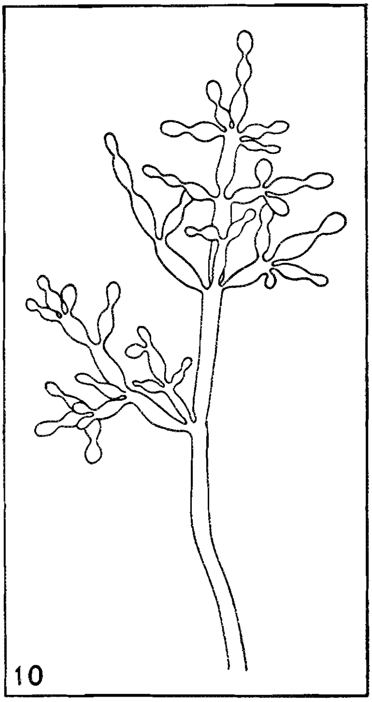

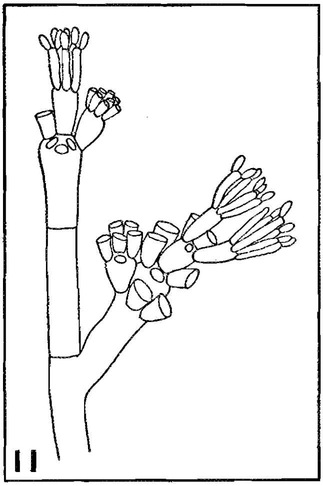

FIG. 10. *Cladosporium avellaneum* forma *avellaneum*, conidiophore and conidia from de Vries (30); slightly reduced from original.

FIG. 11. *Hyaloscypha dematiicola*, part drawing of conidiophore with metulae and conidia from pure culture (DAOM 28286(*b*)); ×1000.

In *Haplographium delicatum* Berk. & Br. (= *H. bicolor* Grove)* (Fig. 11), the type species of *Haplographium* Berk. & Br., I consider that a much modified and very condensed *Cladosporium*-type of conidiophore fructification occurs. The conidiophores of *Hyaloscypha dematiicola* are erect, simple, septate, thick-walled, and brown except at the paler apex and it is altogether a well differentiated structure. At maturity the apex is capped by a ball of slime containing conidia and partially enveloping the other cells upon which they were borne. In pure culture on malt agar the solitary globules of conidia are about 35 μ in diameter and very occasionally up to 45 μ. When neighboring conidial globules touch they unite, with the result that often an extensive sheet of slimy conidia can be formed. Around the apex of the main stalk are borne up to eight oval, pale brown metulae surrounding a central metula which is really a continuation of the growth of the main stalk. Each primary metula bears secondary metulae in the same way that the apex of the main stalk of

---

* *I have shown by pure cultures in Britain that Hyaloscypha dematiicola (Berk. & Br.) Nannfeldt (det. R. W. G. Dennis) is the perfect state of this Haplographium. Both states were found frequently together in Britain (as they are on the type!) and I also find the same association in my collections of this fungus in New York State, U.S., and Ontario, Canada. It has received one independent name in Canada:*

= Scopularia populi Dearn. & Bisby apud Bisby et al. The Fungi of Manitoba. 1929, p. 130.

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the conidiophore bears primary metulae but the secondary metulae are narrower and usually hyaline to subhyaline. Similarly, tertiary metulae (in a perfectly formed head) are borne on the secondary ones; these are hyaline and narrower than the secondary metulae. There can be differentiated, therefore, three rows of metulae which are successively narrower, proceeding distally from the apex of the main stalk of the conidiophore. Each tertiary metula bears an apical conidium produced as a blown-out end (as are the metulae themselves) and three or four lateral and subterminal conidia have been seen attached although perhaps more than this may develop. I have seen no chains of conidia. As detected by their smaller dimensions conidia may be seen to have developed on some secondary metulae in place of one or more tertiary metulae. In depauperate conidiophores even the secondary metulae may be replaced by conidia. The slimy head of this *Haplographium* conidiophore I consider therefore to be homologous with a *Cladosporium* conidiophore but with a more well differentiated conidiophore and condensed and regularly whorled lateral branches; furthermore the crowded primary and secondary branches (metulae) have developed into permanent structures, failing to secede at maturity. The primary and secondary metulae may be considered, paradoxically, to be 'ramo-conidia' which do not secede and which can more obviously be differentiated from the conidia than can the ramo-conidia of *Cladosporium* from the other conidia in the *Cladosporium* chains. In *Hyaloscypha dematiicola* the tertiary metulae may become detached from the secondary metulae and function as conidia but they may be differentiated by their larger size.

Abnormalities in the head of conidial *Hyaloscypha dematiicola* are not uncommon in field collections or pure culture on agar media. Perhaps the most interesting ones are those in which the central primary metula is much longer than the lateral ones thus more obviously indicating the nature of the central metula as being a continuation of the growth of the conidiophore. The central tertiary metula may even bear quaternary metulae. Then again one of the lateral primary metulae may appear as a brown cylindrical cell, larger than the other metulae and resembling a side branch of the conidiophore; like the main stalk this enlarged metula bears a slimy head of metulae and conidia.

It has been claimed (Mason (82)) that the conidia in this fungus are abstricted from the sporophores in immense numbers but I am unable to verify this. In pure culture where development can be observed more easily the slimy head of conidia is more or less hemispherical on the compact branched head of the main stalk of the conidiophore. In a slimy head 40μ in diameter I calculate that there are about 2500 conidia (measuring $3.5 \times 1.5\mu$); this approximates the number which would be borne in a regular head composed of a succession of nine primary, eight secondary, and seven tertiary metulae bearing five apical and subapical conidia.

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Section IB

In Section IB are classified species some of which have a striking morphological similarity with some forms included in Section IA. Now in IA the mycelium is for the most part composed of narrow hyphae whereas in Section IB the hyphae and conidiophores are wide and these often form a superficial weft on natural substrata. In most of the forms included here the conidia develop on specialized terminal or intercalary swellings of the main stalk of the conidiophore or on terminal swellings of lateral branches.

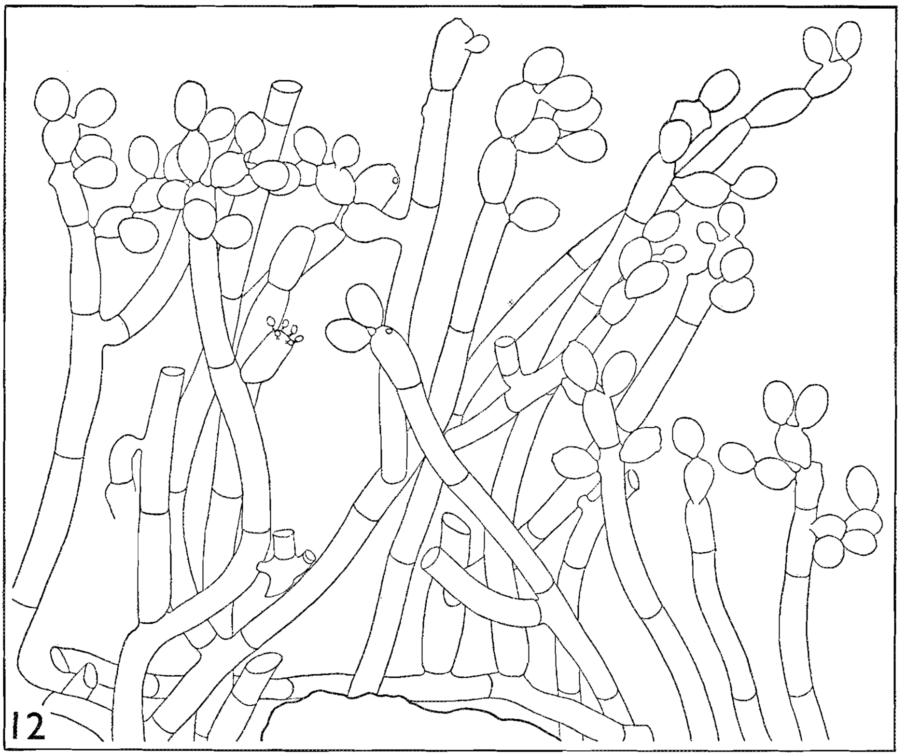

FIG. 12. *Pellicularia pruinata*, conidiophores (one of which bears a basidium), and conidia from Hughes (50); ×500.

In *Pellicularia pruinata* (Bres.) Rogers (Fig. 12) (Hughes (50)) the sparingly branched conidiophores are really of the *Cladosporium*-type (Fig. 10); the long, erect, and wide conidiophores are modified above into a terminal acropetal chain of more or less oval conidia which are denticulate at both ends whilst the lateral branches are also modified into conidia, entirely or for most of their length. In *Oidium aureum* Link ex Fr. (Fig. 13), the type species of the genus, a similar state of affairs is found but the shorter conidiophores are themselves more branched towards the base; they bear a terminal acropetal chain of conidia and lateral ones as well.

The morphology of *Torula ramosa* Fuckel (Fig. 14) is immediately reminiscent of *Oidium aureum* although the dematiaceous nature of the mycelium,

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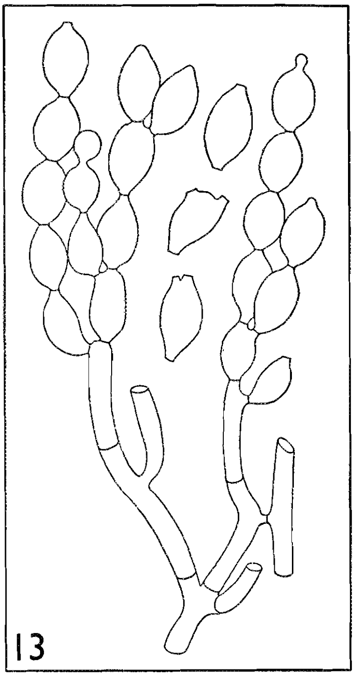

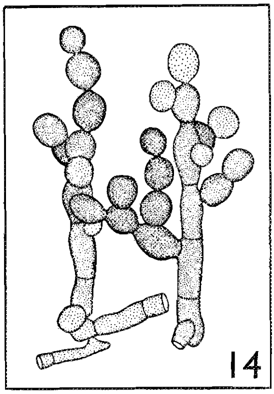

FIG. 13. *Oidium aureum*, conidiophores and conidia (I.M.I. 5366); ×500.
FIG. 14. *Oidium ramosum*, mycelium, conidiophores, and conidia (I.M.I. 6072); ×500.

conidiophores, and conidia does not really fit the fungus for adequate inclusion in the genus *Oidium*; Linder (78) stated that in *Oidium* the conidiophores are never black or fuscous. Another species in Herb. I.M.I. is congeneric with *Torula ramosa* and together these two black molds may well constitute a new genus. At present, however, I prefer to dispose those collections in Herb. DAOM as **Oidium ramosum** (Fuckel) comb. nov.*

In Linder's treatment of the genus *Oidium* Link ex Fr. there seems to be two main groups of species, (1) those in which the conidiophores (often merely repent hyphae) produce vesicles bearing solitary conidia or chains of conidia on denticles or conidiophores with chains of conidia produced directly upon them, and (2) those in which the conidiophores bear a number of conidia solitarily on conspicuous denticles which are not usually restricted to any one cell of the conidiophore and those cells bearing the denticles are not at all or only slightly swollen. (An odd species *Allescheriella crocea* (Mont.) Hughes (50) (= Linder (78) sub *Oidium simile*) (Fig. 46) I consider best classified in *Allescheriella* (Section III) of which generic name this is (as *A. uredinoides*) the type species).

* ≡ *Torula ramosa Fuckel in Symbolae Mycologicae, p. 348. 1870.*
≡ *Torula ramosa Peck in N.Y. State Museum Rept., 32 : 39. 1880 [as 1879].*
≡ *Torula peckii Sacc. & Syd. in Sylloge Fungorum, 14 : 1070. 1899.*

The type collections of both names have been seen; the former at Herb. R.B.G. Kew, England, and the latter at New York State Museum, Albany, N.Y. A recent collection from Canada is DAOM 28726, on wood, Merivale Woods, near Ottawa, Ont., 24.vii.1952.

Some 22 species treated by Linder, including *Pellicularia pruinata* (= *Oidium candicans* (Sacc) Linder) and *Oidium aureum* are found in the first group and amongst themselves show a great deal of variation. In *Pellicularia pruinata*, for instance, some lateral conidial branches are composed of only a single conidium borne on a denticle although most lateral branches are two or three conidia long. There is no clear line separating the two groups. In *Oidium conspersum* (Link) Linder (Fig. 15), the type species of the generic name *Acladium* Link, which would be included in the second group of species the erect conidiophores are terminated by a single conidium and along the upper three quarters of the length of the septate conidiophores are borne solitary conidia on well marked denticles; five other species included by Linder are similar to *O. conspersum* in this way. In *O. conspersum* I have not observed any particular regular order in the production of the conidia other than a more or less simultaneous development or a haphazard one. I agree with

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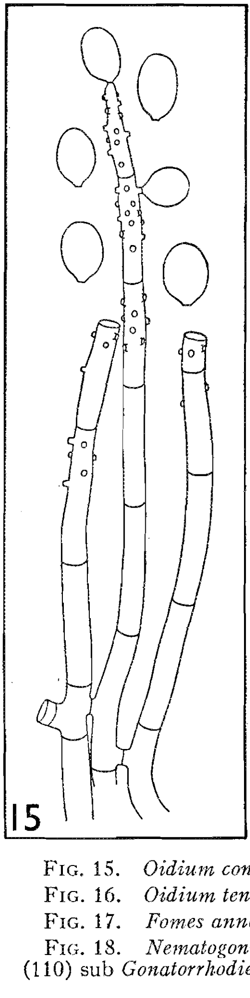

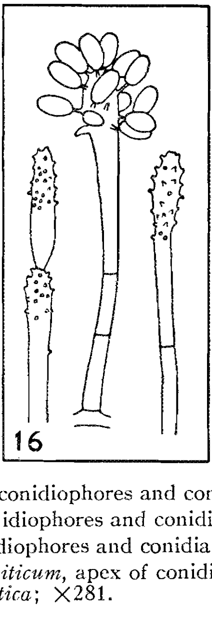

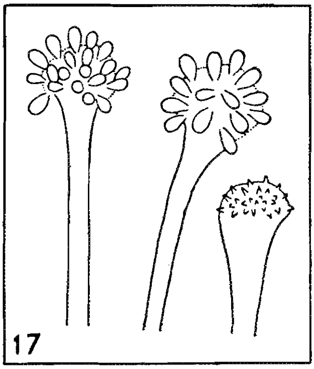

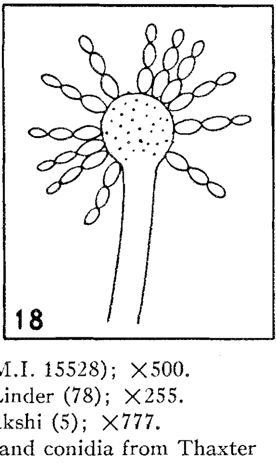

FIG. 15. *Oidium conspersum*, conidiophores and conidia (I.M.I. 15528); ×500.

FIG. 16. *Oidium tenellum*, conidiophores and conidia from Linder (78); ×255.

FIG. 17. *Fomes annosus*, conidiophores and conidia from Bakshi (5); ×777.

FIG. 18. *Nematogonium parasiticum*, apex of conidiophore, and conidia from Thaxter (110) sub *Gonatorrhodiella parasitica*; ×281.

Linder that *O. conspersum* and the similar species are best classified along with *O. aureum*, the type species, even though the conidia are solitary or, as I prefer to look upon it and paradoxical though it may seem, even though the lateral chains of conidia have been reduced to single conidia. In *Oidium* spp., those with chains of conidia have few lateral (conidial) branches whereas in those species producing solitary terminal and lateral conidia the conidiophores bear numerous denticles supporting such solitary conidia.

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If one now considers *Oidium tenellum* (Berk. & Curt.) Linder (Fig. 16) it will be observed that the denticles bearing solitary conidia are numerous and are restricted to the upper regions of one, two, or three terminal cells of the conidiophore; furthermore, these cells are slightly swollen and immediately suggest the conidial apparatus found in *Oedocephalum* (e.g. *Fomes annosus* (Fr.) Cooke, Fig. 17) and a number of other genera whose members have conidia produced on denticles on swollen cells of the conidiophore or its lateral branches. *Oidium tenellum* certainly seems to provide a connecting link between such species as *O. conspersum* and those with the *Botrytis–Oedocephalum* type of fructification. Such genera are briefly mentioned below but it is worth while drawing attention to the fact that *Gonatobotryum fuscum*, *G. apiculatum* (see p. 594), *Nematogonium parasiticum* (see p. 594) and others produce chains of conidia on denticles. In *Gonatobotryum apiculatum* the short chains are seldom branched whilst in *Nematogonium aurantiacum* the chains of conidia, which are characteristically smaller towards the apex of a chain, are always branched.

Oedocephalum spp. are characterized by simple, erect conidiophores producing conidia more or less simultaneously on denticles on a swollen terminal cell (ampulla). Such conidiophores are produced by *Fomes annosus* (Fig. 17) (see Bakshi (5, 6) sub *Oedocephalum lineatum* Bakshi, and Olson (94) sub *Cunninghamella meineckella* Olson); this was observed in 1889 by Brefeld (13) who proposed the generic name *Heterobasidion* for the conidiophores. Brefeld figured a number of conidiophores with lateral branches arising from the terminal ampulla. An *Oedocephalum* conidial apparatus has been reported also for '*Pyronema omphalodes* (Bull.) Fuckel' by a number of authors, e.g. Schmidt (102). *Oedocephalum echinulatum* Thaxter (109) has minutely echinulate conidia; in this publication Thaxter altogether described four species of *Oedocephalum* including *O. verticillatum* Thaxt., an interesting form with verticillate branches bearing terminal, conidium-bearing, denticulate ampullae.

In *Rhopalomyces elegans* Corda a simple conidiophore bears a terminal ampulla bearing colored conidia. Thaxter (109) beautifully illustrated this fungus and also described and illustrated another species *R. strangulatus* Thaxt. Boedijn (11) considered *R. elegans* to be one of the Mucorales.

In *Gonatobotrys simplex* Corda a simple hyaline conidiophore bears a terminal and a number of intercalary ampullae, each roughened by conidium-bearing denticles; the conidia are hyaline and continuous. The fungus was illustrated by Corda (24) and Drechsler (33).

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In *Gonatobotryum fuscum* Sacc. a simple, pale brown conidiophore has the same form as that of the preceding species; the conidia are oval, pale brown, and are borne in chains of two.

In **Gonatobotryum apiculatum** (Peck) comb. nov.* the conidiophores are simple, erect, dark brown with terminal and intercalary ampullae bearing crowded conidia on denticles. The conidia are borne in short, seldom branched chains. The fungus is found on leaf spots of *Hamamelis* in North America and has been figured by Overholts (96) (as *G. maculicola*).

Nematogonium aurantiacum belongs in Section IB; it produces orange colored colonies. The conidiophores have terminal and intercalary ampullae which produce short branched chains of conidia on denticles, the distal conidia being successively smaller. Ayers (3) has described and figured a fungus associated with *Nectria coccinea* (Pers. ex Fr.) Fr. on *Fagus grandifolia* as *Gonatorrhodiella highlei* A. L. Smith (105) (e.g. Reliquiae Farlowianae 998 on *Nectria coccinea* on *Fagus*, Maine, U.S., det. Ayers as *G. highlei*). The fungus in this collection is identical with de Thümen, Mycotheca universalis 1665 on *Platanus occidentalis* in socio *Nectria* sp., France, sub *Nematogonium aurantiacum* Desm., and with Ellis and Everhart, Fungi columbiani 372 on *Magnolia glauca* in socio ?nectriaceous fungus, New Jersey, U.S., sub *Nematogonium aurantiacum*. It seems highly probable to me that the fungus assigned to *Gonatorrhodiella highlei* in North America is *Nematogonium aurantiacum*.

Gonatorrhodiella parasitica Thaxter† (110), the type species of this genus, was described as apparently parasitic on *Hypocrea* and *Hypomyces* from Connecticut; it has hyaline conidiophores which later become pale fawn being simple or sparingly branched, bearing apical and intercalary ampullae. The conidia are borne on denticles, which are crowded on the ampullae, and are in chains of three, the distal conidia being somewhat smaller than the proximal ones (Fig. 18). In its habit of being a consociant of other fungi, its morphology, and the color of mycelium, conidiophores, and conidia, *Gonatorrhodiella parasitica* does not appear to me to be generically distinct from *Nematogonium*; the following new combination is therefore proposed: **Nematogonium parasiticum** (Thaxter) comb. nov.

In *Mycotypha microspora* Fenner (36) the conidiophores have the apex swollen into a cylindrical ampulla; the continuous hyaline conidia are closely packed, being borne solitarily on denticles. Martin (81) considered this fungus to be one of the Mucoraceae and as such was it described by Fenner.

In *Blastophorella* Boedijn (12), based on *B. smithii* Boed., the conidiophore is swollen into a cylindrical ampulla as in *Mycotypha* but the conidia are oval and 1-septate.

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* ≡ *Haplographium apiculatum Peck in N.Y. State Museum Rept., 28 : 62. 1876* [*as 1875*].
≡ *Gonatobotrys maculicola Wint. in Bull. Torrey Botan. Club, 10 : 7. 1883* (*Jan.*).
≡ *Gonatobotryum maculicola* (*Wint.*) *Sacc. in Sylloge Fungorum, 4 : 278. 1886.*

† ≡ *Gonatobotrys lateritia Peck in N.Y. State Museum Bull. 131 : 21. 1909. Peck described his species on Poria sp. on Platanus from Star Lake, St. Lawrence Co., N.Y., U.S.*

Sigmoideomyces dispiroides Thaxter (109), the type species of the genus, and *S. divaricatus* McLean (79) produce conidia on denticles on spherical ampullae which are borne on well differentiated enveloping hyphae.

The botryose clusters of conidia in *Botrytis* spp. are well known and it is to the conidium-bearing swellings of *Botrytis* that the term 'ampullae' was first applied (by Klebahn (74) fide Whetzel & Drayton (114) who used it for *Botrytis convoluta* Whetz. & Drayt.). The term ampulla has been used here in Section IB for the terminal and intercalary swellings bearing conidia which are usually on denticles and which arise more or less simultaneously. In 1887 de Bary (28) drew attention to the simultaneous origin of conidia in *Sclerotinia fuckeliana* (*Botrytis cinerea* Pers. ex Fr.). (Mason (82) first used the term 'radula spores' for the conidia borne all over the surface of the ascospores of *Nectria coryli* Fuckel whilst still within the ascus; but because these spores may be 'the homologues of the usual phialospores' the term radula spores cannot be used for the conidia of the *Botrytis* type of fungus. Later in the same publication, however, Mason used the term for the *Botrytis* conidia which were described as developing without any reference to a growing point. If the conidia of *Nectria coryli* are phialospores then the term radula spore may refer to conidia which are not precisely homologous. In 1937 Mason (82) returned to the subject of radula spores and differentiated the *Nectria coryli* type as 'slimy radula spores' from the 'dry radula spores' of *Botrytis*. Nannfeldt (in Melin and Nannfeldt (87)) used 'radula spores' for the conidia of *Rhinocladiella atrovirens* Nannf. but I find that in this fungus they arise not more or less simultaneously, or without reference to a growing point, but successively as the blown-out ends of successively produced growing points. For these reasons the confused term 'radula spore' is not here applied to the *Botrytis* type of conidium.)

Botrytis conidiophores are produced by *Sclerotinia draytoni* Budd. & Wakef. (Dennis & Wakefield (29)), *S. spermophila* Noble (91), *S. polyblastis* Greg., *S. narcissicola* Greg., and *S. sphaerosperma* Greg. (Gregory (40)) and *Sclerotinia fuckeliana* de Bary (*Botryotinia fuckeliana* (de Bary) Whetz.) which is known generally in its conidial state as *Botrytis cinerea* Pers. ex Fr.

Elaborate ampullae are the conspicuous features of *Botryosporium* spp. *B. longibrachiatum* (Oud.) Maire is not uncommon in glasshouses in Britain whilst *B. pulchrum* Corda is found outdoors; the last named species is illustrated in Fig. 19. Each conidiophore is repeatedly dichotomous and bears the really striking lateral fertile branches.

