118

Conidium development in anamorphs of *Ceratocystis sensu lato*: a review

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The use of mode of conidium development as a characteristic in the taxonomy of the anamorphs of Ceratocystis sensu lato *led to a drastic increase in the number of anamorph genera. This excessive number of anamorph names inspired reconsideration of these genera on the basis of mode of conidium development. This review shows that anamorphs of* Ophiostoma *can be divided into two groups based on the mode of wall building during conidiogenesis. These include both those having apical and ring wall-building development. Patterns of development included in the apical wall-building group are phialidic, annellidic and sympodial development. Following this restricted approach, the total number of anamorph names for* Ceratocystis s.l. *can be considerably reduced. For example, anamorphs of* Ophiostoma *could be* Leptographium, Graphium, Hyalorhinocladiella, Sporothrix *and* Knoxdaviesia.

The mode of conidium development has played a substantial role in the taxonomy of *Ceratocystis* Ell. & Halst. *sensu lato*. Realization that two distinct forms of conidium development exist in this group of fungi dates back to Münch,[1] who recognized the unique nature of the *Chalara* (Cda.) Rabenh. anamorph and established *Endoconidiophora* for *E. coerulescens* Münch, which he considered distinct from *Ceratostomella* Sacc. After Hughes[2] introduced conidium development as a characteristic on which to base the classification of conidial fungi, there was a proliferation of generic names attached to anamorphs of *Ceratocystis s.l.* By the time the most recent monograph of *Ceratocystis* was published,[3] seventeen generic names had been assigned to species of *Ceratocystis* (Table 1). The genus *Knoxdaviesia* Wingfield, van Wyk & Marasas was recently added to this list by Wingfield, van Wyk & Marasas.[4] Most of these genera have been separated according to patterns of conidial development.

The aim of this paper is to review patterns of conidium development in anamorphs of *Ceratocystis*, *Ceratocystiopsis* Upad. & Kendrick and *Ophiostoma* H. & P. Syd. The value of conidium development as a taxonomic criterion is also considered.

Historical background

Endogenous versus exogenous conidia

The historical background of the genus *Ceratocystis s.l.* has been extremely confused. To some extent, this confusion has stemmed from various opinions concerning the anamorphs of these fungi. Amongst the anamorphs of *Ceratocystis*, two distinct patterns of conidial development were recognized by early taxonomists. Endoconidiophora was established for *E. coerulescens* Münch (1902) on the grounds that this fungus had an endoconidial anamorph (*Chalara ungeri* Sacc.). Unbeknown to Münch,[1] *Ceratocystis fimbriata* Ellis and Halsted (1890) also had a *Chalara* anamorph and the establishment of *Endoconidiophora* was in error. Despite this fact, numerous subsequent researchers[5-7] accepted this taxon and erected additional species in *Endoconidiophora*.

After the establishment of *Ophiostoma*, Melin and Nannfeldt[8] subdivided the genus into two groups based on the presence of endoconidial (*Chalara*) anamorphs and those with conidia produced exogenously. Bakshi[9] revived *Ceratocystis*

Table 1. Genera of conidial fungi that have been associated with species of *Ceratocystis* (Cs), *Ceratocystiopsis* (Cp) and *Ophiostoma*.