Chaetosphaeria phaeostroma (Dur. & Mont.) Fuckel is the presumed perithecial state of *Cladotrichum triseptatum* Berk. & Br. and is not uncommon in Britain on old diatrypaceous fungi. The brown conidiophores mixed with concolorous setae form a shining velvety growth; the conidiophores (Fig. 20) are broad, dichotomously branched with intercalary and terminal more or less spherical ampullae upon which oval to oval-cylindric 3-septate conidia arise more or less simultaneously. *Chaetosphaeria fusca* Fuckel, another fungus which is a consociant of sphaeriaceous fungi, I have collected once in Britain

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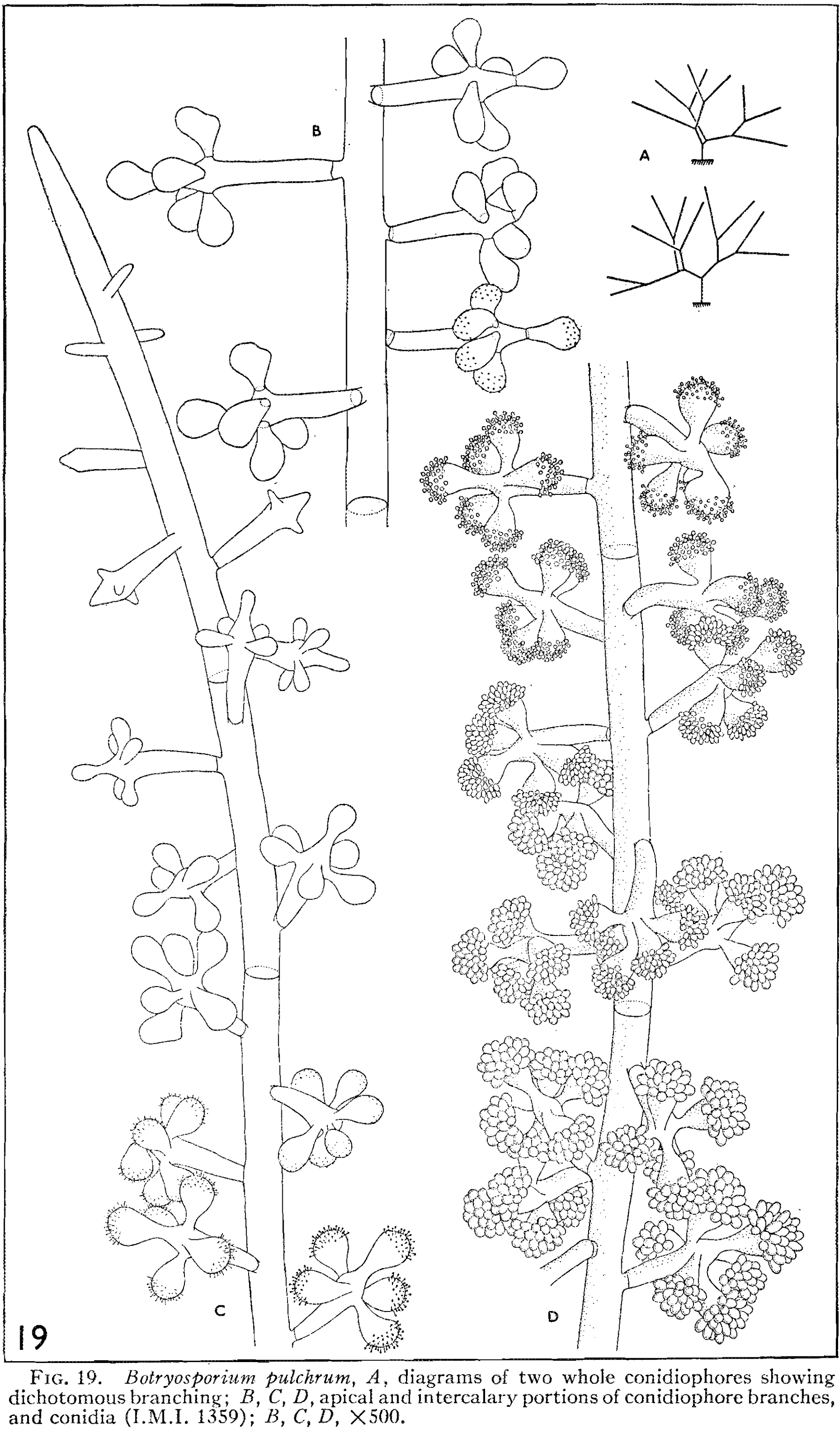

FIG. 19. *Botryosporium pulchrum*, *A*, diagrams of two whole conidiophores showing dichotomous branching; *B*, *C*, *D*, apical and intercalary portions of conidiophore branches, and conidia (I.M.I. 1359); *B*, *C*, *D*, ×500.

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in its presumed conidial state (*Cladotrichum scythophorum* Corda). The sparingly branched and adpressed conidiophores have terminal and intercalary ampullae each bearing a few acropetal chains of waisted-oval, 1-septate conidia, the first conidia of each chain having arisen more or less simultaneously.

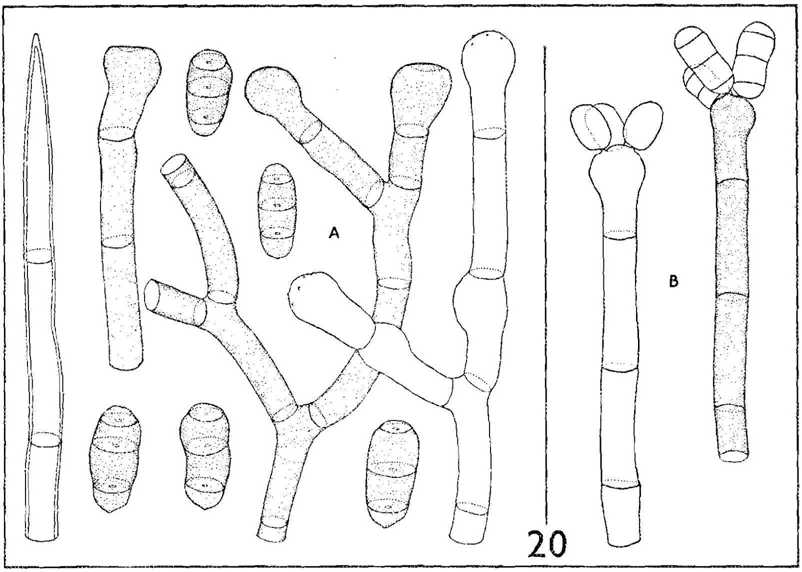

FIG. 20. *Chaetosphaeria phaeostroma*, mycelial seta, portions of conidiophores, and conidia; *A*, I.M.I. 1694; *B*, I.M.I. 1354; ×500.

It is interesting to note that many of the conidial fructifications included in Section IB have been shown to be Basidiomycetes, Phycomycetes, Discomycetes, and Pyrenomycetes; furthermore it appears that they are all perfectly dry-spored.

Section II

The mycelium is immersed or superficial, generally narrow but sometimes as wide as the conidiophores.

In this section the conidia are produced as blown-out ends singly at the apex of the conidiophore and of the successive new growing points which develop just to one side of the previous terminal conidium. At maturity, therefore, a conidiophore or sporogenous cell producing conidia in this way possesses a number of scars; each one of these was in turn terminal (during the development of the now fallen conidium) before being pushed aside by the development of a new growing point. Such conidiophores usually show a perceptible increase in length with the development of each conidium; but in some species a succession of conidia developing on a succession of growing points results not always in a longitudinal extension of the conidiophore or sporogenous cell but the apex becomes swollen with the development of successive conidia.

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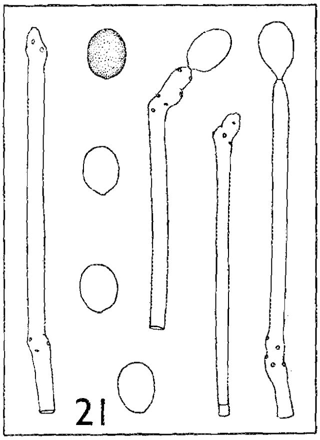

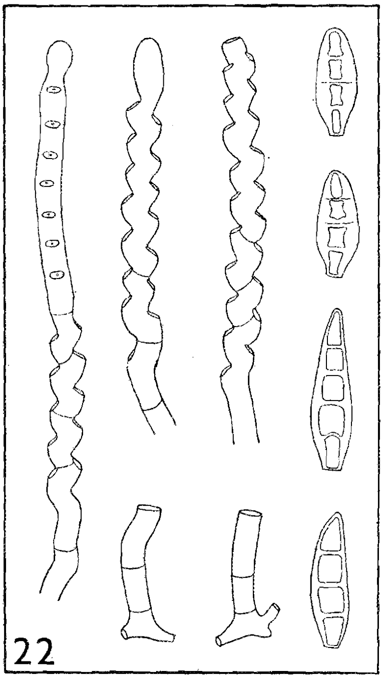

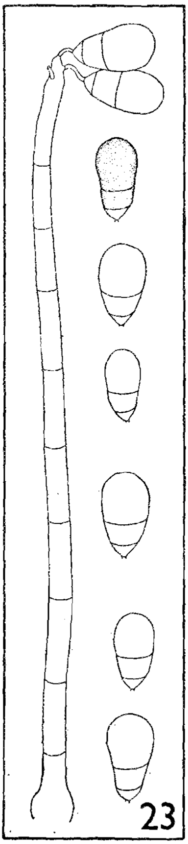

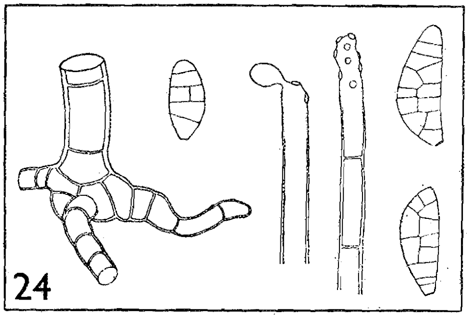

FIG. 21. *Virgariella atra*, apices of conidiophores, and conidia (I.M.I. 27613); ×500.

FIG. 22. *Helminthosporium guareicola*, conidiophores and conidia from Hughes (68); ×500.

FIG. 23. *Brachysporium obovatum*, conidiophore and conidia from Hughes (48); ×500.

FIG. 24. *Dactylosporium macropus*, portions of conidiophores and conidia from Hughes (63); ×500.

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The distance between the successive scars is often fairly constant but in some species it varies considerably; this distance, of course, depends on the activity of the new growing point before blowing-out into a new terminal conidium. In *Virgariella atra* Hughes (Fig. 21; see also p. 654) groups of conidial scars along the length of the conidiophore alternate with smooth portions where there has been no conidium production; I have observed this in cultures of '*Acrothecium simplex* Berk. & Br.' and '*Acrotheca acuta* Grove'*, and also in *Helminthosporium guareicola* Stevens (Fig. 22) (Hughes (68)) and *Daldinia angolensis* (Welw. & Curr.) Sacc. (Hughes (59)). The interrupted conidium production is seen to best advantage in *Arthrobotrys* spp. e.g. *A. superba* Corda (Drechsler (32) and also Matruchot (86)), the resultant conidiophore having the appearance of one of the members of Section IB such as *Gonatobotrys simplex* Corda in which species the conidia on each ampulla arise simultaneously; in *Arthrobotrys* the swellings are the result of the successive development of closely inserted conidia.

A further example is found in *Cordana* sp. I in Herb. DAOM in which a succession of conidia results in a swollen apex to the conidiophore, and furthermore with further growth sterile lengths of conidiophore may eventually alternate with fertile swellings. This is very reminiscent of the illustration by Sibilia (104) of *Arthrobotryella hernica* Sibilia; numerous phaeodidymospores are shown attached to denticles on well differentiated ampullae but I do not know whether the conidia arise in succession or simultaneously. Close observation of the *Echinobotryum* conidia of *Stysanus stemonitis* (Pers. ex Fr.) Corda indicates that these, too, arise in succession, on a short hypha the apex of which becomes swollen as further conidia develop.

In some species e.g. *Brachysporium obovatum* (Berk.) Sacc. (Fig. 23) (Hughes (48)) and *Dactylosporium macropus* (Corda) Harz (Fig. 24) (Hughes (63)) the conidiophores are simple and more or less setose, being dark brown and thick-walled. In '*Helminthosporium simplex* Kunze' (Fig. 25) and '*H. apiculatum* Corda' (Fig. 26), two not uncommon molds of wood in Britain, dematiaceous fusoid conidia are formed successively; both species have been collected in North America. In *Diplorhinotrichum candidulum* v. Höhn. (Fig. 27) the conidiophores are generally short, thin-walled, and more or less hyaline.

In the foliicolous *Camptomeris* spp. (Hughes (66)) well differentiated conidiophores are unilaterally thickened and produced on specialized vesicular supporting-cells which are subglobose to cylindrical with somewhat inflated distal ends. In the *Polythrincium* conidiophores of *Cymadothea trifolii* (Pers.) Wolf (Hughes (66)) conidiophores are also produced on a palisade of cylindrical vesicular cells.

In *Cercospora* spp. the conidiophores are borne on an immersed or semi-immersed stroma and the genus is usually classified amongst the Dematieae. *Isariopsis griseola* Sacc. has almost synnematous conidiophores with conidia like those of *Cercospora* and is classified amongst the Stilbaceae. The genera

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* *Acrotheca acuta Grove is completely out of place in Acrotheca (= Ramularia Unger fide Hughes (49)) and could, I believe, be adequately placed in the genus Rhinocladiella Nannf.*

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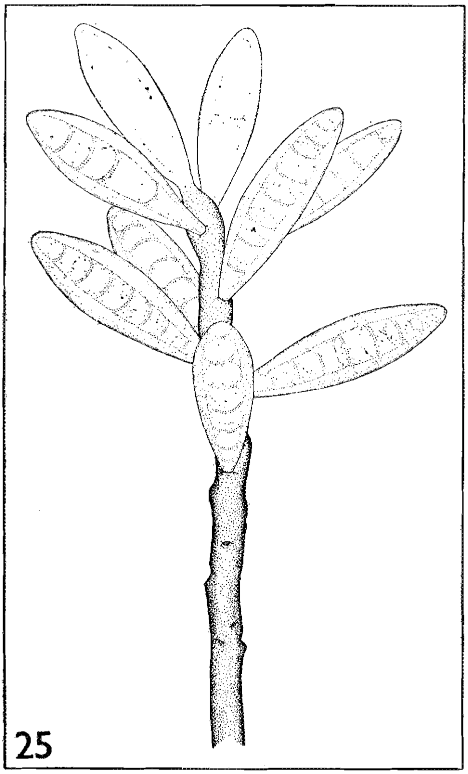

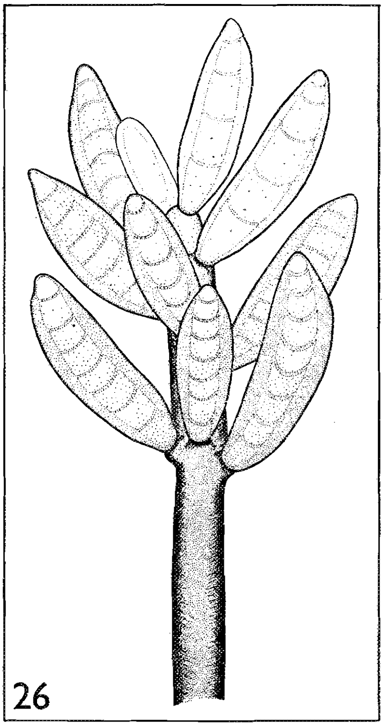

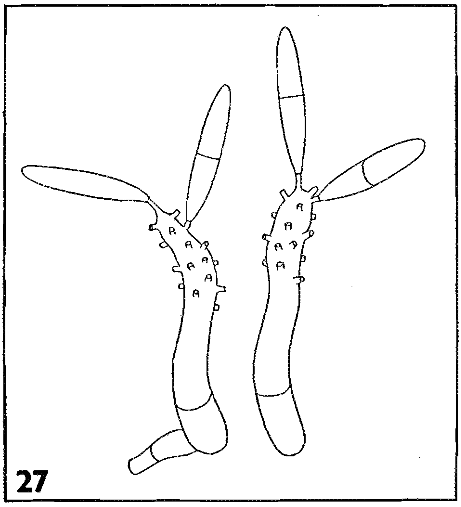

FIG. 25. *Helminthosporium simplex*, conidiophore and conidia (I.M.I. 1353); ×750.

FIG. 26. *Helminthosporium apiculatum*, conidiophore and conidia from pure culture (I.M.I. 1357); ×750.

FIG. 27. *Diplorhinotrichum candidulum*, conidiophores and conidia from Hughes (54); ×1000.

Cercospora and *Isariopsis*, however, are otherwise similar with respect to conidium origin and development and should appear together in any classification. In the hyperparasitic species assigned to *Arthrobotryum*, for want of a better generic name, the conidiophores are in synnemata and the conidia develop as in *Isariopsis*; the type species of *Arthrobotryum* is included in Section III because it has a different type of conidium development. *Phaeoisaria cornui* (Bain.) Mason is another species which produces synnemata and classified here in Section II; it produces amerospores whereas the synnematous *Sclerographium aterrimum* Berk. produces dictyospores (Hughes (60)).

In species usually with mononematous branched conidiophores, conidium production is often restricted on specialized terminal and lateral unicellular sporogenous cells and these are more or less cylindrical, subulate, or flask-shaped. In *Tritirachium* (Fig. 33) and *Calcarisporium* (Hughes (51)) the more or less subulate sporogenous cells are terminal and also in regular verticils below the uppermost septa of the main stalk and they form a wide angle with it. In the *Verticicladium* conidiophores of *Desmazierella acicola* Lib. (Fig. 28)

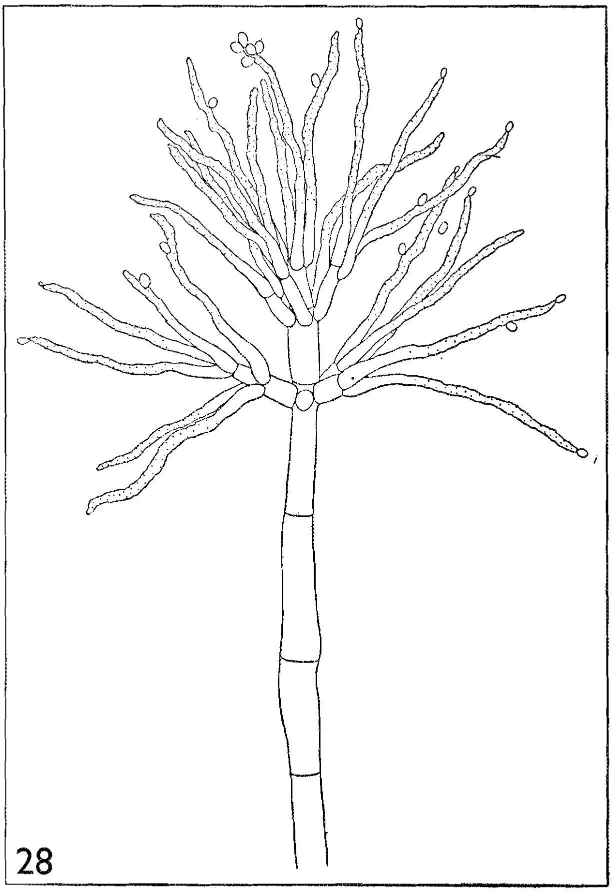

FIG. 28. *Desmazierella acicola*, conidiophore from pure culture, from Hughes (51); ×500.

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the subulate sporogenous cells are borne apically and subapically on secondary lateral branches, themselves borne terminally and in whorls on primary branches.

In *Verticicladiella abietina* (Peck) Hughes (Fig. 29; see also p. 653) long subulate conidiophores bear a slimy head of conidia; primary, secondary, and tertiary branches are adpressed to the main stalk and these bear slightly divergent subulate sporogenous cells which bear conidia as in the *Verticicladium* conidiophores of *Desmazierella acicola.* The presence or absence of slime is used to differentiate the two genera.

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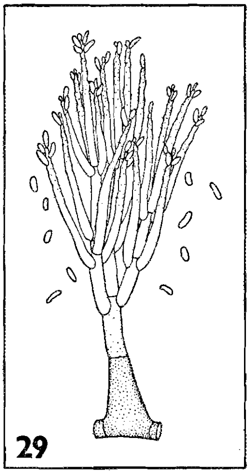

FIG. 29. *Verticicladiella abietina,* short conidiophore, and conidia from pure culture (DAOM 33941); ×1000.

Verticils of sporogenous cells are characteristic of *Costantinella* spp. (Fig. 34) (see Nannf. & Eriks. (89)) and some species of *Hansfordia* (Hughes (51)) and *Nodulisporium* e.g. conidial *Daldinia concentrica* (Bolt. ex Fr.) Ces. & de Not. as described and figured by Molliard (88). In other species of *Hansfordia* and *Nodulisporium,* and in *Virgaria nigra* Nees (Fig. 30) the

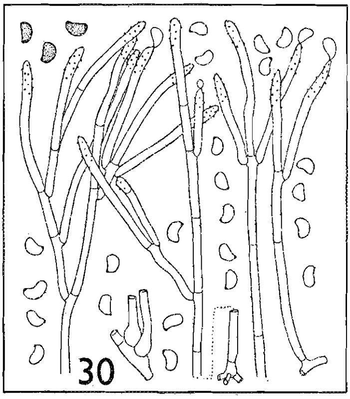

FIG. 30. *Virgaria nigra,* conidiophores and conidia (I.M.I. 40653(*g*)): ×500.

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branching is more or less irregular and the laterals which are fertile are not particularly well differentiated. **Virgaria lignatilis** (Schw.) comb. nov.* is apparently not uncommon in Eastern North America and differs from *V. nigra* only in its shorter conidiophores and slightly smaller conidia.

In *Atractina biseptata* v. Höhnel (Fig. 31), the type species of this genus, primary and secondary branches are crowded and closely adpressed and parallel to each other and more or less parallel also with the erect almost setose mononematous conidiophore. A compact head is thus formed and the tertiary branches take the form of subulate, hyaline sporogenous cells which produce a succession of conidia in slime from a succession of new growing points; at maturity the conidia become 2-septate and the central cell brown, the outer ones remaining more or less hyaline or becoming very pale brown and collapsing readily.†

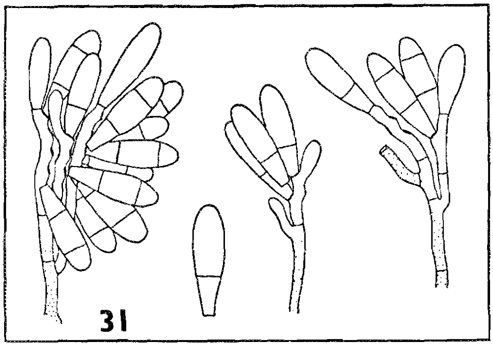

FIG. 31. *Atractina biseptata*, conidiophores and conidia from pure culture (DAOM 29146); ×1000.

Most of the Helicosporeae as treated by Linder (77) may be classified in Section II. In *Helicosporium vegetum* Nees ex Fr.§ the conidia arise in succession on short hyaline lateral sporogenous cells found towards the base of conidiophores but above, only solitary conidia may arise—on short denticles. The succession of conidia is particularly evident in *H. aureum* (Corda) Linder

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* ≡ *Cladosporium lignatile Schw. in Trans. Am. Phil. Soc. II, 4 : 277. 1832.*
= *Botrytis fuliginosa Cooke & Ellis in Grevillea, 6 : 5. 1877.*
= *Botrytis atrofumosa Cooke & Ellis in Grevillea, 6 : 90. 1878.*
≡ *Virgaria atrofumosa (Cooke & Ellis) Sacc. in Sylloge Fungorum, 4 : 281. 1886.*

† *From a study of published descriptions and illustrations it seems very probable to me that Atractina biseptata will finally give way to a much earlier specific epithet and generic name. The following tentative synonymy is being considered at present in Herb. DAOM.*
? = *Graphium macrocarpum Corda in Icones Fungorum, 3 : 13. 1839.*
≡ *Haplographium macrocarpum (Corda) Sacc. in Sylloge Fungorum, 4 : 620. 1886.*
? = *Stachybotrys elata Sacc. in Michelia, 2 : 560. 1882.*
≡ *Sterigmatobotrys elata (Sacc.) Oud. in Nederl. Kruidk. Arch. II, 4 : 548. 1886.*
≡ *Phragmostachys elata (Sacc.) Cost. in Les Mucédinées simples, p. 97, Paris. 1888 [ex errore sub 'P. atra'].*
? = *Scopularia venusta Preuss in Linnaea, 24 : 133. 1851 (see Bayliss Elliott (7)).*

§ *Whilst at the Commonwealth Mycological Institute I germinated the ascospores of Ophionectria cerea (Berk. & Curt.) Ell. & Everh. and pure cultures were obtained. These cultures produced conidiophores and conidia identical with those obtained previously from the cultures prepared from conidia of what was at that time referred to Helicosporium vegetum.*

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(sensu Linder) in which the sporogenous cells are swollen. In *Helicoma mülleri* Corda and other *Helicoma* spp. the conidia may arise on short lateral, finally geniculate branches or in succession on the elongating main stalk of the conidiophore; the lateral sporogenous cells are particularly conspicuous in *H. proliferens* Linder. *Helicomyces roseus* Link ex Fr. (Fig. 32) produces conidia successively at the apex of each new growing point of the conidiophore.