Genus	Comments	References
Acremonium	State present in *O. nigrum*. Possibly reduced form of *Hyalorhinocladiella*	3
Allescheriella	Anamorph of *Cp. retusi* (Davidson & Hinds) Upadhyay. Resembles *Sporothrix*	3
Chalara	Anamorphs of *Ceratocystis s.s.*	11, 33
Gabarnaudia	Anamorphs of *Cs. fimicola* (Marchal) Upadhyay and *Cs. helvellae* (Karsten) Upadhyay	32, 44
Graphilbum	Anamorph of *Cs. sparsa* Davidson and *Ophiostoma ips* (Rumbold) Nannf. Hyaline analogue of *Graphium*	30
Graphiocladiella	Anamorph of *Ophiostoma clavigerum*. No obvious justification for separation from *Graphium*	3, 45
Graphium	Anamorphs of many *Ophiostoma* spp. Incorporates *Pesotum*, *Phialographium* and possibly *Graphiocladiella*, *Graphilbum* and *Hyalopesotum*	29
Hyalodendron	Anamorphs of *O. californica* de Vay, Davidson & Moller; *O. piliferum* (Fries), *O. multiannulatum* (Hedge. & Davidson) Hunt and *O. pluriannulata* (Hedge.) H. & P. Sydow. Probably more correctly *Sporothrix*	3
Hyalopesotum	Anamorph of *O. introcitrina* Olchowecki and Reid. Hyaline analogue of *Pesotum*. Possibly synonymous with *Graphium*	29, 30
Hyalorhinocladiella	Anamorphs of many *Ophiostoma* spp. Hyaline analogue of *Rhinocladiella*	30
Knoxdaviesia	Anamorph of *Cp. proteae*	4
Leptographium	Anamorph of many *Ophiostoma* spp. Includes *Verticicladiella* and *Phialocephala* anamorph of *O. francke-grosmanniae*	42
Pachnodium	Anamorph of *C. cana* (Münch) C. Moreau. Synnematal analogue of *Sporothrix*	30
Pesotum	Sympodial analogue of *Graphium*. Synonym of *Graphium*	27, 29
Phialocephala	Phialidic analogue of *Leptographium*. Purported anamorph of *O. francke-grosmanniae* which was shown to be *Leptographium*	38, 39, 42
Phialographium	State of *C. sagmatospora* Wright & Cain. Synonym of *Graphium*	28, 29
Sporothrix	Anamorph of many *Ophiostoma* spp., often synanamorph with *Graphium*	3, 11
Verticicladiella	Sympodial analogue of *Leptographium*. Synonym of *Leptographium*	2, 23, 42

based on *C. fimbriata* and considered various other generic names, including *Endocondiophora* and *Ophiostoma*, to be synonyms of *Ceratocystis*. The preferential treatment given to the endoconidial state was thus retracted. Hunt[10] followed the example of Bakshi[9] and accepted *Ceratocystis* as incorporating genera such as *Endoconidiophora, Rostrella* Zimmerman, *Grosmannia* Goid. and *Ophiostoma*.

Despite the fact that he viewed *Ceratocystis* as representing a homogeneous group, Hunt[10] recognized that distinct anamorph groups existed. For these he established three sections. They included a section for species of *Ceratocystis* with endoconidial (*Chalara*) anamorphs. Two other sections were established to accommodate anamorphs with conidia produced exogenously but which had macronematous (*Graphium* Corda/*Leptographium* Lagerberg & Melin) (Fig. 1*A*–*H*) and micronematous (mycelial) (Fig. 2*A*–*E*) conidiophores.

De Hoog[11] resurrected the altercation concerning generic names in *Ceratocystis s.l.* and transferred species of *Ceratocystis s.l.* with 'mycelial conidia' to *Ophiostoma*. *Ceratocystis sensu stricto* was then reserved for species with endoconidial anamorphs. This subdivision of *Ophiostoma* and *Ceratocystis* has gained support in recent years from studies on cell wall composition and physiology. For example, the cell walls of those species with *Chalara* states lack cellulose,[12-14] which is present in other species. Similarly, rhamnose has been found in species with conidia produced through apical wall building but not in those with *Chalara* anamorphs.[15,16] Moreover, species of *Ceratocystis s.s.* are unable to tolerate low concentrations of cycloheximide, whereas those of most species of *Ophiostoma* grow in the presence of high concentrations of this compound.[17]

Conidium development in terms of Hughes

The above discussion pertains almost exclusively to the presence or absence of 'endoconidia' and a *Chalara* anamorph. This might well have occurred despite the fundamental work of Hughes,[2] who promoted patterns of conidium development as taxonomic criteria in anamorphic fungi as a whole. However, the mode of conidium development in terms of Hughes[2] has had a pronounced effect on the taxonomy of anamorphs of *Ceratocystis s.l.* other than those genera with *Chalara* anamorphs.

Three distinct types of conidium development introduced by Hughes[2] have been pertinent to anamorphs of *Ophiostoma*. These include blastic annellidic (section III) (Fig. 3*A*), blastic sympodial (section II) (Fig. 3*B*) and blastic phialidic (section IV) (Fig. 3*C*). Hughes[2] recognized the presence of annellations on conidiogenous cells of *L. lundbergii* and suggested that these were distinct from the sympodial development in *Sporocybe abietina* Peck (1879) [= *Periconia abietina* (Peck.) Sacc. 1886), for which he established the new genus *Verticicladiella* Hughes.

The connection between *Leptographium* anamorphs and *Ceratocystis s.l.* was recognized by many early investigators of this group.[10,18-21] Hughes[2] was, however, concerned with

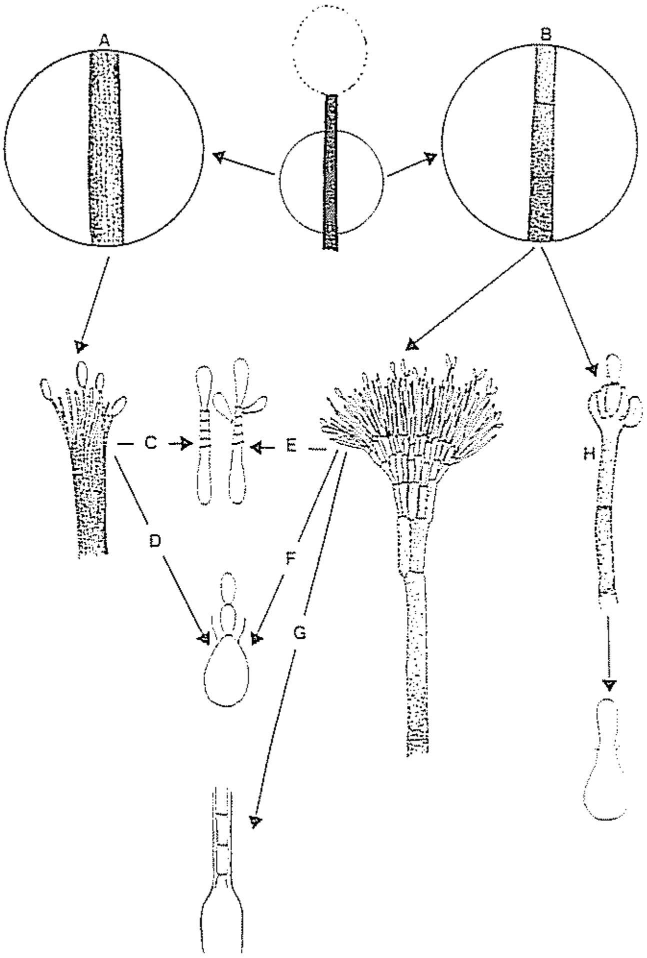


Fig. 1. Anamorphs of *Ceratocystis s.l.* with macronematous conidiophores. *A*, Synnematous conidiophore; *B*, mononematous conidiophore; *C*, *Graphium* (synnematous conidiophore with annellidic conidiogenous cells producing conidia by percurrent proliferation); *D*, *Phialographium* (synnematous conidiophore with phialidic conidial development); *E*, *Leptographium* (mononematous conidiophore with annellidic conidium development); *F*, *Phialocephala* (mononematous conidiophore with phialidic conidiogenous cells by apical wall building); *G*, *Sporendocladia* (mononematous conidiophore producing conidia from phialides by ring wall building); *H*, *Knoxdaviesia* (unbranched mononematous conidiophore).