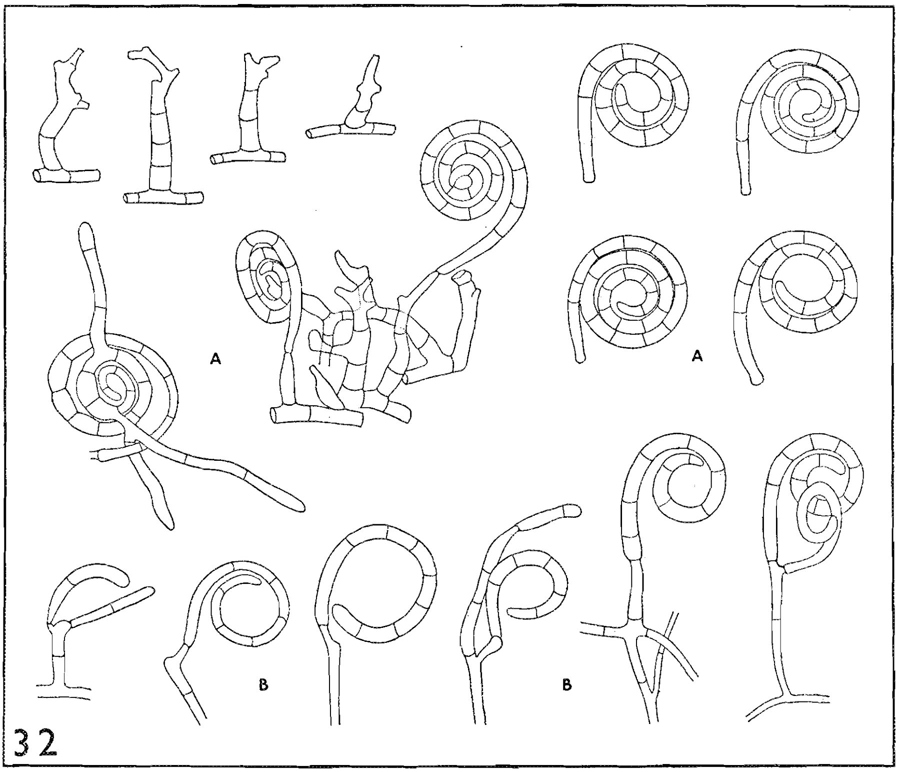

FIG. 32. *Helicomyces roseus*, mycelium, conidiophores, and conidia (I.M.I. 6054(*a*)); *A*, from the host, one conidium is germinating; *B*, from pure culture; ×500.

In most of the conidiophores and sporogenous cells that I have observed, the scars are generally distributed along the sides of the fertile region but I have not observed any spiral arrangement with any degree of certainty. In the conidiophores of *Cymadothea trifolii* the successive new growing points are produced regularly to one side so that after conidia have formed and fallen away the conidial scars are unilateral. In *Tritirachium* spp. (e.g. **Tritirachium hydnicola** (Peck) comb. nov.* (Fig. 33)) and *Beauveria* spp. the conidia are produced regularly to the left and to the right and the fertile region of the sporogenous cell resembles the rachis of a wheat ear and may be conspicuously zigzag. This is characteristic also of *Helminthosporium guareicola* Stevens

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* ≡ *Virgaria hydnicola Peck in N.Y. State Museum Rept., 42 : 32. 1889.*
= *Clonostachys dichotoma A. L. Smith in Trans. Brit. Mycol. Soc. 6 : 56. 1918.*

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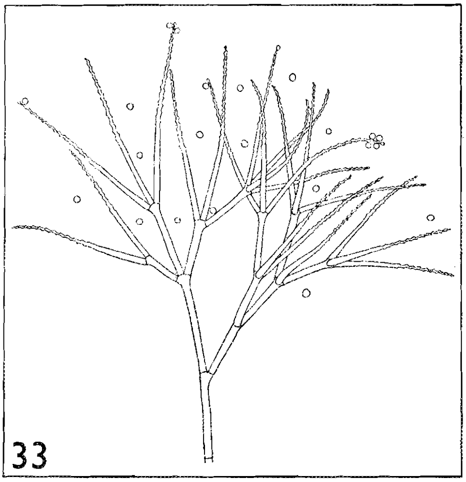
(Fig. 22) in which two or three zigzag fertile portions may be separated by short cylindrical regions which bear no scars and the planes of the separate fertile regions may be different. In *Calcarisporium arbuscula* Preuss, on the other hand, the new growing points develop less regularly and close together in succession so that the restricted fertile region may become swollen, and after the conidia have fallen this is strongly denticulate in all directions (Hughes (51)); occasionally, however, an irregular zigzag apex may result from successive conidium production. In *Costantinella tillettei* (Desm.) Mason & Hughes and in **Costantinella micheneri** (Berk. & Curt.) comb. nov.* (Fig. 34) a single (or double?) row of conidia is produced in linear succession on a somewhat bulbous and eventually recurved apex of the sporogenous cells; such cells are so characteristic that the term *cervix* (pl. *cervices*) was proposed for them by Nannfeldt and Eriksson (89).



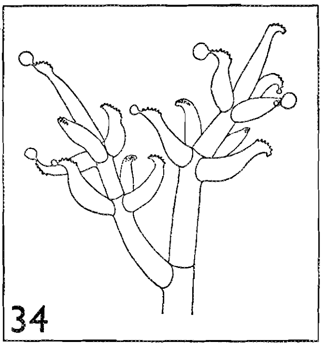


FIG. 33. *Tritirachium hydnicola*, conidiophore and conidia from the type collection; ×500.

FIG. 34. *Costantinella micheneri*, portion of conidiophore, and conidia (DAOM 29409); ×750.

In a number of species, and sometimes genera, the conidia are borne on short stalks and after the conidia have fallen these remain as denticular continuations of the conidiophores; such denticles are characteristic of *Diplorhinotrichum*, *Hansfordia*, *Calcarisporium*, *Phaeoisaria*, *Cacumisporium*, and a number of *Fusicladium* spp.

In species of *Brachysporium* (Fig. 23) and *Camposporium* (Hughes (46)) the conidia are borne on stalks which are cut off by two septa from conidiophore and conidium thus delimiting a separating-cell. In *Beltrania* the separating-cells are much swollen and well differentiated structures (Hughes (54)).

* ≡ *Botrytis micheneri Berk. & Curt. apud Berk. in Grevillea, 3 : 111. 1875.*
= *Verticillium candidum Peck in N.Y. State Museum Rept., 34 : 48. 1883 [as 1881].*
≡ *Costantinella athrix Nannf. & Eriks. in Svensk. Bot. Tidskr. 46 : 122. 1952.*

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In **Streptothrix globosa** (Schw. ex. Fr.) comb. nov.* brown, rough-walled conidia are each borne on a very short separating-cell in succession on the main branches of the much branched conidiophores (Fig. 35) or on the very short predominantly fertile side branches.

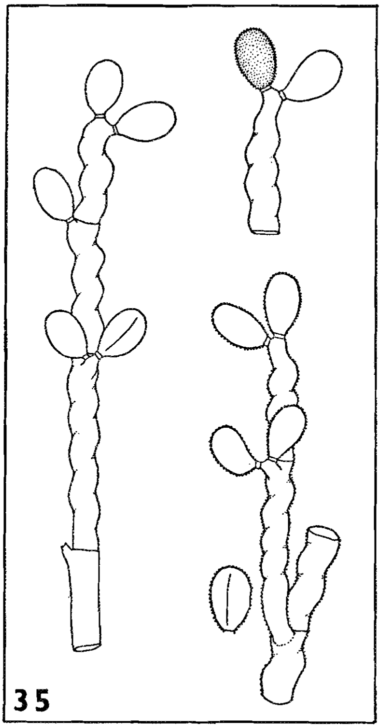

FIG. 35. *Streptothrix globosa*, portions of conidiophores, and conidia (DAOM 34510); ×1000.

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* ≡ *Trichoderma globosum Schw. in Syn. Fung. Carol. Super. p. 77. 1822.*
≡ *Trichoderma globosum Schw. ex. Fr. in Systema Mycol. 3 : 215. 1829.*
≡ *Oidium inquinans Schw. [nom. nov.] in Trans. Am. Phil. Soc. II, 4 : 286. 1832.*
≡ *Torula inquinans (Schw.) Sacc. in Sylloge Fungorum, 4 : 251. 1886.*
= *Streptothrix atra Berk & Curt. apud Berk. in Grevillea, 3 : 107. 1875.*
= *Trichosporium densum Karst. in Hedwigia, 23 : 59. 1884.*
= *Strumella cornyeoidea Sacc. & Wint. in Fungi europaei no. 2984. 1883.*
= *Streptothrix pereffusa Sumstine in Mycologia, 6 : 34. 1914.*

In Herb. DAOM this species is being at present identified on Acer, Betula, Carpinus, Carya, Castanea, Cornus, Corylus, Crataegus, Fagus, Hicoria, Juglans, Quercus, and Tilia. On Quercus and Castanea, in particular, characteristic tuberculariaceous stromata are formed but on the other hosts longer conidiophores are borne on much smaller stromata; I take this to be a host reaction. Davidson (27) published strong evidence in favor of Urnula craterium (Schw.) Fr. being the ascigerous state of Streptothrix globosa (as Strumella coryneoidea). In Streptothrix globosa the conidia are nearly always coarsely roughened and they possess one or two longitudinal slits in the outer wall. In S. mounceae Sumstine the conidia do not possess a slit but a thin, paler, more or less circular area of outer wall just above the base. S. abietina Peck is closely related to but distinct from S. globosa; the wall of the conidium is conspicuously roughened and bears an apical or subapical germ pore.

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Pseudocamptoum fasciculatum (Cooke & Massee) Mason* (see also p. 644) is related morphologically to *Streptorhrix* in that the conidia show similar successive development and possess a longitudinal germ slit.

In *Dicranidion fragile* Harkness (Fig. 36), the type species of *Dicranidion* Hark. (syn. *Pedilospora* v. Höhnel), hyaline staurospores are produced in succession as the blown-out ends of successively developing growing points of the conidiophores. This is the only genus known to me in which staurospores develop in this particular manner.

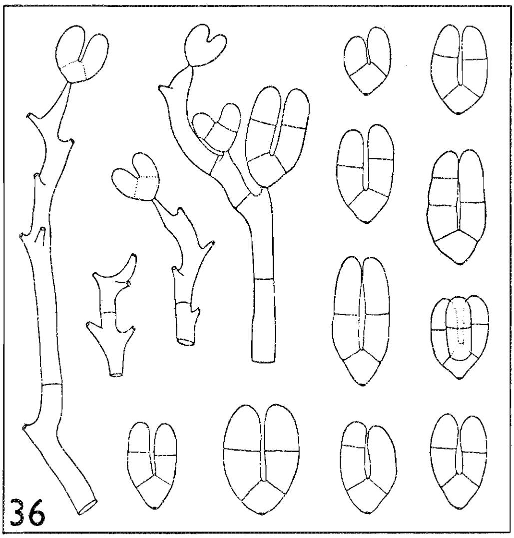

FIG. 36. *Dicranidion fragile*, conidiophores and conidia from the type collection; ×1000.

The primary conidia occasionally produce acropetal chains in Section II; thus in *Ramularia* spp., e.g. *R. onobrychidis* Allesch., each primary conidium (borne directly on the conidiophore) produces a simple or branched chain of conidia in acropetal succession. Similarly in *Heterosporium* spp., acropetal chains may develop from the primary conidia which develop in succession as the blown-out ends of successive new growing points of the conidiophore; some species of this genus have been redescribed and the development of the conidia nicely portrayed by Jacques (72). De Vries (30) transferred most of these to *Cladosporium*.

** = Sporostachys maxima Sacc. in 'Not. Myc. xxiii in Atti Acad. ven.-trent.-istr. p. 92. 1917.'*
≡ Melanographium maximum (Sacc.) Sacc. in Syloge Fungorum, 25 : 937. 1931.

This species is based on C. F. Baker, Fungi Malayana no. 394 sub Sporostachys maxima. Sporostachys is an earlier generic name for Pseudocamptoum and so in all probability is Melanographium Sacc. based on M. spleniosporum Saccardo (101). Mason (82) suggested a still earlier name Cordella Speg., based on C. spinulosa Speg., as being a probable synonym; until the types of the original species of Cordella are examined collections in Herb. DAOM are disposed as Pseudocamptoum fasciculatum.

The conidia in this section are usually dry but they develop in slime in *Verticicladiella abietina* (Peck) Hughes (see p. 653), *Cacumisporium tenebrosum* Preuss (Fig. 37), and *Atractina biseptata* v. Höhnel whilst the conidia are by no means dry in *Helicosporium* spp.* The species included in Section II produce amerospores, didymospores, phragmospores, dictyospores, helicospores, or staurospores.

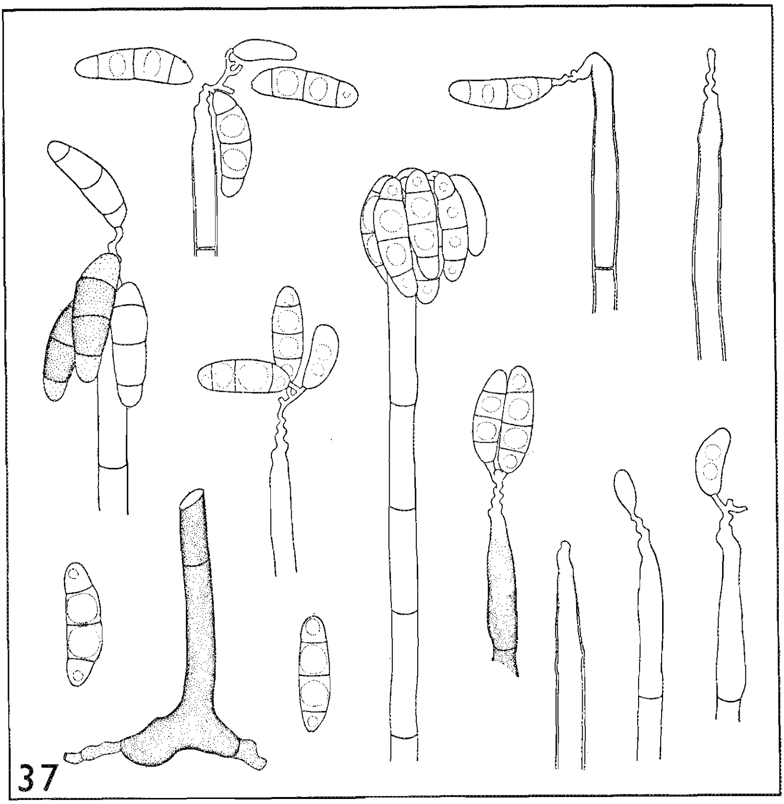

Fig. 37. *Cacumisporium tenebrosum*, conidiophores and conidia (I.M.I. 18435(*b*)); ×500.

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Biggs (8) described and illustrated the successive sympodial production of conidia (as 'oidia') on conidiophores ('oidiophores') in *Corticium coronilla* v. Höhnel & Litsch.

Twyman (111) described the acervuli of *Colpoma quercina* (Fr.) Wallr. and the conidia were shown to arise in the manner characteristic of Section II but the type of conidial fructification was not identified with any separately named member of the 'Melanconiaceae'. As far as I am aware the production of conidia on immersed conidiophores by this method is not common.

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* *In Herb. DAOM three species included in Helicosporium by Linder (77) are considered best classified in the apparently dry spored genus Drepanospora Berk. & Curt. e.g. D. pannosa Berk. & Curt. (= Helicosporium serpentinum Linder), and the Drepanospora conidia of Lasiosphaeria nematospora Linder and L. elinorae Linder.*

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Section III

In this Section are classified fungi whose conidiophores bear a solitary apical usually thick-walled and colored conidium on the main stalk or its branches thereby terminating growth. A plurality of conidia develops from a single conidiophore or single branch only by its proliferation *through* the conidial scar left by the previous conidium with the development of a conidium on the proliferation; by a repetition of this proliferation a succession of conidia is produced accompanied by a successive increase in length of the conidiophore. This increase in length, therefore, occurs by a different method from that described for Section II. When such proliferations and conidium production occur the conidia may not be markedly thick-walled more especially when they are produced in slimy heads.

The mycelium is generally immersed, sometimes superficial.

The conidiophores show considerable variation throughout the Section and is best illustrated by reference to various species. In *Trichocladium opacum* (Corda) Hughes (62) (Fig. 38) the conidiophore may be so small as to be virtually absent as when a conidium is borne directly on one of the semi-immersed mycelial cells; alternately a conidiophore composed of up to three short cells may be developed but even so it is little different from the mycelium. *T. asperum* Harz also shows considerable variation in its conidiophores. In both species of *Trichocladium* the conidia are solitary and as in all members of Section III they develop as blown-out ends.

In some species of *Sporidesmium*, e.g. *S. larvatum* Cooke & Ell. (Fig. 39), the conidiophores may be constantly very short but in others, e.g. **Sporidesmium folliculatum** (Corda) Mason & Hughes comb. nov.[*] (Fig. 40) they may be as long as the conidia.

In *Coniosporium paradoxum* (Corda) Mason & Hughes (Hughes (47)) (Fig. 41) simple or branched and tufted conidiophores, whose component cells become balloon-like at maturity, carry a single, terminal, more or less oval dictyospore. Similar balloon-like conidiophores are also found in '*Sporidesmium*' *nitens* Schw.[**]

In other fungi the conidiophores may be well differentiated, erect, more or less setose, simple, thick-walled, many times septate, and much longer than the conidia; these are found in *Monosporella setosa* (Berk. & Curt.) Hughes

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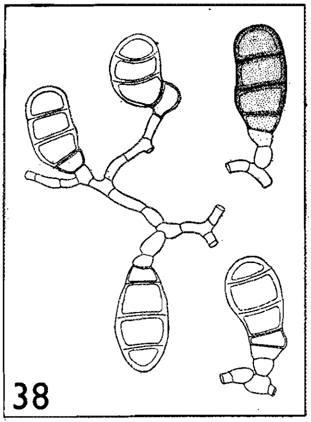
[*] ≡ *Helminthosporium folliculatum Corda in Icones Fungorum, 1 : 13. 1837.*
== *Helminthosporium brachytrichum Cooke & Ellis in Grevillea, 6 : 6. 1877.*
== *Helminthosporium macilentum Cooke in Grevillea, 6 : 74. 1877.*
== *Helminthosporium orthospermum Sacc. & Fairm. apud Sacc. in J. Mycol. 12 : 50. 1906.*
This fungus is as common around Ithaca, N.Y., and Ottawa, Ont., as it is in Britain.

[**] *The late S. C. Damon (26) considered this to be an earlier name for Coniosporium paradoxum which seems to be restricted to the periderm of Betula in Europe, usually in association with the conidial state of Melanomma subdispersum (Karst.) Berl. & Vogl. (== Helminthosporium longipilum Corda == H. arbusculoides Peck!). I have collected 'Sporidesmium' nitens a few times around Ottawa, Ont., and Ithaca, N.Y., on bare wood but never on the periderm of Betula although Melanomma subdispersum is exceedingly common around Ottawa on this host. The european collections of Coniosporium paradoxum are sufficiently distinct from 'Sporidesmium' nitens to merit their being kept separate until pure cultures prove them to be the same.*



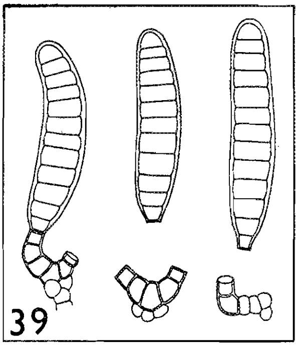
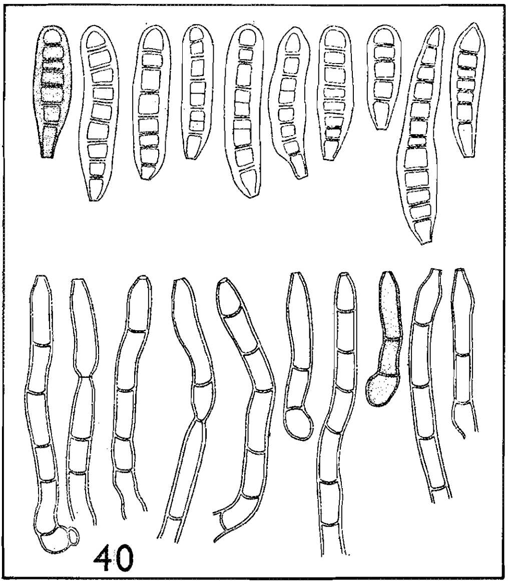


FIG. 38. *Trichocladium opacum*, mycelium, conidiophores, and conidia from Hughes (62); ×500.

FIG. 39. *Sporidesmium larvatum*, conidiophores and conidia (Ellis, N. Am. Fungi, no. 355, on cedar rails); ×500.



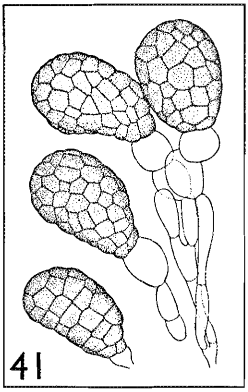


FIG. 40. *Sporidesmium folliculatum*, conidiophores and conidia (I.M.I. 5505); ×500.

FIG. 41. *Coniosporium paradoxum*, conidiophores and conidia from Hughes (47); ×500.

(Fig. 42, and see also p. 654), in *M. sphaerocephala* (Berk. & Br.) Hughes (Fig. 43, and see also p. 654), and in *Farlowiella carmichaeliana* (Berk.) Sacc. (Fig. 44).

In *Bactridium flavum* Kunze (Fig. 45) and *B. fulvellum* Berk. the conidiophores are tufted and form a tuberculariaceous fructification; each conidiophore is more or less irregularly branched and is in fact a more or less undiffer-

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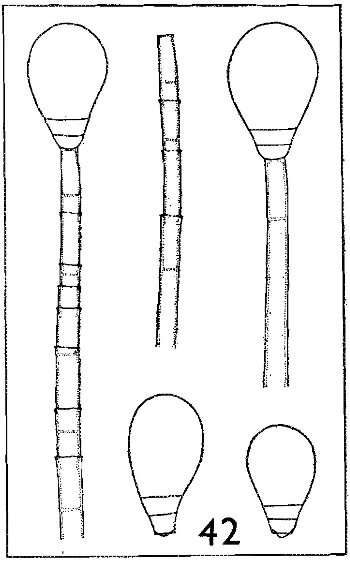

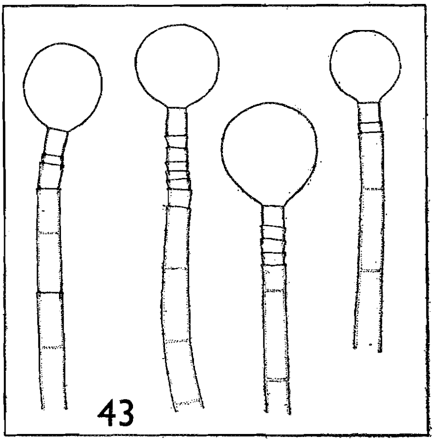

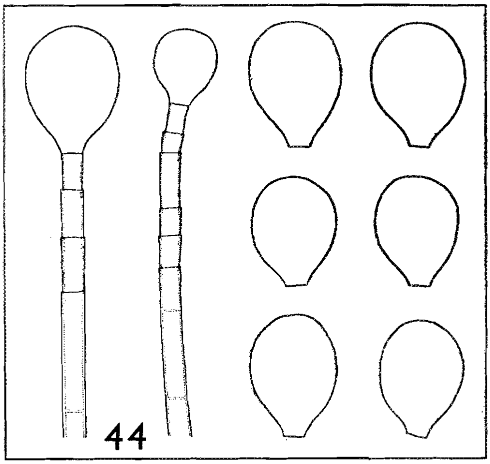

FIG. 42. *Monosporella setosa*, conidiophores and conidia (DAOM 29291(*a*)); ×500.

FIG. 43. *Monosporella sphaerocephala*, conidiophores and conidia (DAOM 29423(*a*)); ×500.

FIG. 44. *Farlowiella carmichaeliana*, conidiophores and conidia (I.M.I. 7040); ×500.

entiated, septate, aerial, branched hypha bearing solitary apical conidia. In Section III, I classify *Allescheriella crocea* (Mont.) Hughes (50) (Fig. 46) which seems to be morphologically related to *Coccospora agricola* Goddard (White and Downing (115)). *Allescheriella crocea* has wide mycelium and its affinities may well be with the Basidiomycetes. Linder (78) included this fungus as '*Oidium simile* Berk.' (see Hughes (50)) but the development of thick-walled conidia on lateral branches, not denticles, places the fungus in Section III.