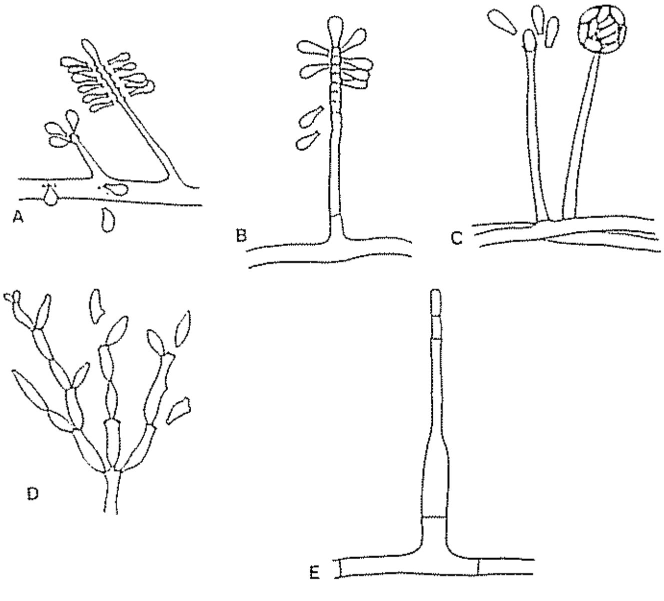


Fig. 2. Anamorphs of *Ceratocystis s.l.* with micronematous conidiophores. *A*, *Sporothrix* (sympodial proliferation producing holoblastic conidia and each former conidiogenous locus is marked by a prominent denticle); *B*, *Hyalorhinocladiella* (sympodial proliferation leaving flat, low-profile, ring-like scars on the surface of the conidiogenous cell); *C*, *Acremonium* (characterized by single, erect, slender, hyaline, phialidic conidiogenous cells bearing clusters of conidia around the tips); *D*, *Hyalodendron* (ambiguous conidiogenous cells producing one or more conidia on short denticles at the tips of, or in whorl along the sides of, simple or branched conidiophores); *E*, *Chalara* (conidia produced in basipetal chains from phialidic conidiogenous cells with long, cylindrical collarettes and deep-set, conidiogenous, loci-borne on simple conidiophores).

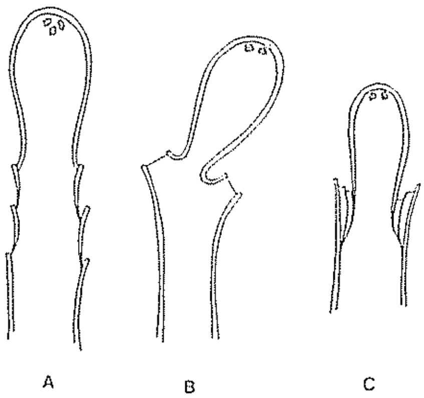


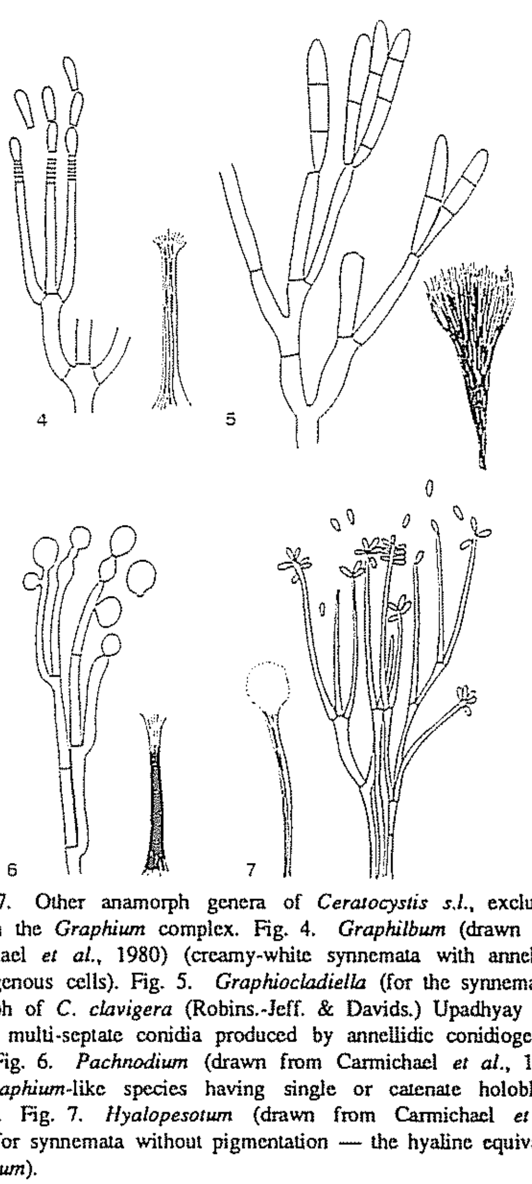
Fig. 3. Three of the patterns of conidium development assigned to sections introduced by Hughes:[2] *A*, blastic annellidic (section III); *B*, blastic sympodial (section II); *C*, blastic phialidic (section IV).

conidium development alone and made no connection between his work on *Leptographium* and the taxonomy of *Ceratocystis s.l.* Despite this fact, the establishment of *Verticicladiella* with *V. abietina* (Peck) Hughes as the type species came to have a pronounced effect on the taxonomy of *Ceratocystis* anamorphs.

In 1961, Kendrick published the first of a series of studies on the *Leptographium* complex[22–26] in which he applied the new taxonomic criteria introduced by Hughes. The genus *Phialocephala* Kendrick was established for those *Leptographium*-like fungi in which conidia were produced from phialides (Fig. 1*F*).[23] These included species such as *P. bactrospora* Kendrick with deep-set tubular collarettes, and others with less distinct or flared collarettes such as *P. canadensis* Kendrick. Connections between *Phialocephala* and *Ceratocystis* had yet to be established.

In the second of his series of papers, Kendrick[23] treated the genus *Verticicladiella*. In this study, seven species including five new taxa were considered. Some of these were known as anamorphs of *Ceratocystis s.l.* At least six other species of *Ceratocystis* were known to have anamorphs belonging in the *Leptographium* complex but these were not considered. Clearly, at the time, the importance of anamorph/teleomorph connections was less strongly emphasized than it is today. Significant emphasis was also being placed on anamorph taxonomy, particularly in terms of conidium development and 'Huesian' characters.

The extensive and fundamental work of Kendrick firmly established the use of conidium development as a taxonomic criterion in anamorphs of *Ceratocystis s.l.* This logically led to the subdivision of *Graphium* (Fig. 1*C*), the synnematal analogue of *Leptographium*. Thus, Crane and Schocknecht[27] established *Pesotum ulmi* (Schwarz) Crane & Schocknecht and *P. piceae* Crane & Schocknecht, for the sympodial anamorphs of *O. ulmi* (Buism.) Nannf. and *O. piceae* (Münch) H. & P. Sydow, respectively. In these species, conidia were believed to develop sympodially as opposed to percurrently such as in the case of *Graphium*. Upadhyay and Kendrick[28] followed this example and erected *Phialographium* for *P. sagmatospora* Upadhyay & Kendrick, the anamorph of *Ceratocystis sagmatospora* Wright & Cain, in which conidia were purportedly produced in phialides. Subsequently, numerous anamorphs of *Ceratocystis s.l.* have been assigned to various of these genera although few binomials have been provided.[29] Additional genera such as *Graphilbum* Upadhyay & Kendrick (Fig. 4), *Graphiocladiella* Upadhyay (Fig. 5), *Pachnodium* Upadhyay & Kendrick (Fig. 6), and *Hyalopesotum* Upadhyay & Kendrick (Fig. 7), although not based entirely on conidium development, have been segregated from *Graphium*, *Pesotum* and *Phialographium* (Fig. 1*C, D*).[30]



Figs 4–7. Other anamorph genera of *Ceratocystis s.l.*, excluding those in the *Graphium* complex. Fig. 4. *Graphilbum* (drawn from Carmichael *et al.*, 1980) (creamy-white synnemata with annellidic conidiogenous cells). Fig. 5. *Graphiocladiella* (for the synnematous anamorph of *C. clavigera* (Robins.-Jeff. & Davids.) Upadhyay with one- to multi-septate conidia produced by annellidic conidiogenous cells). Fig. 6. *Pachnodium* (drawn from Carmichael *et al.*, 1980) (for *Graphium*-like species having single or catenate holoblastic conidia). Fig. 7. *Hyalopesotum* (drawn from Carmichael *et al.*, 1980) (for synnemata without pigmentation — the hyaline equivalent of *Pesotum*).