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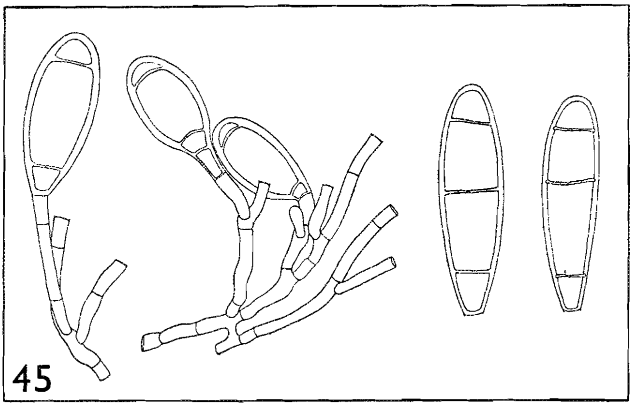

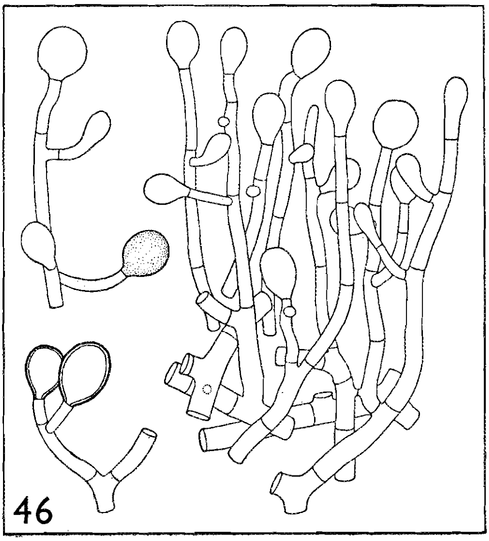

FIG. 45. *Bactridium flavum*, conidiophores and conidia (I.M.I. 33713); ×200.
FIG. 46. *Allescheriella crocea*, conidiophores and conidia from Hughes (50); ×500.

In *Arthrobotryum stilboideum* Cesati (Hughes (55)) and *Leptographium lundbergii* Lagerb. & Melin a more or less penicillate type of branching is observed; the conidiophores are synnematous and simply penicillate in the first and mononematous and repeatedly penicillate in the second; slimy heads of conidia are produced by both. *Stysanus* produces synnematous fructifications and the branching is subpenicillate being most evident at the ends of the central conidiophores. *Scopulariopsis* differs from *Stysanus* mainly in the absence of synnemata but dry conidia develop in both.

The genus *Phragmocephala* Mason and Hughes (85) is included in this Section; the species have mononematous, synnematous, or more or less tuberculariaceous conidiophores. It appeared to the authors of this name that the three generic names required for such species in the Saccardoan scheme would separate obviously related species.

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Now the important feature of Section III is the development first of a solitary conidium at the apex of the conidiophore and its branches thus terminating their growth. There can usually be observed direct continuity between the wall of the conidiophore and that of the conidium. In most cases only a single conidium is produced at each end as in *Phragmocephala* (excluding *P. setosa*, see p. 654), *Bactridium* spp., and some *Sporidesmium* spp. Whereas acropetal chains of conidia are found in Sections I, II, and VI (p. 629) I have never found them in this present Section. A plurality of conidia in Section III can arise only as explained below.

In the West African *Annellophora africana* (Hughes (57)) (Fig. 47), for example, the first conidium is terminal and after seceding the conidiophore proliferates *through* the terminal scar and the apex of the proliferation blows out into another conidium which is cut off from the proliferated conidiophore by a septum; this septum appears at a variable distance above the scar of the first conidium. A series of such proliferations with a single conidium produced at each new level results in a closely or distinctly annellated appearance of the conidiophore. Such a conidiophore with annellations is so characteristic that it is considered worth while proposing the term '*annellophore*' for it. Annellophores, indicating this curious succession of proliferations and terminal conidia are far more general in the Hyphomycetes (and perhaps the Coelomycetes) than has previously been suspected and on the whole little or no attention has been given to annellations in published descriptions and illustrations.

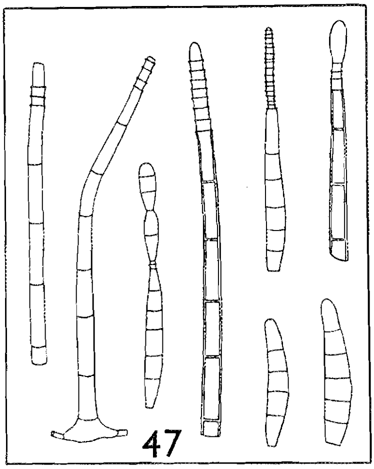

FIG. 47. *Annellophora africana*, conidiophores and conidia from Hughes (57); ×500.

Annellophores which are simple, well differentiated, and septate are found in *Ceratosporella* (Hughes (53, 65)), *Triposporium* (Hughes (53)), *Monosporella* (Figs. 42, 43, 44), *Podoconis* spp. (Hughes (67, 68)), and some *Sporidesmium* spp. Arnaud (1) described his genus *Bainieria* for the single species *B. hyalina* Arn. in which he drew attention to the origin of the conidia being the same as that found in conidial *Venturia inaequalis* (Cooke) Wint. [*Spilocaea*] and *Chaetotrichum* Sydow (≡ *Annellophora* Hughes).

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But annellations are by no means restricted to such unbranched and more or less setose conidiophores; they are to be found, perhaps more commonly, in other genera in which the actual sporogenous cells are unicellular and well differentiated from that part of the conidiophore that supports them, or a distinct support for them may be absent especially in some foliicolous species.

In conidial states referable to *Spilocaea*, *Mastigosporium*, *Stigmina*, *Pollaccia*, and *Deightoniella* (Hughes (59, 69)), all leaf parasites, the annellophores are usually short, single-celled, more or less cylindrical or flask-shaped structures. In *Spilocaea* states the annellations are very conspicuous, but the reverse is true of *Pollaccia* and *Mastigosporium* in which the annellophores are hyaline or subhyaline. In leaf parasites such as these there is an advantage in producing short conidiophores in view of their exposed position. I have also seen conspicuous annellations in the *Septoidium* conidiophores of some species of *Parodiopsis*.* These form-genera are scattered throughout the Saccardoan classification.

On the other hand annellations are characteristic of the sporogenous cells which are supported on distinct mononematous or synnematous stalks. In *Scopulariopsis brevicaulis* (Sacc.) Bain. (Fig. 48, *A*-*D*), which may be regarded as the type species of this genus, the sporogenous cells are annellophores; they have been called phialides and also 'sterigmata' (as in *Penicillium*) but neither term seems to me to be suitable. When young, the annellophores are flask-

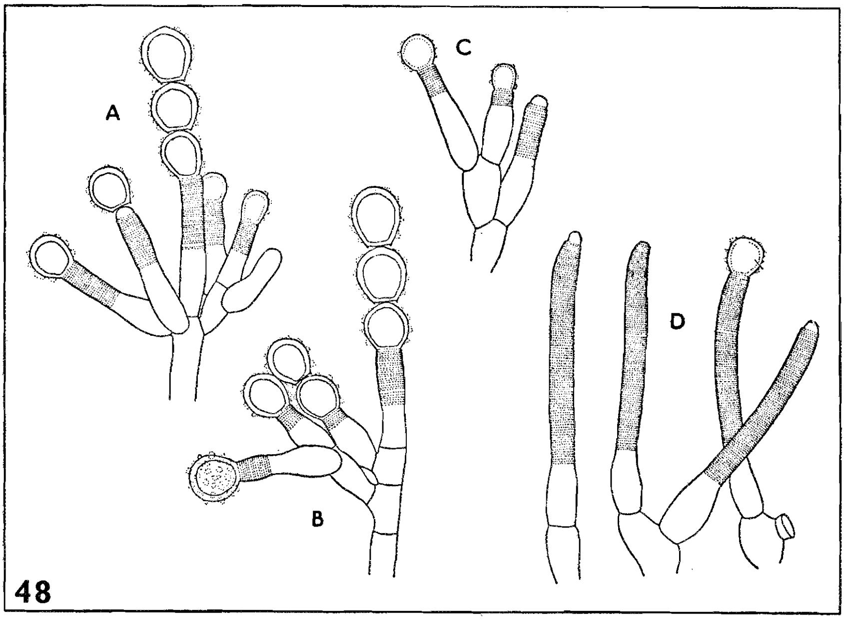

FIG. 48. *Scopulariopsis brevicaulis*, conidiophores and conidia; DAOM 29102, *A*, *B*, from pure culture four weeks old: DAOM 33997, *C*, from two-weeks-old pure culture; *D*, from eight-weeks-old culture; ×1000.

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* *In addition to the Septoidium conidia, most Parodiopsis spp. produce microconidia on long conidiophores by the method characteristic of Section II.*

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shaped with a short, almost cylindrical neck (Fig. 48, *A*, *B*, *C*); in older annellophores (Fig. 48, *D*) the necks are longer by virtue of the greater number of annellations. The conidia have a flattened base encircled by a minute frill; they persist in long fragile chains but these are not true chains in the sense that those of *Xylohypha nigrescens* (Fig. 1) or *Septonema secedens* (Fig. 4) are true chains. It is interesting to note that most illustrations of *Scopulariopsis* spp. show the cylindrical ends of sporogenous cells and the descriptions usually give a wide range for the length of sporogenous cells; this is to be expected considering the method of conidium production. Characteristic of false basipetal chains is the fact that the conidium at the apex of the annellophore is more or less mature before the new one developing below detaches it from the annellophore. The occurrence of chains of conidia developing from annellophores is facultative but obligate in *Xylohypha*, *Bispora*, and indeed all other fungi producing acropetal chains.

The sporogenous cells of *Stysanus** *stemonitis* (Pers. ex Fr.) Corda (Fig. 49) have been called phialides but close examination will show them to be annellophores, with the annellations by no means inconspicuous. As with *Scopulariopsis* (Fig. 48) young annellophores have very short cylindrical necks which increase in length as successive annellations develop. Similar annellations are found in **Stysanus purpureofuscus** (Fr.) comb. nov.** (Fig. 50) and *Trichurus gorgonifer* Bain. (Fig. 51).

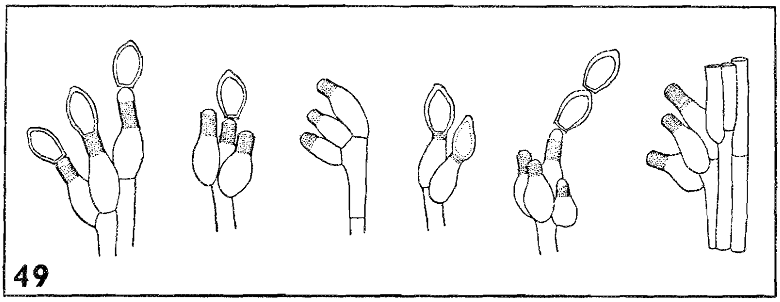

FIG. 49. *Stysanus stemonitis*, portions of synnema, and conidia (I.M.I. 22419): ×1000.

Phaeoscopulariopsis Ota (95) was published for two species, *P. paisii* (Poll.) Ota (≡ *Torula paisii* Poll.) and *P. bestae* (Poll.) Ota (≡ *Torula bestae* Poll.). I have seen an isolation of *Phaeoscopulariopsis paisii* (I.M.I. 36480) and the sporogenous cells are annellophores. Now this genus is precisely

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* *In Pycnostysanus azaleae (Peck) Mason the dry head of conidia is on a stalk as in Stysanus but the conidia develop in acropetal chains as in Xylohypha (Section IA, p. 582) and not from annellophores. Pycnostysanus must be classified in Section IA.*

** ≡ *Aspergillus purpureofuscus Fr. in Systema Mycologicum, 3 : 388. 1832.*
≡ *Aspergillus purpureofuscus Schw. in Trans. Am. Phil. Soc. II, 4 : 282. 1832.*

There seems to be no doubt that Fries obtained a specimen from Schweinitz and I consider both names to be based on the same collection, being thereby obligate synonyms. I.M.I. 34001(c) (Fig. 50) is the same thing.

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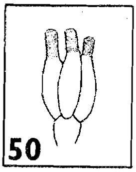

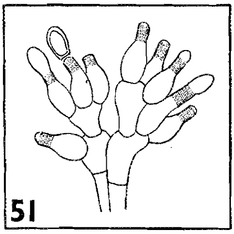

FIG. 50. *Stysanus purpureofuscus*, portion of synnema (I.M.I. 34001(*c*)); ×1000.
FIG. 51. *Trichurus gorgonifer*, portion of synnema, and conidia (I.M.I. 7393); ×1000.

Scopulariopsis with dark colored conidia and is an earlier name for *Masoniella* G. Smith (107) which is based on *M. grisea* (Smith) Smith. The type isolation of *M. grisea* (DAOM 29438) produces chains of conidia from annellophores.

It was suggested by Hughes (55) that the sporogenous cells of *Arthrobotryum stilboideum* Cesati bore annellations; of this I am now convinced following an examination of an isolation of this fungus. In pure culture *A. stilboideum* produces a black slimy mass of conidia; the synnemata are not well differentiated but the annellations on the end cells of the conidiophores can be observed more readily.

The genus *Bactrodesmium* is of particular interest as a member of Section III; it seems to be separable from *Bactridium*, type species *B. flavum* (Fig. 45), only on account of its dematiaceous conidia. In *B. flavum*, *Bactrodesmium abruptum* (Berk. & Br.) Mason & Hughes (Fig. 52), *B. fasciculare* (Corda) Mason & Hughes (Fig. 53), and **Bactrodesmium spilomeum** (Berk. & Br.) Mason & Hughes comb. nov.* (Fig. 54) the conidia are solitary on the ends of branched conidiophores; in *B. masonii* Hughes (Fig. 55, and see also p. 654), however, the conidiophores are likewise branched but grow through the conidial scars of former conidia to produce a proliferation whose apex swells out into another conidium. Two or three conidia may be formed in this way on what may now be called annellophores in this species. When an apparent chain of two conidia is observed (Fig. 55), and this is not uncommon, then this is a false chain, homologous with that produced by *Stysanus stemonitis* or *Scopulariopsis brevicaulis*, the conidia having developed in basipetal succession. The production of annellations in *Bactrodesmium masonii* and their absence in the closely related *B. spilomeum* is further evidence to support the inclusion, in one Section, of those fungi which produce solitary conidia and those which produce a succession from annellophores. Conidiophores with and without annellations are also found in the different species of *Podoconis* (Hughes (67, 68)) and *Sporidesmium*; for example, they are absent in *Podoconis macrura* (Sacc.) Hughes and *Sporidesmium folliculatum* (Fig. 40) but are

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* ≡ *Sporidesmium spilomeum Berk. & Br. apud Rabenhorst in Fungi europaei, no. 1162. 1868.*

This name was omitted from Saccardo's Sylloge Fungorum and from the List of British Hyphomycetes (Wakefield and Bisby (112)), but it was one of the two species mentioned when Cooke proposed the new name in Grevillea, 12 : 35. 1883, the first being S. abruptum Berk. & Br.

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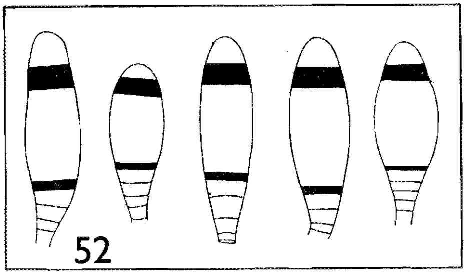

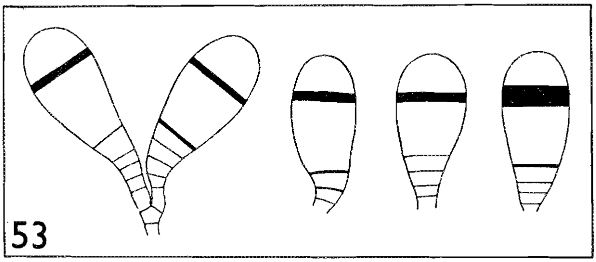

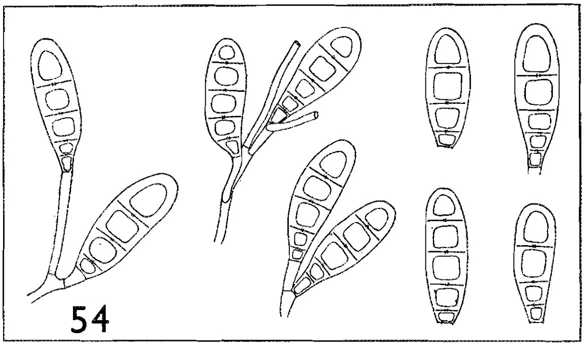

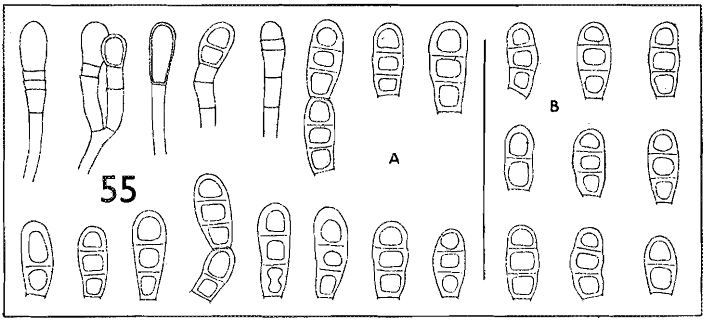

FIG. 52. *Bactrodesmium abruptum*, conidia (I.M.I. 19039); ×500.

FIG. 53. *Bactrodesmium fasciculare*, conidia (I.M.I. 14014); ×500.

FIG. 54. *Bactrodesmium spilomeum*, conidiophores and conidia (I.M.I. 14486); ×500.

FIG. 55. *Bactrodesmium masonii*, conidiophores and conidia; *A*, from I.M.I. 19219(*y*); *B*, I.M.I. 19652(*c*); ×500.

produced in *Podoconis bicolor* Hughes, *P. alta* (Preuss) Mason & Hughes (Fig. 56), and in **Sporidesmium densum** (Sacc. & Roum.) Mason & Hughes comb. nov.* (Fig. 57).

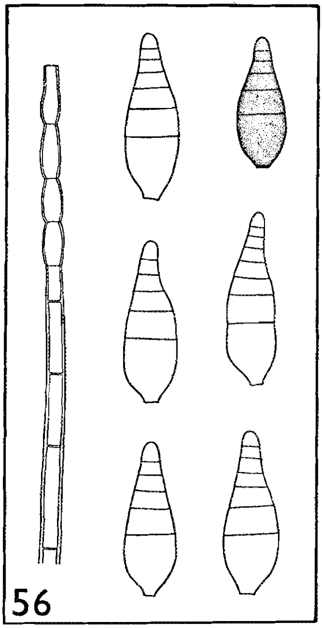

FIG. 56. *Podoconis alta*, conidiophores and conidia from Hughes (67); ×500.

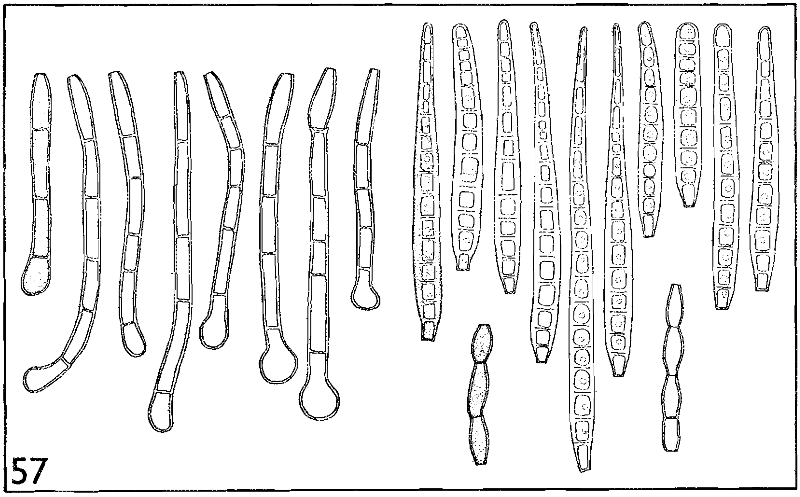

FIG. 57. *Sporidesmium densum*, conidiophores, detached annellations, and conidia (I.M.I. 6784); ×500.

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* ≡ *Helminthosporium densum Sacc. & Roum. in Rev. Mycol. 3 : 29. 1881.*

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In **Thyrostromella negundinis** (Berk. & Curt.) comb. nov.* the subhyaline annellophores form a compact palisade on an erumpent stroma; the conidia are 2-septate and brown. **Thyrostromella pedunculata** (Ell. & Everh.) comb. nov.** (Fig. 58) is only critically distinct from *T. negundinis* on their respective hosts, *Sambucus* and *Acer negundo*, although pure cultures may show them to be identical. In *T. pedunculata* the annellophores are brown and annellations very conspicuous with their diameter decreasing perceptibly with each successive conidium. The conidia are dry, 2-septate, slightly constricted, thick- and dark-walled, rounded at the apex, and flattened at the base which bears a conspicuous frill. In **Thyrostromella sambucina** (Ell. & Everh.) comb. nov.† (Fig. 59) the annellations on the more or less cylindrical

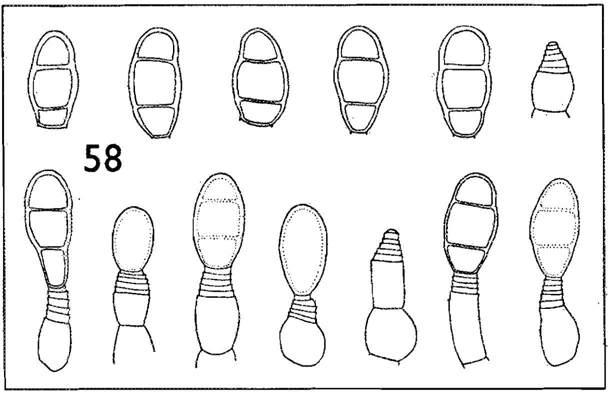

FIG. 58. *Thyrostromella pedunculata*, conidiophores and conidia (DAOM 1749); ×500.

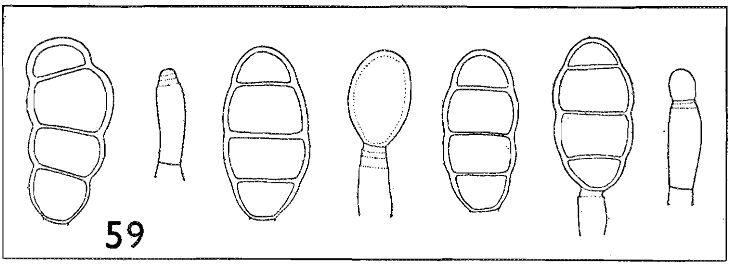

FIG. 59. *Thyrostromella sambucina*, conidiophores and conidia from the type collection; ×500.

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* ≡ *Coryneum negundinis Berk. & Curt. apud Berk. in Grevillea, 2 : 153. 1874.*
= *Coryneum negundinis Ell. & Everh. in Bull. Torrey Botan. Club, 24 : 292. 1897.*
≡ *Coryneum septosporioides Sacc. & Syd.* [*nom. nov.*] *in Saccardo's Sylloge Fungorum, 14 : 1022. 1899.*

** ≡ *Brachysporium pedunculatum Ell. & Everh. in Proc. Acad. Nat. Sci. Phil. 47 : 440. 1895.*
≡ *Exosporium pedunculatum (Ell. & Everh.) W. B. Cooke in Mycologia, 41 : 617. 1950.*

† ≡ *Coryneum sambucinum Ell. & Everh. in Bull. Torrey Botan. Club, 24 : 467. 1897.*
= *Exosporium sambuci Tracy & Earle apud Greene in Plantae Bakerianae, I : 36. 1901.*

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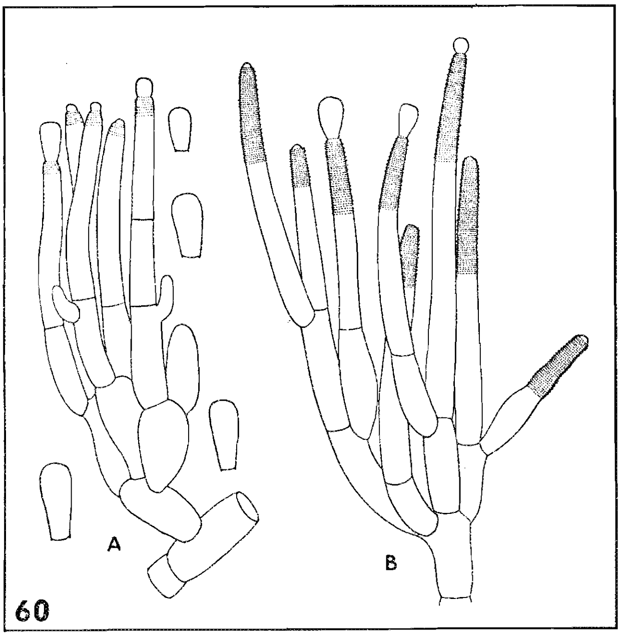
annellophores are not so conspicuous as in *T. pedunculata*. The conidia are 3-septate, thick- and dark-walled, slightly constricted, and somewhat flattened at the basal scar provided with a marginal frill.

In the conidia produced from annellophores it will at once be noticed (e.g. Figs. 55, 58, 59) that the majority of them have a somewhat flattened base as wide as the apex of the annellophore, with a minute frill of ruptured outer wall around it. This frill is obvious in colored conidia and is indicative of the double nature of the wall of the conidium, but the presence of the frill in hyaline conidia can more easily be observed using phase contrast equipment. The successive annellations may have a more or less constant diameter as in *Venturia inaequalis* and *Stysanus stemonitis* (Fig. 49) but in others e.g. *Thyrostromella pedunculata* (Fig. 58) successive annellations are narrower so that the width of the scars on the conidia varies accordingly.