In addition to having anamorphs in the *Leptographium* and *Graphium* complexes, species of *Ceratocystis s.l.* have anamorphs, either reported to belong to, or described, in a number of other genera. The most common of these are *Sporothrix* Hekt. & Perkins (Fig. 2*A*), for which many species are of unknown teleomorph affiliation,[11] and *Hyalorhinocladiella* Upadhyay & Kendrick which was specifically established for anamorphs of *Ceratocystis s.l.*[30] Both genera have conidiophores that are micronematous and mycelial in nature but they can usually be distinguished easily on the basis of their conidium development. Sporothrix produces conidia through sympodial proliferation of the conidiogenous cells and distinct denticles remain after secession of conidia (Fig. 2*A*).[11] In contrast, *Hyalorhinocladiella* was described by Upadhyay & Kendrick[30] (Fig. 2*B*), particularly for anamorphs of *Ceratocystis s.l.* that were *Rhinocladiella* Nannfeldt-like but hyaline. Interestingly, many species of *Ceratocystis s.l.* with synnematal *Graphium* anamorphs also have distinct *Sporothrix* synanamorphs.

The genus *Knoxdaviesia* was recently described by Wingfield *et al.*[4] as accommodating *K. proteae* (Fig. 10), the anamorph of *Ceratocystiopsis proteae* Wingfield, van Wyk & Marasas. This unusual fungus, resembling genera such as

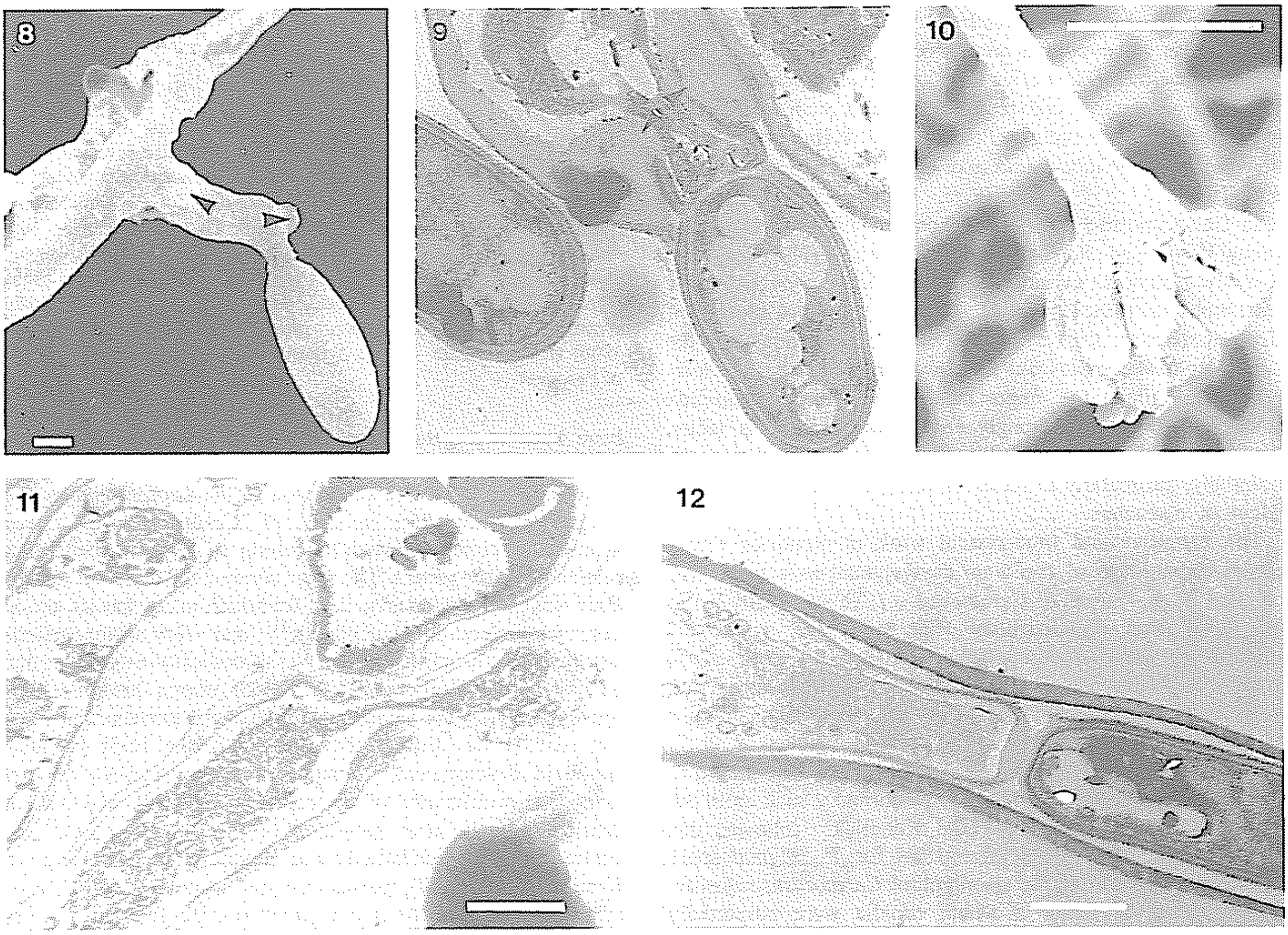
Phialocephala, Stachybotrys Corda and *Custingophora* Stolk, Hennebert & Klopotek occurs in *Protea* L. infructescences, a unique environment for species of *Ceratocystis s.l.* Conidiogenous cells are phialidic with distinct periclinal thickening and there is no evidence of percurrent proliferation of the conidiogenous cell above the apex of the collarette (Fig. 1*H*).[31] In our opinion, they do not resemble those of any other anamorphs of *Ceratocystis s.l.*, thus justifying the existence of the genus.