When conidia with a flattened base and a minute basal frill are observed then close examination may show that they have developed from annellophores. Now *Leptographium lundbergii* Lagerb. & Melin (Fig. 60) for some time proved to be difficult to dispose suitably in a system of classification because conidium development was not understood; the bases of the hyaline oval-oblong conidia are somewhat flattened and bear a marginal frill around the scar. The more or less subulate or flask-shaped end cells of the mononematous penicillately branched conidiophores show the presence of extremely



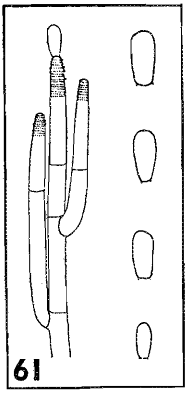


FIG. 60. *Leptographium lundbergii*, fructifications from pure culture (DAOM 22593); *A*, seven days old; *B*, 23 days old; ×1000.

FIG. 61. *Leptographium* sp., small fructification from pure culture (DAOM 28732(*b*)); ×1000.

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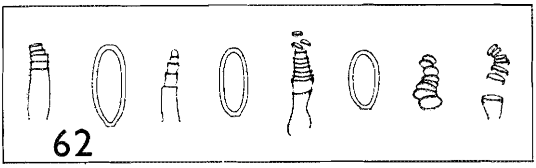
inconspicuous annellations so they are annellophores.* The difference in length between annellophores from a seven-days-old and a 23-days-old pure culture is shown in Fig. 60. The disposition of *L. lundbergii* along with *Stysanus*, *Trichurus*, *Scopulariopsis*, and *Arthrobotryum* then became necessary and its location there seems now so very obvious and natural.

DAOM 28732 (b), an isolation from rotting timber, produces slimy heads of conidia on a mononematous conidiophore branched penicillately at the apex; in this fungus the annellations are conspicuous (Fig. 61).

Shaw and Hubert (103) regarded *Hantzschia* Auersw. to be an earlier synonym of *Leptographium*** but in this paper the former is included in Section IV because the sporogenous cells are considered to be phialides and the latter is included here in Section III because of its annellophores.



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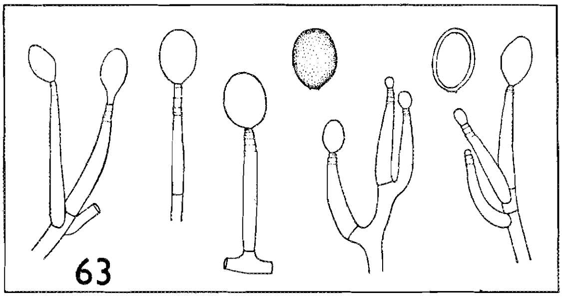

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FIG. 62. *Melanconis juglandis*, conidiophores and conidia (DAOM 35198); ×500.
FIG. 63. *Melanconis stilbostoma*, conidiophores and conidia from pure culture (DAOM 28797); ×500.

In the *Melanconium* state of *Melanconis juglandis* (Ell. & Everh.) Graves (Fig. 62), and in *M. stilbostoma* (Fr.) Tul. (Fig. 63) as isolated from *Betula papyrifera* twigs in Canada I find the sporogenous cells to bear well developed annellations. This is particularly evident in *Melanconis juglandis* in which the annellations are pale brown but so delicately attached to each other that in a crushed preparation they may become detached and appear as distinct rings as shown in Fig. 62.

In a number of illustrations of cross sections of coelomycetous fructifications the sporogenous cells have been figured as more or less cylindrical with a flattened apex; furthermore, the conidia of such fungi are often shown with a flattened base and a minute marginal frill. It is not improbable that such

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* *Perhaps these are the structures which Falck (35) termed 'ampliphialides'.*

** *However, these authors proposed retaining the use of Leptographium because Hantzschia Grunow had been proposed independently for a genus of diatoms; Hantzschia Grunow is a later homonyn of Hantzschia Auersw., as these recent authors pointed out, and to reverse the general procedure in view of the priority of the fungus genus would lead to confusion and has no justification whatsoever.*

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conidia will be found to have developed from annellophores. On the whole the precise method of conidium development in the Coelomycetes has been neglected, granted the conidiophores are usually extremely small, but from a few personal observations and reference to some published descriptions and illustrations I gather that they may well show the same types of development as encountered in those Fungi Imperfecti with exposed conidiophores. When the types of development in the Coelomycetes become known, the 'Melanconiales' are particularly suited for investigation, then the group may be incorporated with the Hyphomycetes and major groupings differentiated on the type of conidium development rather than on the enclosed or exposed position of the conidiophores. Mason (83) stressed the overemphasis of sporodochia, pycnidia, and acervuli in the current classification too, but my approach to this conclusion differs from his.

Section IV

In this section are included those form-species whose conidia (phialospores) develop from phialides. The term phialide is here restricted to those unicellular structures which are usually terminal, but sometimes intercalary as well, on simple or branched conidiophores; they are oval to subcylindrical to flask-shaped or subulate often with a well differentiated basal swelling and a narrower distal neck, with or without a terminal collarette; from the apex of each phialide develops a basipetal succession of phialospores without an increase in the length of the phialide itself. If the phialide does proliferate e.g. in *Catenularia* (see below), then a plurality of conidia develops at each level. Not uncommonly a phialide may possess two or three collarettes in which case the term polyphialide can be applied to it (e.g. *Lasiosphaeria hirsuta*, in Hughes (52)).

In *Sporoschisma* spp. (Hughes (45)) are found the largest phialides I have ever seen and because of their great dimensions they show clearly the events occurring during phialospore development. The stalked phialides in *S. mirabile* Berk., the type species (Fig. 64), are up to 320μ long, consist of a bulbous base leading above to a 1- to 3-septate stalk which then enlarges into a slightly swollen part which then narrows again into a more or less cylindrical tube closed at the rounded apex. Up to three phialospores are laid down within the cylindrical tube from the apex backwards; finally the thinner-walled apical cap of the phialide is torn off presumably by pressure from within. The uppermost phialospore has a rounded apex and is usually shorter and has fewer septa than the others and when pushed out from below is usually found with the torn-off apex of the phialide capping its distal end. A similar type of development can be observed also in *S. saccardoi* Mason & Hughes, *S. juvenile* Boud., and in **Chalara insigne** (Sacc., Rouss., & Bomm.) comb. nov. (≡ *Sporoschisma insigne* Sacc., Rouss., & Bomm.*).

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* *Chalara insigne lacks the capitate hyphae which are so characteristic of the three species of Sporoschisma redescribed by Hughes (45); in this paper Chalara insigne was redescribed as Sporoschisma insigne. I collected this in September, 1952, in excellent condition on an old Poria in N.Y. State, U.S.*

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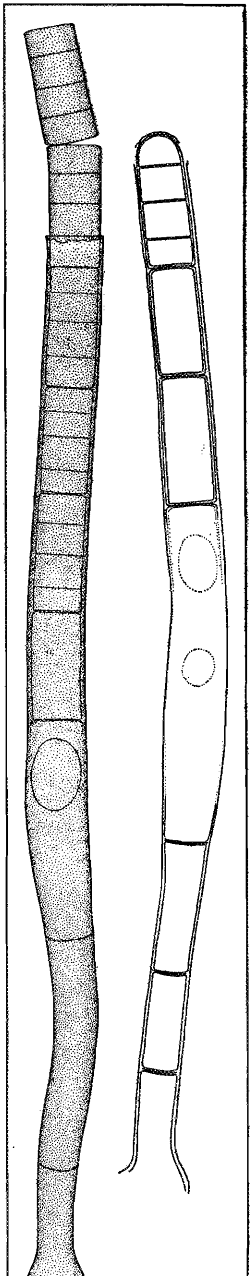

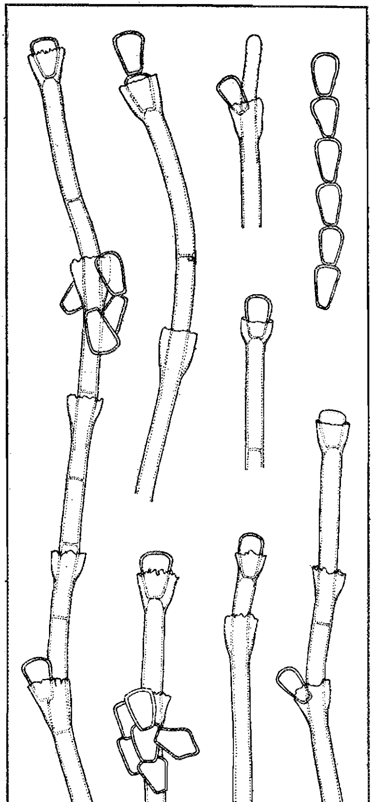

FIG. 64. *Sporoschisma mirabile*, young and mature phialides with phialospores from Hughes (45); ×500.

FIG. 65. *Catenularia cuneiformis*, phialides and phialospores (I.M.I. 49478); ×500.

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Brierley (15) described the development of the 'endoconidia' of '*Thielavia basicola* Zopf' [*Thielaviopsis basicola* (Berk. & Br.) Ferr.] and the sequence of events is similar to that found in *Sporoschisma*.

In *Catenularia cuneiformis* (Richon) Mason (Fig. 65) the conidiophores are simple, erect, and at maturity bear a terminal funnel-shaped collarette and usually up to four intercalary collarettes through which the conidiophore has proliferated. The first collarette is formed by the laying down inside the slightly enlarged apex of the conidiophore of a single cuneate phialospore and the irregular breakup of the wall of the apex of the original swelling to form the funnel-shaped structure. A succession of phialospores develops as in *Sporoschisma* by the proliferation of the phialide into the collarette and the cutting off of single cell units. Phialospores generally mature before another is produced below them but this is not always so in *S. juvenile* in which the phialospores may emerge from the collarette whilst still hyaline and continuous although more distal conidia in the chain are brown and 3-septate.

In DAOM 33739 (Fig. 66), disposed for the time being with two other isolates from rots of wood of *Betula lutea* from New Brunswick (33740, 33761) as *Phialophora* sp. 4, a most interesting type of phialide fructification is found. These phialides are in penicillate fascicles; their basal part is more or less oval and at maturity each has a long, cylindrical, and conspicuous collarette.

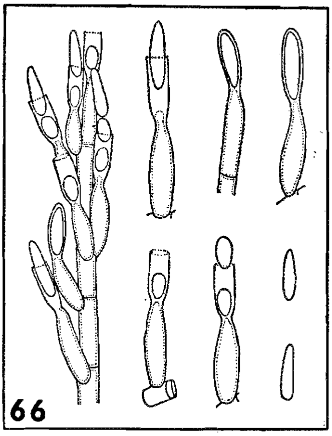

FIG. 66. *Phialophora* sp. 4, phialides and phialospores (DAOM 33739); ×1000.

Early stages show that the first phialospore which is laid down within the unbroken extension of the phialide is long and cylindric-oval; a break occurs towards the apex of the outer wall very probably because of continued growth of the first phialospore and the inability of the outer wall to grow any further. The first long phialospore is thus freed and when it has seceded the collarette becomes very evident. Subsequent phialospores are oval and only about half as long as the first phialospore or the collarette. This accounts for the two types of phialospores, the long and the short, found in all preparations of the three isolates of *Phialophora* sp. 4.

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In other species of *Phialophora*, e.g. *P. fastigiata* Lagerb. & Melin (Fig. 67), the phialide may have a shorter collarette, often about a half as long as the phialospore. In most species of *Phialophora* that I have examined the first formed phialospore differs but little from the subsequent ones.

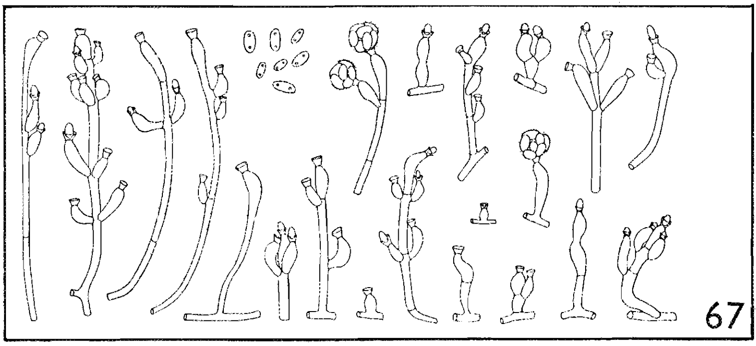

FIG. 67. *Phialophora fastigiata*, hyphae, phialides, and phialospores from Hughes (52); ×500.

It would seem, therefore, that in many phialides the first phialospore is truly endogenous and develops within the unbroken outer wall of that part of the phialide distal to the neck. After the rupture of the wall the first phialospore which, in some cases, has reached maturity, is liberated and the collarette becomes evident. The position of the break in the outer wall, originally enclosing the first phialospore will determine the length of the collarette. Subsequent phialospores are not precisely endogenous even though they may be sunken to a greater or lesser degree within the open collarette.

In *Fusarium semitectum* Berk. & Rav. (DAOM 34095, det. W. L. Gordon) the first phialospore develops as a blown-out end of the apex of a cell which is the phialide initial. No double wall can be differentiated but when this first phialospore secedes a break in the wall occurs where the initial is separated from the phialide by a constriction and a minute cylindrical collarette becomes differentiated; a barely visible frill is sometimes seen just above the base of this first phialospore and is that part of the wall which was connected to the collarette. The first formed phialospores are usually smaller and less curved than those which follow.

In *Fusariella* spp. (Hughes (44)) the phialospores remain attached in chains and each phialospore is attached to the second cell from the apex of the phialospore below it; this is due to the lateral and curved growth of that spore during development. In *F. atrovirens* Sacc. and *F. obstipa* (Pollack) Hughes it was possible to see that the apical or first formed phialospore in the chain is always straight, the subsequent ones being distinctly curved. *F. atrovirens* is illustrated in Fig. 68.

In the phialides of *Menispora* spp. the outer wall enclosing the first phialospore initial is ruptured at a very early stage when the initial is quite small so

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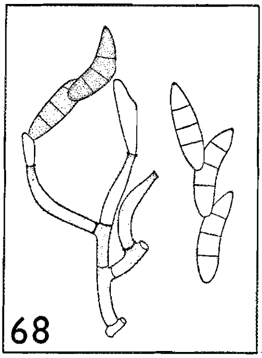
that a distinct collarette is present during the later stages in the development of the first phialospore. In *Menispora tortuosa* Corda (Fig. 69)* and *M. ciliata* Corda, two common fungi of wood and bark in Britain, phialides are borne singly or in small groups on short stalks towards the bases of erect conidiophores which may be coiled or flexuous above. The phialides are more or less cylindric-oval and recurved at the narrowed apex so that the collarette is directed towards the base. The phialospores are 3-septate in *M. tortuosa* (≡ *Eriomenella tortuosa* (Corda) Peyronel), and continuous in *Menispora ciliata* Corda, being once ciliate at both ends in the two species; they form slimy fascicles lying alongside the phialide from which they developed.



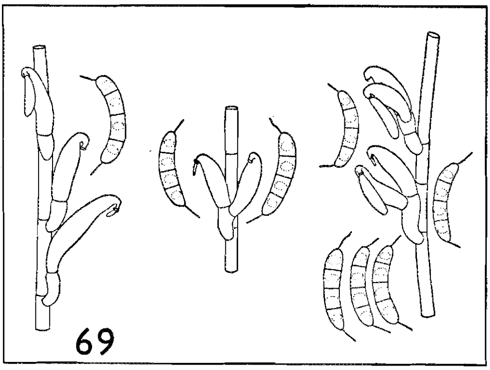


FIG. 68. *Fusariella atrovirens*, phialides and phialospores from Hughes (44); ×500.
FIG. 69. *Menispora tortuosa*, phialides and phialospores (I.M.I. 20037(*d*)); ×500.

In the *Tubercularia* fructifications of *Nectria cinnabarina* (Tode ex Fr.) Fr. the conidia-bearing hyphae are the ultimate ends of more or less verticillately branched hyphae arising from the stroma. The fertile hyphae are long, usually simple, hyaline, and septate. At the apex of these and just below most of the transverse septa are upwardly directed short branches bearing what I take to be a cylindrical collarette. The phialospores are produced successively in large numbers and result in the conspicuous orange-colored fructifications. The presence of a linear series of sporogenous cells is not common in the Hyphomycetes.

Phialide-bearing fungi are extremely numerous and no attempt can be made in a short paper to give an account of the various forms displayed by the fructifications. Some phialide-bearing species have been described by Cain (19) and Hughes (52, 58) to mention but two of numerous authors who have dealt with like forms.

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* *Six recent collections in Canada (Ontario) are very close to M. tortuosa but the 3-septate phialospores are more strongly ciliate; the phialides are more numerous on the short lateral stalks, often appearing digitate, and the apex of each is not recurved so that the phialospores come to be grouped in slimy fascicles perched on the apex of the phialides and not alongside them as in M. tortuosa.*

Section V

In this section are classified those fungi which develop basipetal chains of conidia from poorly differentiated conidiophores which possess a generative or meristematic region towards the apex with the result that the conidiophore merges imperceptibly with the chain of conidium initials which exhibit a gradual maturation towards the distal end of the chain.

In 1952 Hughes (64) discussed two species, the conidial state of *Hysterium insidens* Schw. (Fig. 70) (= *Sirodesmium granulosum* de Not) and *Sirodesmium diversum* (Cooke) Hughes (≡ *Torula diversa* Cooke) (Fig. 71); these were illustrated and described. In these two species the conidial fructifications are pustular and the dry chains of dark brown conidia arise in basipetal succession from simple or branched radiating conidiophores. Close examination shows that the conidia merge imperceptibly with the conidiophores and it is impossible definitely to indicate where the conidiophore ends and conidium initials begin. This is because the conidiophore is meristematic at its upper end so that a basipetal chain of conidium initials develops; the maturation of conidia is a slow process and in *Hysterium insidens* in particular all stages from amerospores through phragmospores to large dictyospores can be seen in a single chain.

In the publication cited attention was drawn to the similarity between this type of development and that described by Yarwood (117) for the *Acrosporium* (*Oidium* auct.) conidia of the powdery mildew *Erysiphe polygoni* DC. (Fig. 72). By direct observations Yarwood observed the presence of a generative cell [marked 'x' in the figure] elongating and dividing to produce a conidium initial at the apex and a lower cell that retains its generative capacity.

When Mason and Hughes (Hughes (47)) made the combination *Coniosporium peziza* (Cooke & Ellis) (≡ *Sporidesmium peziza* Cooke & Ellis) they were wrong. The conidia in this fungus are in basipetal chains and the fungus is a *Sirodesmium*, hence **Sirodesmium peziza** (Cooke & Ellis) Mason & Hughes comb. nov.*

In *Coniothecium betulinum* Corda (see below) a section through a pustular fructification shows the conidia to be finally dictyospores and they develop in basipetal chains from more or less undifferentiated hyphae of the semi-immersed stroma.

In *Trimmatostroma salicis* Corda, the type species of this genus, the fructifications are pustular as in the foregoing. The conidia arise in basipetal chains from more or less undifferentiated hyphae of the semi-immersed stroma. This genus is usually classified amonst the phragmosporae but a number of conidia will be seen to possess one or more longitudinal septa. I do not understand how *T. salicis* and *Coniothecium betulinum* can be held in different genera, to say nothing of different groupings. In both species no acropetal conidia develop but branched chains occur in both, especially in *Trimmatostroma salicis* where the origin of a branch is often at a triradiate conidium or at a conidium bearing a short lateral outgrowth at right angles usually and in no

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* ≡ *Sporidesmium peziza Cooke & Ellis in Grevillea, 4 : 178. 1876.*

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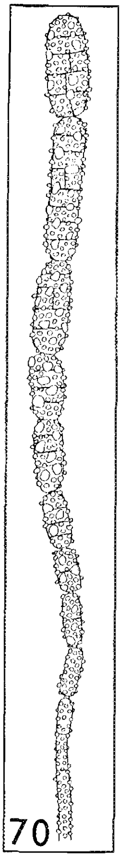

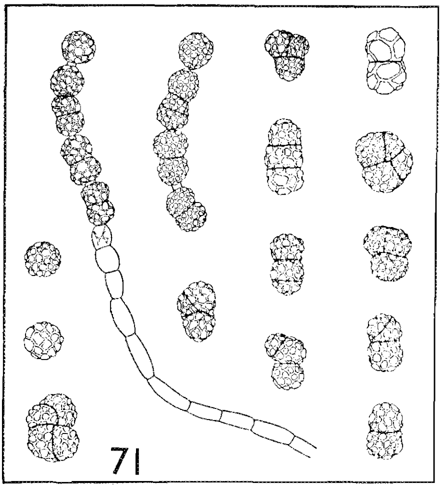

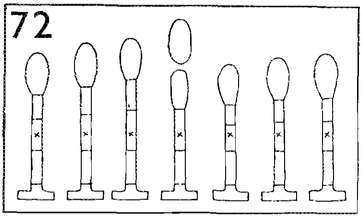

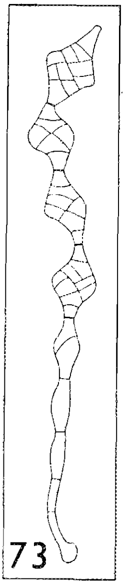

FIG. 70. *Hysterium insidens*, isolated conidiophore and chain of conidia from Hughes (64); ×500.

FIG. 71. *Sirodesmium diversum*, conidiophore and conidia from Hughes (64); ×500.

FIG. 72. *Erysiphe polygoni*, development of conidia from Yarwood (117); reduced from original.

FIG. 73. *Phragmotrichum chailletii*, conidiophore and conidia from Reliq. Farl. no. 665 on *Abies*; ×500.

regular position with regard to the linear part of that particular conidium. I believe the lateral branches have arisen by a lateral (as well as a longitudinal) swelling of a conidium initial; septation is followed by the longitudinal expansion of one cell and the lateral expansion of the other to produce a basipetal chain similar to the main chain on which it is borne.

In *Coniothecium atrum* Corda (22), the type species of the genus, the conidia were described as embedded in slime and one of the illustrations is described thus: 'Sporenhaufschen in Wasser zerfliessend, und die braune Gallerte und die Sporen.' Eleven species classified subsequently by Corda in *Coniothecium* seem to have little in common with the type species. *C. betulinum* is one of these; in Herb. DAOM the collections of this species are disposed as **Trimmatostroma betulinum** (Corda) comb. nov.*

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* ≡ *Coniothecium betulinum Corda in Icones Fungorum, 1 : 2. 1837.*

It is interesting to note that most *Sirodesmium* spp., *Trimmatostroma salicis*, and *T. betulinum* produce pustules of dry phaeospores.

In DAOM 29327 and the collections issued in Reliquiae Farlowianae no. 200*a*, *b*, sub *Stilbum glomerulisporum* Ell. & Everh. [nomen nudum], the white or cream colored fructifications may be tuberculariaceous or stilbaceous. The conidia arise in basipetal succession from single or from two neighboring cells of conidiophores which possess a generative region towards the apex. The mature dictyosporous or bulbil-like hyaline conidia are composed of adpressed and coiled outgrowths of the initial cells; they remain in long chains even in teased preparations and the individual conidia are often separated the one from the other by one or two unchanged cells of the hypha from which they have developed. The fungus is not a *Stilbum* but I know of no generic name wherein it can adequately be classified when it is described.

It appears that this type of conidium development is to be found amongst fungi classified in the Coelomycetes. In the pycnidia of the European *Alysisporium rivoclarinum* Peyronel (97) the pycnospores were figured as arising in basipetal succession with a very gradual transition from pycnospore initials to mature pycnospores. Furthermore they are held apart at maturity by a hyaline disjunctor (compare with conidial *Hysterium insidens*) and it seems very probable that the type of development in Peyronel's species is similar to that which is characteristic of Section V. In *Phragmotrichum chailletii* Kunze (Fig. 73) there is a basipetal succession of conidia as in the conidial chains of *Sirodesmium* and their gradual maturation is readily observable in sections through the fructifications.

In the 'Melanconiaceous' fungus described and figured in Grove (41) as *Septotrullula bacilligera* var. *cambrica* Grove & Rhodes the conidia arise in basipetal chains and show a gradual maturation. A large number of genera of the Coelomycetes (Sphaeropsidales, Melanconiales) are described with spores in chains; it seems to me to be essential to know exactly how the chains arise; I know of no pycnidial fungus in which the pycnospores arise in acropetal succession.

The gradual basipetal maturation of the conidia suggests that food material passes up the chain of developing initials. The conidia are in true chains.

Section VI

The main character possessed by species being included in this section is the apparent development of solitary conidia at minute, single, or numerous pores in the wall of the conidiophore. The effect of this on the apex of the conidiophore or wherever such conidia are produced and the base of the conidium is very striking. The apex of the conidiophore is nearly always rounded and the outer and inner walls come to an end abruptly thus delimiting a more or less cylindrical pore. The base of the conidium is also usually rounded and a morphological scar such as a conspicuous tear or break in the wall is absent; the base of the conidium may be truncate but nevertheless the outer wall of the conidium is continuous all round the base except for the basal pore.

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The torn outer wall such as found in conidia of Sections I, II, and III for instance is absent. In some of the conidia produced in Section III the scar may be visible as a flat and thickened area at the base of the conidium; such clearly demarcated and thickened areas are not found in the conidia of Section VI. It is necessary to mention at the outset that I have found the main character of Section VI to be a difficult one but, for all that, I believe that it brings together fungi to form a homologous group of very closely related genera; the need for further morphological studies in this group is stressed.

In some species the conidiophore is simple and the apical conidium checks all further growth. Lateral conidia, however, may develop in verticils below the uppermost septa or irregularly along the length of the conidiophore and in such cases chains of conidia may occur. These lateral conidia, like the apical ones, fall readily from their attachment and although darker colored areas on the conidiophore marking the point of their insertion may be completely absent, the seat of their former attachment can easily be located by the presence of the minute pores.

In *Exosporium tiliae* Link ex Wallr. (Fig. 74), for instance, the apex of the conidiophore is rounded and shows the pore clearly; in a young collection a conidium initial makes its appearance as a minute hyaline bulb at the pore just as if it had resulted from a blowing out of the inner wall of the conidiophore. During further development the initial increases in length and width and its base comes to lie over a part of the rounded apex of the conidiophore but in no instance can I observe direct continuity between the outer wall of the conidiophore with that of the conidium. In *E. tiliae* and some species of *Helminthosporium* (sensu stricto) the base of the conidium, more especially the terminal ones, is dark brown and turbinate. The conidiophores are minute in *Exosporium tiliae* and cover the surface of large superficial hemispherical stromata; only solitary conidia develop on these conidiophores. The only

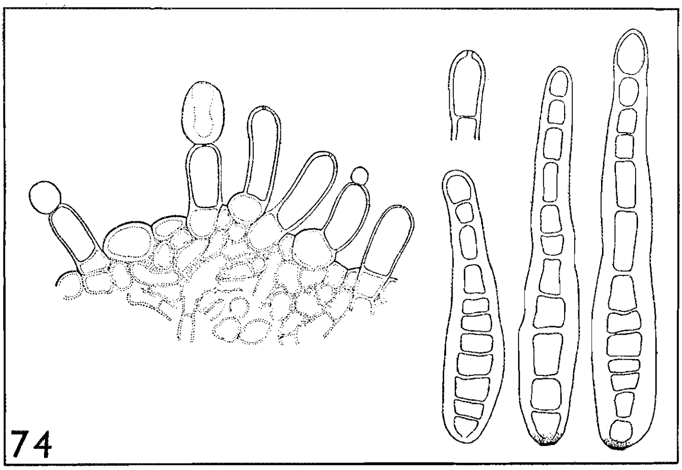

FIG. 74. *Exosporium tiliae*, conidiophores and conidia (I.M.I. 6787); ×500.

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other true *Exosporium* spp. known to me are *E. biformatum* v. Höhn. which I collected on *Fagus sylvatica* wood (the type host) in England (I.M.I. 10912 (*b*)), and *E. cespitosum* Ell. & Barth.

In *Helminthosporium velutinum* Link ex Fr., the type species of *Helminthosporium*, the conidia develop terminally and in more or less regular verticils below the terminal conidium and below the uppermost septa (Fig. 75) of the subulate conidiophore.

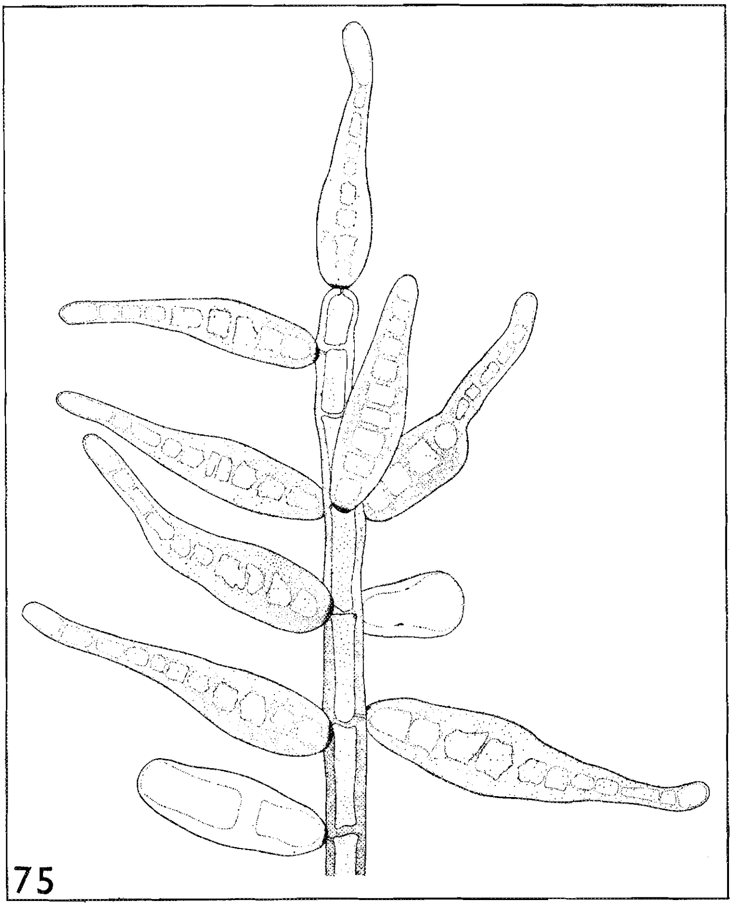

FIG. 75. *Helminthosporium velutinum*, apex of conidiophore with conidia from pure culture (I.M.I. 349(*a*)); ×500.

In **Helminthosporium atrovirens** (Harz) Mason & Hughes comb. nov.*, (Fig. 76) well known as the cause of silver scurf of potato tubers, the conidia develop exactly as in the type species of *Helminthosporium* and the new combination becomes necessary.

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* ≡ *Spondylocladium atrovirens Harz in Bull. Soc. Imp. Moscow, 44 : 42. 1871.*

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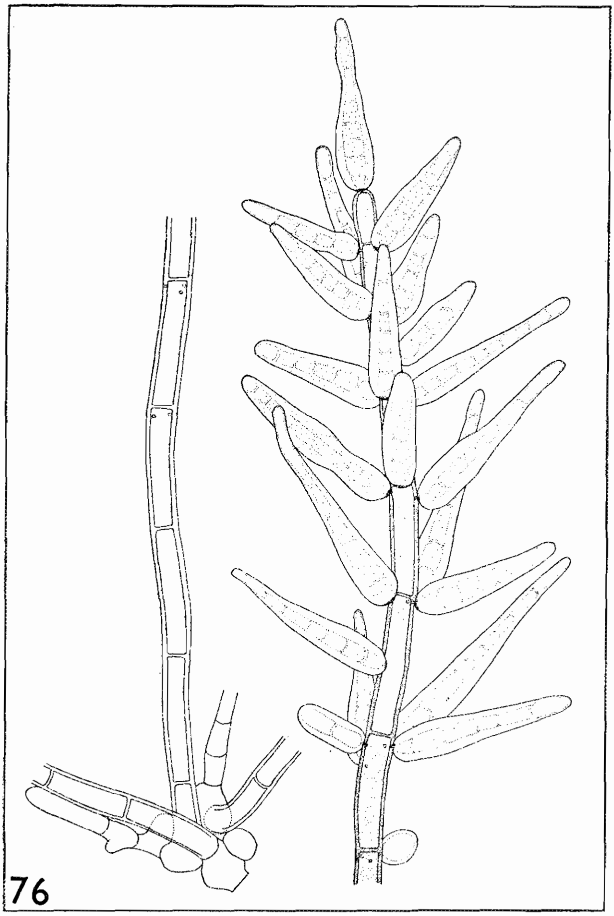

FIG. 76. *Helminthosporium atrovirens*, conidiophore and conidia (I.M.I. 1685); ×500.

In *H. microsorum* D. Sacc. (Fig. 77) conidiophores are in tufts on dead twigs of *Quercus ilex*; they bear a terminal conidium and one or two lateral conidia as well.

'*Helminthosporium tiliae* Fr.' is very similar to *H. microsorum* but the conidiophores bear only solitary terminal conidia (Fig. 78).

An unidentified *Massaria* (I.M.I. 19472(*a*, *b*)) on *Quercus* grew in association with a *Helminthosporium*; conidiophores and conidia of the *Helminthosporium* developed from ascospores in pure culture. As far as I am aware this is the first time that a true *Helminthosporium* has been connected with a perfect state.

In *Helminthosporium smithii* Berk. & Br. (Fig. 79) solitary conidia are produced at the apex of conidiophores which may then proliferate through the apical pore and form another conidium at the apex of the proliferation; two

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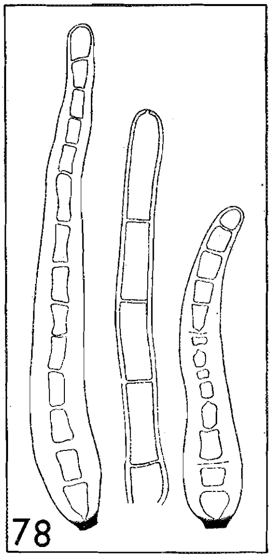
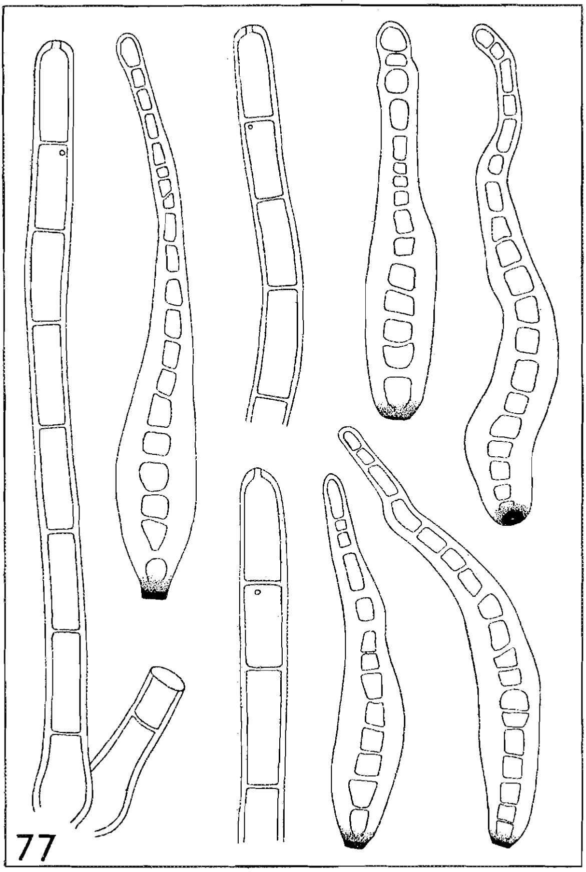




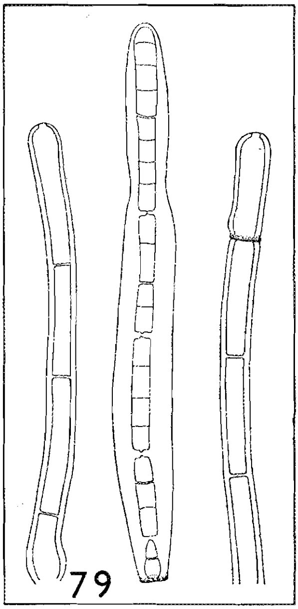


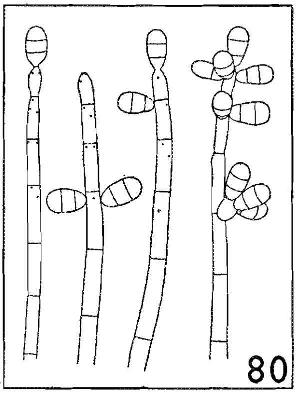
FIG. 77. *Helminthosporium microsorum*, conidiophores and conidia (I.M.I. 19654); ×500.

FIG. 78. '*Helminthosporium tiliae*', conidiophore and conidia (I.M.I. 9070); ×500.

FIG. 79. *Helminthosporium smithii*, conidiophores and a short conidium (I.M.I. 31422); ×500.

or three such proliferations have been seen. This, of course, is characteristic of *Corynespora cassiicola* (Berk. & Curt.) Wei (113) which may also form short acropetal chains of conidia.

In **Spondylocladium obovatum** (Cooke & Ellis) comb. nov.* (Fig. 80) a not uncommon Eastern North American Hyphomycete of rotten wood and bark the conidiophore bears irregular lateral whorls of conidia which leave characteristic pores after seceding. The terminal conidium, however, arises obviously as a blown-out end of the apex of the conidiophore but a further note on this apparent anomaly is given on p. 640.



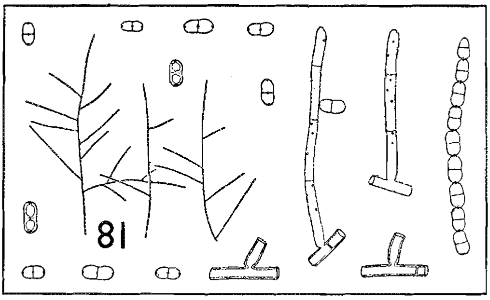


FIG. 80. *Spondylocladium obovatum*, conidiophores and conidia (DAOM 29394(*a*)); ×500.

FIG. 81. *Diplococcium spicatum*, conidiophores and conidia (I.M.I. 27623); ×500 except low power outlines of entire conidiophores which are ×50.

In *Diplococcium spicatum* Grove (Fig. 81), the type species of *Diplococcium*, the main stalk of the conidiophore is erect, more or less straight, and it bears up to nine 'lateral branches' which form a wide angle with the main stalk; these may themselves bear upwardly directed laterals. Along the terminal portion of the main stalk and along the length of the lateral branches are found minute scattered pores which denote the place of the former attachment of long, fragile, acropetal chains of subhyaline didymospores.

In **Diplococcium uniseptatum** (Berk. & Curt.) comb. nov.** the simple conidiophores bear numerous scattered pores at which usually solitary, brown, 1-septate, readily seceding conidia are borne.

In **Diplococcium indivisum** (Sacc.) comb. nov.† a common mold of wood and bark around Ottawa, Ont., and Ithaca, N.Y., the simple conidiophores bear numerous scattered pores at which solitary, brown, continuous conidia develop.

In the *Stemphylium* conidial apparatus of *Pleospora herbarum* (Pers. ex Fr.) Rabenh. (see Wiltshire (116)) and in *Stemphylium sarcinaeforme* (Cav.) Wiltshire (116) (Fig. 82) solitary conidia are produced on branched or unbranched conidiophores which proliferate through the pore left by one

* ≡ *Acrothecium obovatum Cooke & Ellis in Grevillea, 5 : 50. 1876.*

** ≡ *Virgaria uniseptata Berk. & Curt. apud Berk. in Grevillea, 3 : 145. 1875.*
≡ *Cladotrichum uniseptatum (Berk. & Curt.) Sacc. in Sylloge Fungorum, 4 : 373. 1886.*
= *Cladosporium aterrimum Ell. & Everh. in Proc. Acad. Phil. 1894 : 378. 1894.*

† ≡ *Virgaria indivisa Sacc. in Michelia, 2 : 560. 1882.*

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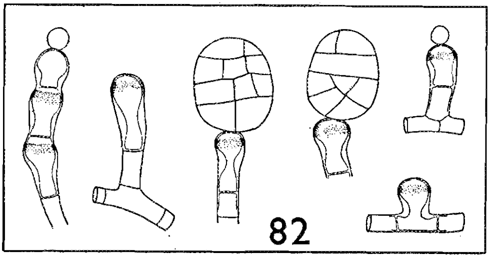

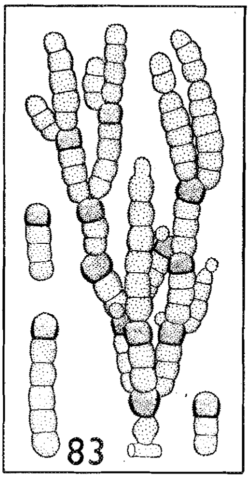

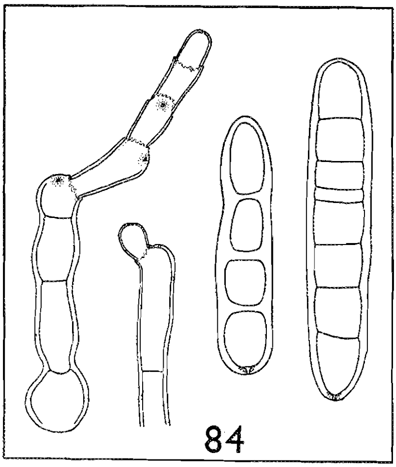

FIG. 82. *Stemphylium sarcinaeforme*, conidiophores and conidia (DAOM 14970); ×500.

FIG. 83. *Torula herbarum*, conidiophore, conidial chains, and conidia (I.M.I. 15281); ×500.

FIG. 84. *Helminthosporium teres*, conidiophores and conidia (DAOM 1056); ×500.

conidium and then produce another conidium at the apex of the proliferation. Occasionally the proliferation will be just lateral to the apical conidium which remains attached.

In *Torula herbarum* Link ex Fr. (Fig. 83) terminal cells of the conidiophore are not unlike those of *Stemphylium* prior to proliferation; in *T. herbarum*, however, up to three conidia may be borne on the end cell of the conidiophore and branched acropetal chains of phragmospores develop. The apical cell of each conidium within the chain is usually characteristically darkened and thickened like the terminal cell of the conidiophore.

In '*Helminthosporium teres*' Sacc. (Fig. 84) the first conidium is terminal. Then the conidiophore develops a growing point just below the apex and if the outer wall of the conidiophore has hardened then the inner wall bursts through it, grows upward, and displaces the pore left by the apical conidium, and then produces another terminal conidium. A succession of such new growing points arises in this way so that the once terminal pores become lateral in position. The apex of the conidiophore and the base of the conidium are similar in possessing a pore and furthermore, within each apical and basal

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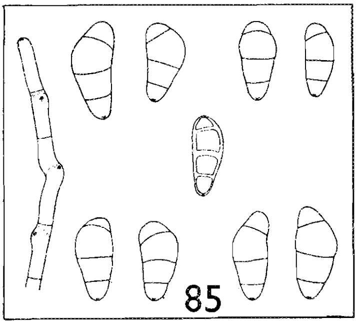
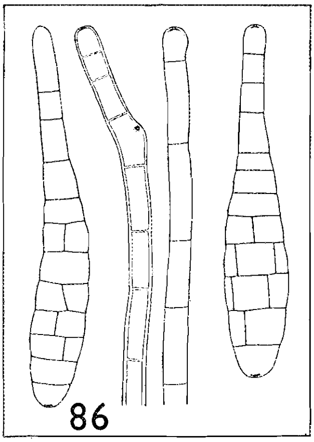
cell of conidiophore and conidium respectively, just below (or above) the pore is a brown ring which gives a characteristic appearance in side view. A thickened hilum as often found in Section III is not seen here. In some graminicolous species assigned to *Helminthosporium* the base of the conidium may be truncate just as in some conidia of *H. velutinum* and related species.

The production of successive conidia in *Curvularia* spp. e.g. *C. lunata* (Wakker) Boedijn (Fig. 85) is similar to that found in *Helminthosporium teres* Sacc.





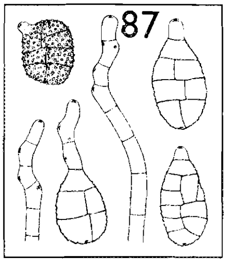


FIG. 85. *Curvularia lunata*, conidiophore and conidia (DAOM 14976); ×500.
FIG. 86. *Alternaria brassicae*, conidiophores and conidia (DAOM 14161); ×500.
FIG. 87. *Alternaria consortiale*, conidiophores and conidia (DAOM 14937); ×500.

In *Alternaria* spp. solitary or acropetal chains of conidia develop on conidiophores which may or may not increase in length with further conidium production. In *A. brassicae* (Berk.) Sacc. (Fig. 86) chains of conidia and increase in length of the conidiophore occur apparently only in pure culture. In **Alternaria consortiale** (Thüm.) Groves & Hughes comb. nov.* (Fig. 87), on the other hand, chains of conidia are not infrequent and the conidiophore may become markedly geniculate following the development of successive new growing points each terminating in a single conidium or a chain of conidia.

In *Dendryphion comosum* Wallr., the type species of Wallroth's genus, the growth of the erect main stalk of the conidiophore is usually terminated by a conidium which then develops an acropetal chain of similar conidia. In the meantime lateral branches, often in whorls, have arisen below the apex and these are also branched and bear acropetal chains of conidia.

In *Dendryphion laxum* Berk. & Br. (Fig. 88) the branching of the conidiophore is not usually so pronounced; the lateral branches produced, usually below the terminal conidial chain, produce a succession of subterminal growing

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* ≡ *Macrosporium consortiale Thüm. in Herb. myc. oecon. no. 450. 1876.*
≡ *Stemphylium consortiale (Thüm.) Groves & Skolko in Can. J. Research, C, 22 : 196. 1944.*

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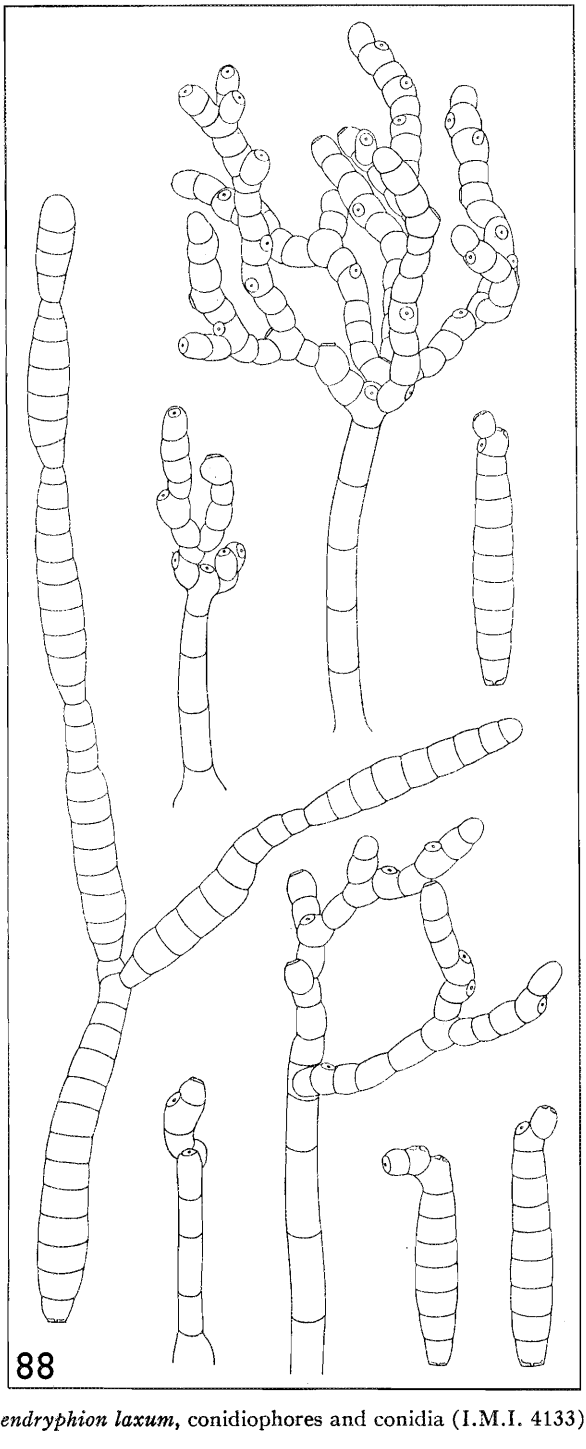

FIG. 88. *Dendryphion laxum*, conidiophores and conidia (I.M.I. 4133); ×500.

points each terminating in an acropetal chain of phragmospores. The chains may be branched and the apex of a conidium may proliferate like the apex of one of the lateral branches.

In **Dendryphion interseminatum** (Berk. & Rav.) comb. nov.* the branching of the conidiophore is not so localized as in the preceding species; the conidiophores are nodulose indicating where a number of conidia have arisen. The conidia are usually formed in short acropetal chains. The genus *Dendryphiella* is based on this species and I see no reason for holding this distinct from *Dendryphion* merely on account of the looser and longer branches. The catenulate conidia have basal and apical pores and the point of attachment of conidia to the conidiophores is also marked by a pore. The fungus can be excluded from *Heterosporium*, on account of the method of conidium development; in this paper *Heterosporium* is included in Section II.

In the next genus described, a solitary conidium terminates the growth of the main stalk of the conidiophore; primary, secondary, tertiary, and even quaternary distinct lateral branches arise each in turn being terminated by a solitary conidium. In *Dendryphiopsis atra* (Corda) Hughes (Figs. 89, 90, see also p. 655) the main stalk retains that form which it reached at the formation of the apical conidium. Lateral branches arise by bursting through the outer wall of the conidiophore, develop apical conidia, and a dichasium-like head is the result. Corda (25) figured long chains in this species but an authenticated (possibly type) collection shows only solitary conidia. *D. atra* is one of the commonest wood and bark hyphomycetes of the Ottawa district and is equally common around Ithaca, N.Y. It has received at least one independent name in North America.

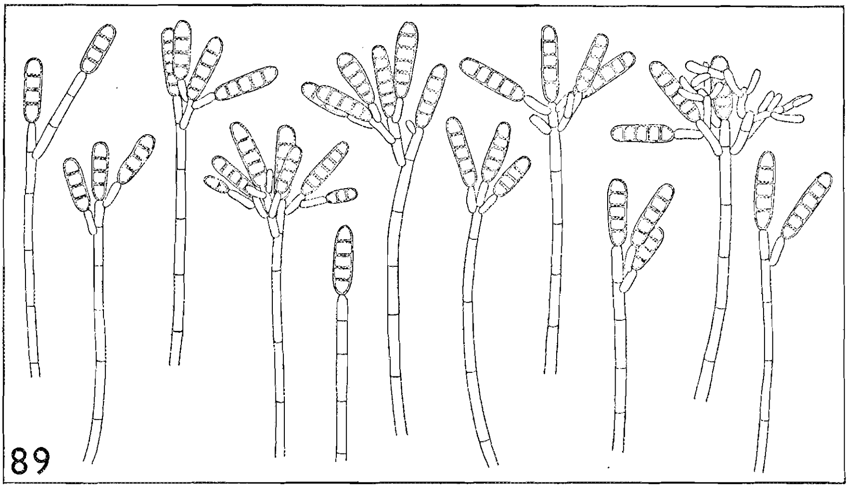

FIG. 89. *Dendryphiopsis atra*, conidiophores and conidia (I.M.I. 4493); ×165.

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* ≡ *Helminthosporium interseminatum Berk. & Rav. apud Berk. in Grevillea, 3 : 103. 1875.*
≡ *Dendryphiella interseminata (Berk. & Rav.) Bub. & Ran. in Ann. Mycol. 12 : 417. 1914.*

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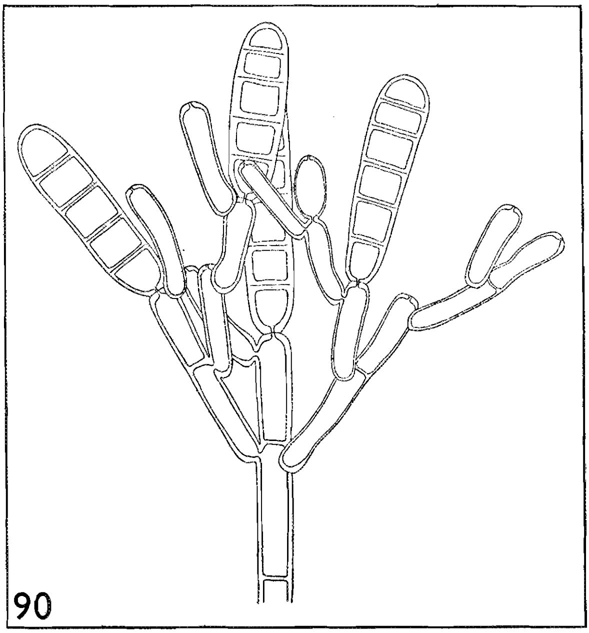

FIG. 90. *Dendryphiopsis atra*, conidiophore and conidia (I.M.I. 4493); ×500.

In '*Helminthosporium stemphylioides* Corda' (≡ *Brachysporium stemphylioides* (Corda) Sacc.) (Fig. 91) the scattered conidiophores are inflated at the

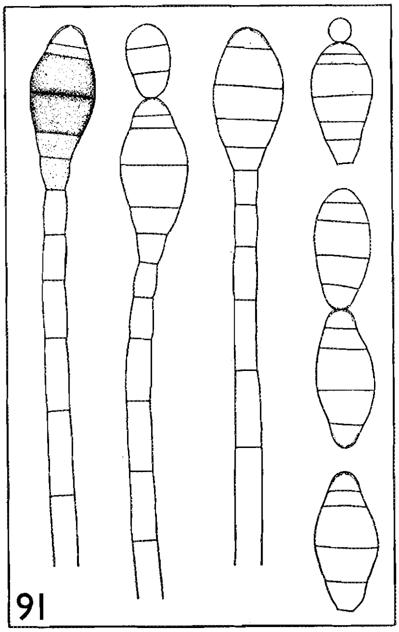

FIG. 91. '*Helminthosporium stemphylioides* Corda', conidiophores and conidia (I.M.I. 19219(*j*); ×500.

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apex into conidium-like structures which may secede at maturity but apparently with difficulty. Before seceding, however, each of these will have borne at its apex a single unbranched chain of conidia whose development necessitates the classification of this fungus in Section VI. It will be remembered that the apical conidium of *Spondylocladium obovatum* (Fig. 80) is a blown-out end of the conidiophore and is more persistent than the lateral ones which develop as in *Helminthosporium velutinum.*

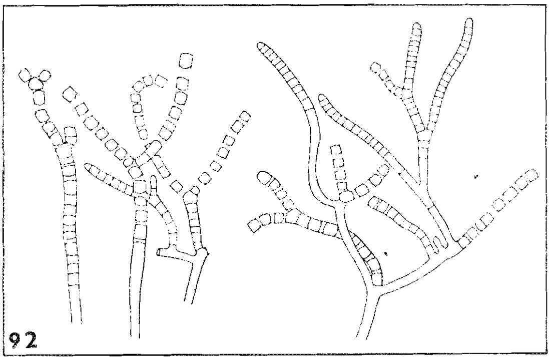
In 1951 Hughes (53) suggested that the four-armed conidia of *Tripospermum eggelingii* Hansf. might have developed at pores. No further material of this or congeneric species has been seen.

Admittedly the character used in delimiting Section VI may be a difficult one but it is extremely evident in large numbers of species which have other characters in common; many have determinate conidiophores and a characteristic conidial shape and structure. I feel that a useful purpose is being served in drawing attention to this type of development by basing a Section on it.

Section VII

In this section are classified those species whose conidia arise from the septation and breaking-up of simple or branched hyphae.

In **Coremiella ulmariae** (MacWeeney) Mason comb. nov.* (Figs. 92, 93) the conidiophores are in tufts and each grows apically and branches irregularly or somewhat dichotomously to become arborescent towards the apex. Transverse septa are laid down in basipetal succession in the upper branches and neighboring or alternate cells develop thicker walls, a process which also takes place basipetally. The intermediate cells lose their contents entirely and the lateral walls remain thin, collapse inwards, and finally break readily to free the oblong or cubical conidia. The conidium it will be realized has developed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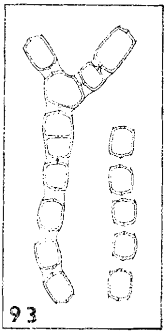
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FIG. 92. *Coremiella ulmariae*, conidiophores (I.M.I. 8977); ×315.
FIG. 93. *Coremiella ulmariae*, portions of chains of conidia (I.M.I. 8977); ×750.

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* = *Stysanus ulmariae McWeeney in Irish Naturalist, 4 : 277. 1895.*

The genus Coremiella was published by Bubák & Krieger (Bubák (18)) for the single species C. cystopoides which they illustrated.

within the outer wall of the original hypha and the characteristic papilla and minute pore of the end walls are clearly visible; conidia which have seceded show a minute frill at each end, this being the remains of the outer wall, of the original hypha belonging to one of the collapsed cells. Only the terminal branches of conidiophores become modified into conidia.

In *Geotrichum* sp. (DAOM 29164, Fig. 94) more or less undifferentiated, simple or branched, hyaline hyphae develop septa in basipetal succession; each cell becomes thicker-walled and secedes by the breaking down of the outer wall and a separation of the transverse wall which is presumably a double structure. The conidia are hyaline and oblong at maturity but yellow in mass in this particular isolate.

Langeron (76) has illustrated *Geotrichum candidum* Link ex Sacc. and also reproduced a figure by Arnaud and Barthelet (2) of *G. purpurascens* (Bon.) Sacc., both species producing conidia in the manner described here.

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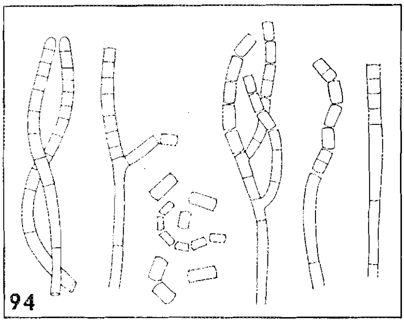

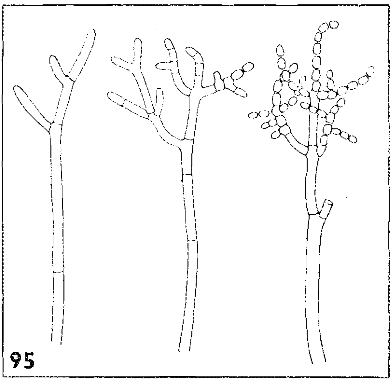

FIG. 94. *Geotrichum* sp., conidiophores and conidia (DAOM 29164); ×750.
FIG. 95. *Oidodendron griseum*, conidiophores with branched apices at various stages of development and fragmentation, from pure culture (I.M.I. 45947); ×750.

In *Oidiodendron griseum* Robák (98) the more or less well differentiated pale brown main stalk of the conidiophore branches irregularly towards the apex and finally septates basipetally, the cells becoming rounded off, slightly roughened, and colored (Fig. 95). At maturity the conidia fall very readily leaving the erect main stalk of the conidiophore with the stumps of former branches at the apex.

Such a breaking-up of hyphae into conidia is seen in *Hendersonula toruloidea* Nattr. (Nattrass (90) and Hughes (59)). On *Manihot utilissima* the fungus forms blister-like swellings under the periderm and these are filled with conidia which have developed in this manner. The formation of conidia can be well studied in pure culture on agar media.

Brodie (16) described the formation of 'oidia' by *Coprinus lagopus* (Fr.) Fr. Normal 'oidiophores' have an erect stalk with a sparingly branched apex bathed in a drop of liquid; the apical branches segment basipetally into the 'oidia'. This is reminiscent of *Oidiodendron* but here the conidial heads are dry.

Brodie (17) also described the basipetal formation of uninucleate 'oidia' in *Collybia velutipes* (Curt. ex Fr.) Quél. by the successive division of the single nucleus of a hypha and the successive segmentation of that hypha. Chains of conidia so formed usually separate in water. This type of development from a more or less undifferentiated hypha is reminiscent of *Geotrichum*.

Kaufert (73) illustrated and described the production of binucleate and uninucleate conidia from coremia on 'dicaryotic' and 'haploid' mycelia respectively of *Pleurotus corticatus* Fr. The conidia are yellow-brown and are formed in a liquid resulting in glistening black masses. The free ends of the hyphae at the tips of the coremia were stated to break up 'in a basipetal manner into chains of conidia'. Such synnemata (coremia) are reminiscent of *Coremiella*, but in the type species of this genus the conidia are dry.

Drechsler (31) illustrated and described 18 species of *Actinomyces*; he stated that 'sporogenesis commences at the tip by the insertion of regularly spaced septa, and proceeds downward towards the base of the filament'; such filaments are frequently spiral. The method of conidium development by basipetal fragmentation certainly suggests that *Actinomyces* should be included in Section VII.

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Section VIII

In this section are included those species whose conidiophores elongate by a basal growing point. The conidiophore itself may arise from a barrel-shaped or flask-shaped conidiophore mother-cell which usually bears a terminal, often atypical conidium prior to development of the conidiophore. The conidia of mature conidiophores are either borne solitarily at the apex or apically and irregularly on short stalks along the increasing length of the conidiophore, or apically and in whorls between thickened septa of the conidiophore. All the conidia arise as blown-out ends and the oldest conidia are usually towards the apex and the youngest towards the elongating base of the conidiophore.

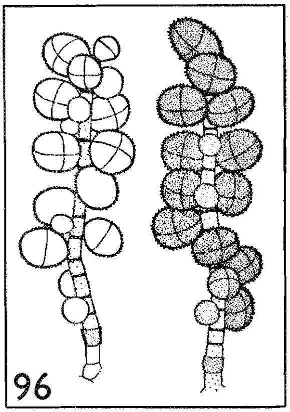
The various species produce fructifications which are usually pustular, superficial, and with dry powdery conidia. The conidia are mostly colored and may be amerospores or septate in such a way that the conidia are composed of a flattened or irregular plate of 4, 8, or 16 cells. The amerospores are usually flattened, almost lenticular and bivalvate with a longitudinal germ slit. Mason (82) proposed the tribe 'bivalvae' to contain such genera as *Papularia*, *Arthrinium*, *Camptoum*, 'and presumably *Pseudocamptoum*'.

In *Papularia* spp. (see Ellis *et al.* (34) with illustrations) the fructifications may be superficial or immersed and then erumpent. The conidiophores are delicate and hyaline and I consider them to have arisen from conidiophore mother-cells. The first conidium is formed at the apex and subsequent ones are borne laterally on an elongating conidiophore in such a way that the youngest conidia are mostly found towards the base. Mature conidia are more or less circular and bivalvate.

In *Arthrinium* spp. (Ellis *et al.* (34) with illustrations) the conidiophore mother-cells and conidiophores are more or less well developed and with the conidia form dark brown to black, powdery, superficial, raised fructifications. The conidiophores possess dark brown to black septa between which are borne the angular to bicornate and flattened conidia each with a longitudinal germ slit. The first conidium is terminal and is often abnormal; other conidia arise in succession towards the younger base of the conidiophore although the sequence is often broken by the delayed appearance of some conidia amongst fully formed ones.

In *Endocalyx* spp. (Hughes (68)) the fructifications are semi-immersed; the conidiophores are filamentous and elongate by a basal growing point. The conidia are sessile or shortly stalked and at maturity, flattened, smooth or with ornamentations, continuous, colored, and with a longitudinal germ slit.

In *Dictyoarthrinium* spp. (Figs. 96, 97) (Hughes (59)) the conidiophores possess dark cross-walls and a single terminal, and lateral whorls of conidia borne between the dark transverse septa. The conidia are flattened, roughwalled, and quadrately septate; they are four-celled in *D. quadratum* Hughes and composed of a flat plate of 16 cells in *D. africanum* Hughes. The conidiophores elongate by a growing point either within or just above the conidiophore mother-cell and the youngest conidia are generally found towards the base. I observed no germ slits in the conidia of either species. The fructifications are similar to those of *Arthrinium* spp.



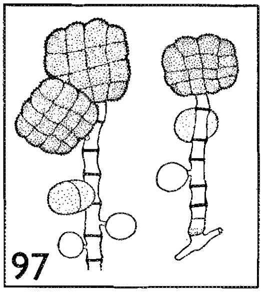


FIG. 96. *Dictyoarthrinium quadratum*, conidiophores and conidia from Hughes (59); ×500.

FIG. 97. *Dictyoarthrinium africanum*, conidiophores and conidia from Hughes (59); ×500.

In *Spegazzinia tessarthra* (Berk. & Curt.) Sacc. (Fig. 98) and *S. tessarthra* var. *deightonii* (Hughes (68)) the conidiophores arise from conidiophore mother-cells and bear the single terminal conidium prior to elongation. At maturity the conidiophores are of two kinds, micro- and macro-conidiophores, each bearing different kinds of conidia, a single one at the apex of each. The macro-conidiophores are dark brown and do not possess black and wide transverse septa. The conidia of the species and its variety do not possess a germ slit.

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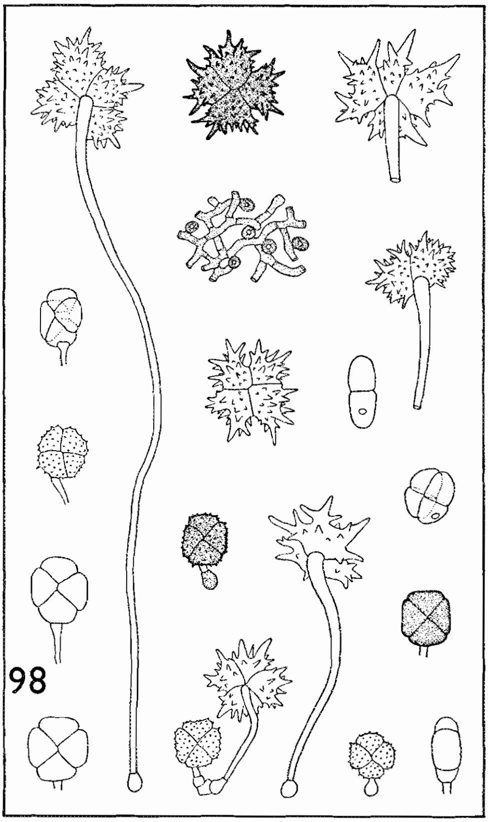

FIG. 98. *Spegazzinia tessarthra*, mycelium, conidiophores, and conidia from Hughes (68); ×500.

(The flattened conidia of *Pseudocamptoum fasciculatum* (Cooke & Massee) Mason have a longitudinal germ slit but this species cannot be classified in this section. In the first place the conidiophores do not arise from conidiophore mother-cells and they elongate by means of a terminal growing point which ultimately blows out into a conidium; a succession of conidia then develops, each conidium being the blown-out end of successively produced growing points just lateral to the previous conidium. *Pseudocamptoum* is classified in Section II.)

Graphiola spp. are currently classified in the *Graphiolaceae* of the Ustilaginales although their location there has always been regarded as dubious. Of *G. borassi* Sydow & Butler (108) the authors stated that the fungus has nothing in common with the Ustilagineae. I believe *Graphiola* spp. such as *G. phoenicis*, *G. thaxteri*, *G. congesta*, and *G. borassi* Syd. & Butl. should be classified amongst the Fungi Imperfecti; these are far more closely related to *Endocalyx* spp. than their usual inclusion in the Ustilaginales would suggest. The illustrations of *Graphiola thaxteri* Fischer (Fig. 99) and *G. congesta* Berk. Rav. by Fischer (38) certainly suggest a basal elongation of the conidio-

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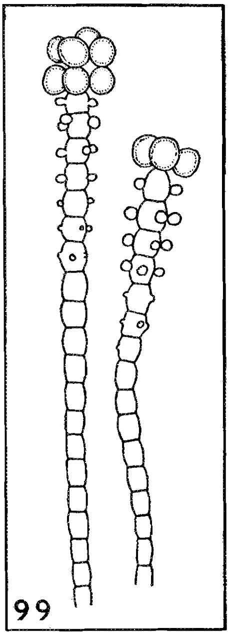
phores on which conidia develop laterally apparently in basipetal succession as in *Endocalyx* (Hughes (68)). The illustrations of conidiophores of *G. phoenicis* Poit. (Fischer (37)) are very much like those of *G. thaxteri.* Sydow and Butler's (108) figures (Fig. 100) indicate a basal elongation of conidiophores in *G. borassi,* the individual cubical cells of which develop three to eight linear conidia mostly at the corners; the cubical cells themselves finally secede from each other and presumably function as conidia.



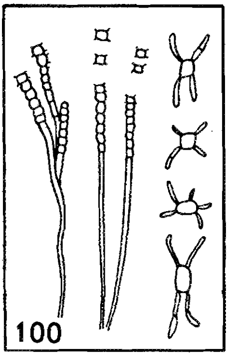


FIG. 99. *Graphiola thaxteri,* isolated conidiophores and conidia from Fischer (38); ×1170.

FIG. 100. *Graphiola borassi,* isolated conidiophores (×486) and conidia (×810) from Sydow and Butler (108).

Discussion

In the preceding pages I have attempted to arrange some Hyphomycetes into sections wherein the types of conidiophore and conidium development and structure are the primary differentiating characters. I believe that these sections show a measure of uniformity including interesting variations on distinct themes which cannot be obtained by using in a major sense the characters employed in the older classifications. Whether this uniformity will be retained by including a far greater number of genera remains to be seen. I have not included the singularly curious type of development of the isthmospores (Hughes (68)) of *Trichothyrium asterophorum* (Berk. & Br.) v. Höhn. and *T. reptans* (Berk. & Curt.) Hughes which develop from and are supported at maturity each by two 'conidiophores'; isthmospores would I believe require to be classified as Section IX. Furthermore, there may well be other types of conidium development which may not fit adequately into any of the sections delimited. But these data and this classification into major groupings are presented in the belief that a more rational classification in the Hyphomycetes (or Fungi Imperfecti as a whole) will be evolved only when those early stages of conidium development are more clearly understood; such terms as 'budded-off' or 'abstricted' when applied to conidia, without reference to what has actually happened or is actually happening to the conidiophore, do not seem to help very much.

I hope this paper will stimulate not criticisms alone but criticisms accompanied by details of early conidium development more definite than have appeared in the past.

Whereas a large number of well or poorly differentiated terms are available for various spore forms the reverse seems to be true for 'conidiophores'. This term has been used very loosely in the above account but the need for more precise terms is evident. In *Dendryphiopsis* and *Verticicladium*, for instance, when the main stalk and branches are referred to as branched conidiophores it does not specify any distinctive type of compound lateral branches borne on a main stalk. The term conidiophore can be used satisfactorily only for simple conidia-bearing structures.

In mononematous and synnematous fructifications the actual structures bearing the conidia may be well differentiated. The *phialide* can I believe have a precise meaning and implies a unicellular structure. The term *annellophore*, however, can apply to the long multiseptate conidiophore of *Annellophora* as well as to one of the annellated sporogenous cells of *Stysanus* and I believe a distinction needs to be drawn. In Section II conidia develop in the same way on the long multiseptate conidiophore of *Virgariella* as they do on one of the ultimate unicellular sporogenous cells of a *Verticicladium* or *Costantinella* fructification; in the last named it will be remembered that the unilateral, linear, close succession of conidia led to the term 'cervix' but as far as I am aware this can only be used for two (and a possible third) species of *Costantinella*. No precise term for the conidiophore or sporogenous cell of Section II have been proposed but such a term would greatly facilitate the description of many Fungi Imperfecti. The terms acrogenous and acropleurogenous can be used equally well for a few distinct types of conidiophores. Furthermore, there seem to be no terms available to indicate precisely the characters of conidiophores of Sections I, V, VI, VII, or VIII.

A number of interesting examples of outward similarity between fructifications in the various Sections occur. For instance slimy heads of hyaline amerospores on mononematous, dematiaceous conidiophores are produced by *Haplographium*, *Verticicladiella*, *Leptographium*, and *Hantzschia* but conidium development is different in all four and necessitates their segregation into Sections I, II, III, and IV respectively. Furthermore a comparison of the following is interesting: *Calcarisporium* [II] and *Verticillium* [IV]; *Gonatobotrys* [I] and *Arthrobotrys* [II]; *Heterosporium* [II], *Cladosporium* [I], and

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Oidiodendron [VII]; *Spilocaea* [III] and *Fusicladium* [II], to mention only a few examples of parallelism involving distinct types of conidium development.

Nuclear behavior during conidium production has been neglected. The nuclear phenomena during conidium (oidium) production, by the method of Section VII, in *Collybia velutipes* have been described by Brodie (see p. 642). Some further examples are included here.

Nobles (92) stated that in *Peniophora allescheri* (=*P. mutata* (Peck) v. Höhn. & Litsch. fide Dr. Nobles, personal communication) successive division of the single nucleus in the oedocephaloid conidiophore head resulted in 2, 4, 8, 16, or more nuclei. 'The nuclei take up their positions around the inner surface of the distal half of the conidiophore........... At this stage the slender tapering sterigmata push out and a swelling, the developing conidium, appears on the end of each. While the spore is still small a nucleus migrates into it...........'. Uninucleate conidia in the oedocephaloid conidiophores of *Corticium effuscatum* Cooke & Ellis were shown to arise in a manner similar to the aforementioned (Nobles (93)).

Constance Loveland (unpublished researches) informs me that a similar behavior of the nuclei is seen in *Botrytis* spp. In *B. allii* single nuclei migrate into the conidium initials and divide once so that the conidia are binucleate. In *B. cinerea* and *B. streptothrix* (Cooke & Ell.) Sacc. a number of nuclei migrate into each conidium initial from the ampulla on which the conidia develop. I know of no publications dealing with nuclear phenomena in any of the other species included in Section I and which do not show such a simultaneous development of conidia.

Biggs (8) described and illustrated the successive sympodial production of conidia [as 'oidia'] in cultures of *Corticium coronilla* v. Höhn. & Litsch. Of interest is the demonstration of successive divisions of the nucleus of the conidiophore [as 'oidiophore']; one of the daughter nuclei passes to the tip of the growing point which is cut off as a conidium whilst the other divides again and one of the daughter nuclei then passes to the tip of a new growing point which has developed to one side of the base of the previous conidium. This process is repeated a number of times. This method of conidium production is characteristic of Section II but details of nuclear behavior in any other members are unknown to me. It would be extremely interesting to know the nuclear content and behavior in say *Arthrobotrys* spp. during development of conidia (see p. 599).

Backus and Keitt (4) studied nuclear phenomena in *Venturia inaequalis* and found the cells of the vegetative mycelium, conidiophore, and conidium to be uninucleate. It would appear from their illustrations that a daughter nucleus resulting from the division of the conidiophore nucleus migrates into the conidium initial which is then cut off by a cell wall. This is similar to the method described by Biggs (8) except that the successive conidia in *V. inaequalis* are produced by successive proliferations *through* the old scar (Section III). I find no reference to similar work on *V. pirina* Aderh. which produces conidia as in Section II.

Martens and Vandendries (80) described and illustrated three types of accessory spores in *Pholiota aurivella* Batsch. Their semidiagrammatic illustrations are reproduced here as Fig. 101 in which *A* shows 'oidiophores' with basipetal segmentation into 'oidia', the main stalk being terminated by a 'chlamydospore'; *B*, shows a solitary terminal 'chlamydospore' and *C*, fusiform conidia arising successively at the apex of a conidiophore by the blowing out of successive new growing points. In this fungus, therefore, we find three types of conidium development as characteristic of Section II (Fig. 101 *C*), Section III (Fig. 101 *B*), and Section VII (Fig. 101 *A*).

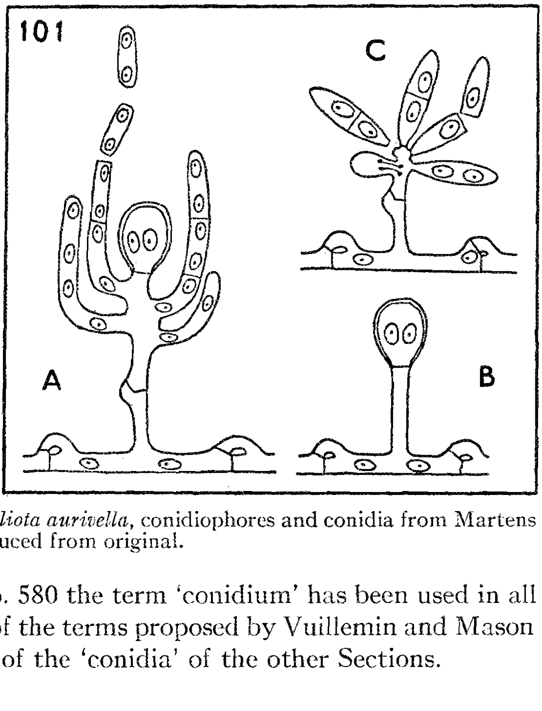

FIG. 101. *Pholiota aurivella*, conidiophores and conidia from Martens and Vandendries (79); slightly reduced from original.

As stated on p. 580 the term 'conidium' has been used in all Sections except IV. But some of the terms proposed by Vuillemin and Mason may be usefully applied to some of the 'conidia' of the other Sections.

Section I.—Because of developmental similarity between say the *Oidium* fructifications of *Pellicularia pruinata* and the fructifications of *Cladosporium* the two parts A and B of Section I were at first combined. The result was a heterogenous group. More uniformity in both Sections was obtained by separating into A those species with predominantly narrow mycelial hyphae and into B those with predominantly wide mycelial hyphae.

In Section IA the conidia are nearly always in chains; they are '*blastospores*' (arising as globular buds or blown-out ends) and their development in acropetal chains is inferred by this term.

In Section IB the conidia are very commonly solitary and I call them *solitary blastospores*; when they occur in botryose clusters the conidia are *botryose solitary blastospores* as in *Botrytis* and *botryose blastospores* in *Gonatobotryum* or *Nematogonium* in which fungi the conidia are in chains. The conidia in this Section are nearly all dry.

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Section II.—The conidia are '*terminus spores*'; in many instances, e.g., *Ramularia* and *Heterosporium*, the terminus spores may bud at the apex and produce *blastospores* but in the chains produced the basal or primary conidium is a terminus spore. In *Arthrobotrys* the conidia may develop in clusters and such conidia may be described as *botryose terminus spores.* Terminus spores are nearly always dry, but produced in slime in a few instances.

Section III.—The conidia are '*chlamydospores*' and are usually produced at the apex of a hypha; they are solitary and usually large, thick-walled, and dark colored but may be small, hyaline, and not particularly thick-walled especially when developing in slimy heads. It will be remembered that intercalary chlamydospores occur in many fungi and both terminal and intercalary chlamydospores may be produced by the same fungus. When chlamydospores are terminal, annellations may be produced on the conidiophores (*annellophores*) and *successive chlamydospores* may remain loosely attached in chains.

The disadvantage of the character implicit in the term annellophore is the great difficulty that may be encountered in observing the actual annellations more especially in those species whose annellophores are narrow and hyaline. Nevertheless it seems to be such a well established mode of producing a plurality of terminal chlamydospores on a single conidiophore in the Hyphomycetes, and in the Coelomycetes apparently, that it must be taken into account in the future if conidium origin is to play any part at all in classification. (The annellations of Section III are comparable with the 'caps' formed in *Oedogonium* during cell formation (Fritsch (39))). The chlamydospores are nearly all dry.

Section IV.—The conidia are '*phialospores*' and are produced in basipetal succession from *phialides* which may or may not possess a very evident collarette. If the spores produced 'on the surface' of the ascospores of *Nectria coryli*, whilst still within the ascus, are the homologues of phialospores as suggested by Mr. Mason (82) then they may be called *radula phialospores.* The term *polyphialide* was proposed by Hughes (52) to include phialides which produce more than one open end from each of which a basipetal succession of phialospores is produced.

Langeron (76) included as phialides the annellophores of *Venturia inaequalis* [Sect. III], the conidiophores of *Erysiphe graminis* DC. [Sect. V], the sporogenous cells of *Beauveria bassiana* (Bals.) Vuill. [Sect. II], the sporogenous cells of '*Haplographium delicatum*' [Sect. IA] in addition to the true phialides of say *Stachylidium* and *Acrostalagmus* [*Verticillium*].

Mason (83) has pointed out that amongst fungi with phialides there is an 'obvious transition between genera characterized by slimy phialospores to other genera characterized by dry phialospores'.

Section V.—The conidia may be termed *meristem arthrospores* and they occur in true chains; their basipetal development, due to the meristematic growth of the conidiophore, seems to me to necessitate a special term for them although they appear to be related to the arthospores dealt with in *Section VII.* Meristem arthrospores are usually dry.

Section VI.—The conidia may be called *porospores.* In *Helminthosporium velutinum* a solitary apical and lateral porospores in verticils are produced whilst in '*H. teres*' successive *terminus porospores* develop. Chains of porospores occur in *Diplococcium spicatum* and *Dendryphion* spp. Porospores are dry.

Section VII—The conidia have been called '*arthrospores*' and this seems to be a perfectly suitable term for conidia which arise from the fragmentation of conidiophores of determinate length. Arthrospores may be dry or slimy.

Section VIII.—The conidia are blown-out ends and are borne either singly at the apex or singly at the apex and laterally, generally in basipetal whorls. Mason (82) proposed the term 'radula thallospores' for the conidia of *Papularia* but I doubt whether this term can be used for Section VIII in its entirety. But the hall mark of this Section is the basal elongation of the conidiophores and these may be called *basauxic conidiophores.* The conidia are dry.

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Because a taxonomic species is entitled to one and only one Latin binomial, some difficulty is experienced with the Fungi Imperfecti. Where a particular taxon has no recognized perfect state and is known to produce two or more imperfect states then any of the states is eligible to provide the generic name regardless of the relative position of the states in any scheme of classification. But which state should be chosen to supply the generic name for the taxon? Or is the particular association of different states to be the basis of a new generic name?

Mason (83) has drawn attention to a splendid example of a fungus described under seven binomials each generic name employed indicating the type of state under consideration. As Mason so rightly pointed out 'It is now, I think, generally agreed that seven binomials for one species are too many'.

It is interesting to observe that the generic name *Chalaropsis* Peyr. is based on a polymorphic species with two types of fructifications or states which would, separately, be classified in Sections IV (phialospores) and II (terminus spores) (see Mason (84)); the production of the two states is, I take it, obligatory for inclusion in *Chalaropsis.* The two types of conidium-bearing structures usually have a common stalk in *Chalaropsis thielavioides* Peyr., the type species, and also in *Ceratostomella radicicola* Bliss (10) (*Chalaropsis* state). The name '*Chalaropsis* pro parte', therefore, could be included in each of two Sections of the classification outlined above. *Thielaviopsis basicola* (Berk. & Br.) Ferr. (see Arnaud and Barthelet (2)) shows a similar association of distinct states also usually borne on a common stalk; the two states would be included, separately, in Sections IV (phialospores) and presumably II (chlamydospores). As Mason (84) has pointed out the two states of

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Chalaropsis thielavioides Peyr. had already been described by McAlpine as '*Cylindrium intermixtum*' (phialospores) and '*Coniosporium radicicola*' (terminus spores). The former state could, I believe, be classified in *Chalara* but I know no generic name which would include comfortably the latter state. Is it advisable to base a generic name on the association of two states of one fungus? Now Mason (82) stated 'that the most urgent business of systematic mycology among the imperfect forms . . . must be to recognize whether a form-genus is founded on a phialospore form or is based on some other spore form . . .' But the form genera *Chalaropsis* and *Thielaviopsis* are each based on two different states or spore-forms although one state is common to both; I believe that such a practice is undesirable because the names are double form generic names relying on the presence of two distinct states for their precise application.

Not many 'species' of Fungi Imperfecti show such a constant association of two states on a common stalk; on the other hand most 'species' show a spasmodic occurrence of different states invariably on distinct stalks and furthermore many 'species' exhibit such different states only in pure culture on agar media.

If a fungus imperfectus shows itself to be polymorphic then it seems best to choose for the generic name of the taxon that state which is considered to be most frequent or constant in occurrence, most conspicuous, or most readily identifiable; but of course this is, for the most part, what has been done in the past. It would appear, therefore, that the choice of generic name for a polymorphic fungus imperfectus is entirely an arbitrary one. In such a polymorphic taxon, therefore, the generic name is the result of classifying one of the states or spore forms to the exclusion of all others (except in *Chalaropsis* for instance). But what of the states whose production is not implied by the generic name chosen? Mason advocated the use of differential names for classifying spore forms [states] and this seems to be the only way out with the Fungi Imperfecti. The subsidiary states may be referred to as *Hyalodendron* blastospores, *Cephalosporium* phialospores, etc., as the case may be, without the unnecessary new combinations. If no suitable qualifying generic name is available precisely to indicate the type of subsidiary state then this can be referred to by the use of spore terminology alone; but for this to work, of course, it is necessary to establish types of conidium development on a firm basis. The alternative is a multiplicity of names, that is, as many names for each species as any author considers there are of recognizable states.

Cooke's (21) concluding remarks in a note on 'Spores and Sporidia' are as follows: 'Subsidiary names are constantly being given to spores having a peculiar mode of generation or of development, and so long as these terms are understood and restricted to their original characteristics they are useful . . . . .'

In the scheme outlined above I have incorporated some old and some new ideas with old and new names for conidiophores and conidia. It is hoped that this comprises another step forward in the quest for a rational classification of those states currently classified as Hyphomycetes.

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I.M.I. 349(*a*), on *Ligustrum ovalifolium*, Lambourne Hill, Perranzabuloe, West Cornwall, England, U.K., 16.xi.1944; 462, on *Fraxinus excelsior*, Mickleham, Surrey, England, U.K., 5.vi.1932; 1353, on *Crataegus oxyacantha*, Kingthorpe Woods, Yorks., England, x.1945; 1354, on *Fagus sylvatica*, Kingthorpe Woods, Yorks. England, x.1945; 1357, on wood, Kingthorpe Woods, Yorks., England, x.1945; 1359, on *Urtica* stems, Kingthorpe Woods, Yorks., England, x.1945; 1685, on *Solanum tuberosum*, England, xi.1945; 1694, 'Kings Cliffe', *Cladotrichum triseptatum* folder in Herb. R.B.G. Kew [no further data]; 4133, on *Urtica dioica*, Hampton Court, Middlesex, England, ii.1946; 4333, on *Urtica dioica*, near Aberystwyth, Wales, U.K., 25.iii.1946; 4493, on *Fagus sylvatica*, Boxhill, Surrey, England, 13.iv.1946; 5366, on wood, Norbury Park, England, 12.v.1946; 5505, on *Ulmus* sp. wood, Scarthingwell Park, Tadcaster, Yorks., England, 11.v.1946; 6054(*a*), on *Fagus sylvatica* wood, Tothill, Surrey, England, 7.vii.1946; 6072, on *Quercus* sp. wood, Ranmore, Surrey, England, 13.vii.1946; 6784, on *Quercus* wood, Mulgrave Woods, Yorks, England, 14.ix.1946; 6787, on *Tilia europea*, Forge Valley, Yorks, England, 16.ix.1949; 7040, on *Fagus sylvatica*, Arncliffe woods, Yorks, England, 17.ix.1946; 7393, isolated from Orange, Calcutta, India, 1939; 8977, on *Ranunculus* leaf, Simondsdyke Wood, England, 22.i.1946; 9070 (slide ex) *Conoplea tiliae* folder in Herb. Persoon in Herb. Lugd. Bat. No. 910, 263-286; 9882, on *Quercus* sp., Ranmore, Surrey, England, 6.i.1947; 14014, on *Fraxinus excelsior*, Howldale, Yorks, England, 13.iv.1947; 14486, on *Fraxinus excelsior*, Howldale, Yorks, England, 12.iv.1947; 15281,

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on *Cladium mariscus*, Pool Marsh, Wheatfen Broad, Norfolk, England, 8.v.1947; 15528, on *Fagus sylvatica*, Ranmore, Surrey, England, 25.v.1947; 18435(*b*), on wood, Birmingham, England, ix.1947; 19039, on *Fraxinus excelsior*, Exeter, Devon, England, 14.ix.1947; 19219, on *Fagus sylvatica* cupules, near Masham, Yorks, England, 11.x.1947; 19654, on *Quercus ilex* twigs, Italy (D. Sacc., Fungi, Ven. Nov.); 20037(*d*), on *Betula*, Ranmore, Surrey, England, 14.xii.1947; 22419, on wood, Earls Court, London, England, 25.i.1948; 27623, on *Sorbus aucuparia*, Limb Valley, Yorks, England, 10.iv.1948; 31422, on *Ilex aquifolium*, near Masham, Yorks, England, 28.iv.1948; 33713, on *Fagus sylvatica*, Ranmore, Surrey, England, 23.i.1949; 34001(*c*), on *Brassica* sp., near Stoke Poges, Bucks, England, 23.i.1949; 40653(*g*) on *Sorbus aucuparia*, near Masham, Yorks, England, 15.iv.1950; 45947, isolated from soil, Sussex, England, xi.1950; 49478, on *Fagus sylvatica*, Ranmore, Surrey, England, ii.1952.

New Species, New Genera, New Combinations

Twenty-nine new combinations have been made throughout the text on pp. 582, 585 (two), 586, 587, 591, 594 (two), 603, 604, 605, 606, 609, 615, 616, 618, 619 (three), 622, 627, 628, 631, 634 (three), 636, 638, and 640, and six are proposed below.

A discussion, with fuller descriptions and further illustrations, of the new taxa described and reasons for many of the new combinations will be given in subsequent publications.

Section II: **Verticicladiella** gen. nov.

Fungi Imperfecti hyphomycetes.

Conidiophora sicut *Verticicladii* (typus *V. trifidum* Preuss) sed capitulo mucoso; ramulis primariis, secondariis, tertiisque plus minusve parallelis, adpressisque; cellulis sporogenis sub-parallelis.

Conidia continua, hyalina, ovata vel paulo curvata, laevia, acropleurogena in cellulis sporogenis in capitulum mucosum oriunda.

Species typica: **Verticicladiella abietina** (Peck) comb. nov.

≡ *Sporocybe abietina* Peck in N.Y. State Museum Rept. 31 : 45. 1879.

≡ *Periconia abietina* (Peck) Sacc. in Sylloge Fungorum, 4 : 273. 1886.

Section II: **Virgariella** gen. nov.

Fungi Imperfecti hyphomycetes, saprophytici.

Conidiophora longa, solitaria, simplicia, septata, crasso-tunicata, atro-brunnea.

Conidia sphaeroidea vel ovata, continua, atro-brunnea, laevia, sicca, crasso-tunicata, acropleurogena.

Species typica: **Virgariella globigera** (Sacc. & Ell.) comb. nov.
≡ *Virgaria globigera* Sacc. & Ellis apud Sacc. in Michelia, 2 : 578. 1882.

Species aliae: **Virgariella fusca** (Cooke) comb. nov.
≡ *Haplaria fusca* Cooke in Grevillea, 6 : 141. 1878.
≡ *Virgaria fusca* (Cooke) Sacc. in Sylloge Fungorum, 4 : 281. 1886.
= *Virgaria olivacea* Ell. & Everh. in Bull. Torrey Botan. Club, 10 : 97. 1883.

Virgariella atra sp. nov.

Coloniae atrae, effusae.

Mycelium immersum vel semi-immersum, ex hyphis ramosis, pallide-brunneis vel brunneis, septatis compositum.

Conidiophora solitaria, erecta, plus minusve rigida, recta, aliquando flexuosa, atro-brunnea, septata, crasso-tunicata, subcylindracea, usque ad 180μ longa, 3.5-5μ crassa, basi usque ad 6.5μ inflata. Crescentia conidiophori indefinita ut in finem cicatrices dispositi sunt in symplegmis intercalaribus.

Conidia subsphaeroidea vel ovata, continua, atro-brunnea, laevia, sicca, crasso-tunicata, acropleurogena, 13-13.5 × 9.7-12μ.

Habitat in ligno putrido *Fraxini excelsius*, Maltby, Yorkshire, Anglia, 9.iv.1948. I.M.I. 27613 (typus).

Section III: **Monosporella** gen. nov.

Fungi Imperfecti hyphomycetes saprophytici.

Conidiophora solitaria, simplicia, septata, crasso-tunicata, plus minusve subulata, brunnea, per proliferationes successivas cylindraceas elongascentia.

Conidia solitaria in primis in apice conidiophori et deinde successivarum proliferationum oriunda, sphaeroidea vel pyriformia, continua vel 2-septata, atro-brunnea vel brunnea, laevia, sicca.

Species typica: **Monosporella setosa** (Berk. & Curt.) comb. nov.
≡ *Monotospora setosa* Berk. & Curt. apud Berk. in Grevillea, 3 : 101. 1875.
≡ *Phragmocephala setosa* (Berk. & Curt.) Mason & Hughes in Naturalist, Lond. 1951 : 97. 1951.

Species aliae: **Monosporella sphaerocephala** (Berk. & Br.) comb. nov.
≡ *Monotospora sphaerocephala* Berk. & Br. in Ann. Mag. Nat. Hist. III, 3 : 361. 1859.
≡ *Halysium sphaerocephalum* (Berk. & Br.) Vuillemin in Bull. Soc. Sci. Nancy, III, 11 : 167. 1911.

A *Monosporella* conidial apparatus is also produced by *Farlowiella carmichaeliana* (Berk.) Sacc.

Section III: **Bactrodesmium masonii** sp. nov.

Sporodochia punctiformia, atra, dispersa, usque ad 170μ diam.

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Conidiophora brevia, ramosa, septata, usque ad 37μ longa, hyalina vel subhyalina, basi 2.5-3μ, apicem versus usque ad 6μ crassa, per 1-3 proliferationes successivas cylindraceas elongascentia.

Conidia solitaria in primis in apice conidiophori et deinde successivarum proliferationum oriunda, ovata, 1-2 plerumque 2-septata, paulo constricta, crasso-tunicata, apice rotundata, basi plana cicatrice conspicuo praedita, pallide-brunnea, laevia, 18-26 × 8-10μ.

Habitat in cupulis emortuis *Fagi sylvatici* in terram; prope Masham, Yorkshire, Anglia, 11.x.1947, I.M.I. 19219(*y*) (typus); Boxhill, Surrey, Anglia, 22.xi.1947, I.M.I. 19652(*c*).

Section VI: **Dendryphiopsis** gen. nov.

Fungi Imperfecti hyphomycetes saprophytici.

Conidiophora: Stipes erectus, septatus; ramuli laterales primarii, secondarii, ternarii, quandoque quaternii, solitarii vel plerumque bini oriundi, plus minusve in formam dichasii. Stipes, ramulique poro singulo apicali praedita.

Conidia singula in ramo, in apicibus stipitis ramulorumque oriunda, subcylindracea, utrinque rotundata, crasso-tunicata, 2-6-septata, laevia, fortiter colorata, facile secedentia, basa poro praedita.

Species typica: **Dendryphiopsis atra** (Corda) comb. nov.
≡ *Dendryphion atrum* Corda in Icones Fungorum, 4 : 33. 1840 (sub '*Dendryphium*').
≡ *Dendryphion ellisii* Cooke in Grevillea, 7 : 7. 1878 (sub '*Dendryphium*').

Identical with *D. atra* or only critically distinct from it are the following:

Helminthosporium nanum Nees in Das System der Pilze und Schwamme. 1817.

Helminthosporium obtusissimum Berk. & Curt. apud Berk. in Grevillea, 3 : 103. 1875.

Dendryphion crustaceum Ell. & Everh. in Webber Rept., Nebr. Bd. Agr. 1889 : 85. 1890 (sub '*Dendryphium*').

Dendryphion pachysporum Ell. & Everh. in Proc. Acad. Phil. 1891 : 92. 1891 (sub '*Dendryphium*').

Acknowledgments

It is a pleasure here to record my extreme indebtedness to Mr. E. W. Mason under whose guidance and inspiration I studied Hyphomycetes, at the Commonwealth Mycological Institute, and also in the field. Without such an experience this paper could not have been written; if I have misinterpreted the Hyphomycetes as classified here then the fault is mine.

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NOTE: Since this article went to press *Streptothrix* conidiophores have been obtained from pure cultures of *Urnula craterium* (Schw.) H. (See p. 606).

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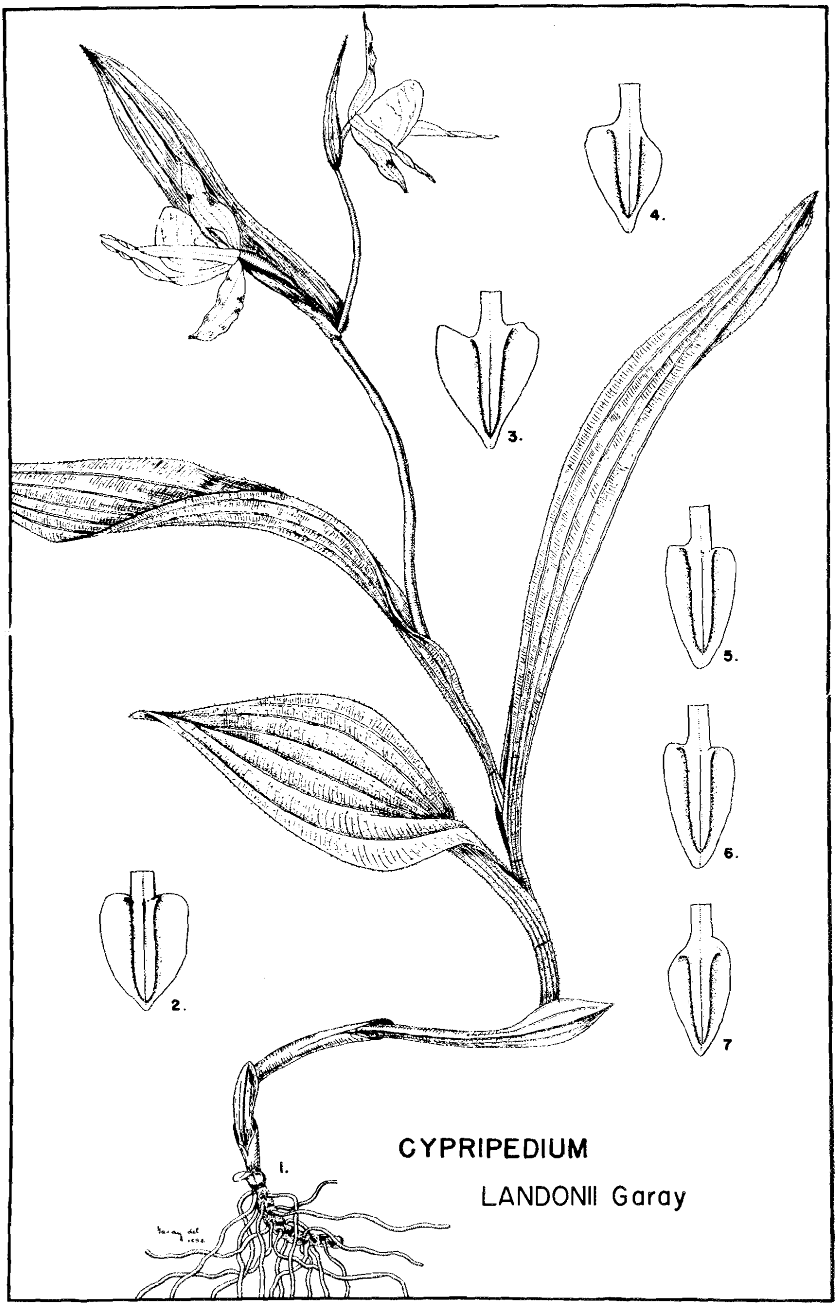

FIG. 1. Plant about one half of the natural size. FIGS. 2-7. Various staminodes approaching the shape of the parents, ×2. FIG. 2. Similar to *C. Calceolus* var. *parviflorum* Fern. FIGS. 3-4. Close to × *C. Favillianum* Curtis. FIGS. 5-7. Resembling *C. candidum* Muhl.

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