Other genera that have been assigned to anamorphs of *Ceratocystis s.l.* include *Allescheriella* Berl., *Acremonium* Link (Fig. 2*C*), *Gabarnaudia* Samson & Gams, and *Hyalodendron* Diddens (Fig. 2*D*). Based on preliminary studies, we believe that those species assigned to *Hyalodendron* could probably be accommodated in *Sporothrix*. We also doubt the validity of the reported *Acremonium* state in *Ophiostoma nigrum* (Davidson) De Hoog & Scheffer.[3] The existence of *Gabarnaudia* states for *C. fimicola* (Marchal) Upadhyay and *C. helvellae* (Karsten) Upadhyay was recognized by Samson,[32] who suggested that this anamorph could be used to distinguish *Spaeronaemella* Karst. from *Ceratocystis* and other related genera.

Patterns of conidium development

In the foregoing historical account, an attempt has been made to introduce anamorph genera that have been associated with species of *Ceratocystis s.l.*, particularly in terms of their conidial development. There has clearly been an excessive number of anamorph genera used for this group of fungi. In this section, using the results of recent studies on conidium development, we attempt to analyse patterns of conidium development encountered in anamorphs of *Ceratocystis s.l.* From this point on, unless otherwise indicated, *Ceratocystis* is used in the strict sense and refers to species with *Chalara* anamorphs. *Ophiostoma* is used for all additional species.[33] Although we refer to *Ceratocystiopsis*, this genus is considered to be in contention[34] and probably synonymous with *Ophiostoma*.

In this account of patterns of conidium development in *Ophiostoma* and *Ceratocystis*, we accept the concepts and use the terminology recently introduced by Minter, Kirk and Sutton,[35] Minter *et al.*[36] and Minter, Sutton and Brady.[37] We therefore differentiate between holoblastic phialides with conidia developing through apical wall building (Fig. 2*C*) and thallic phialides where conidia develop by means of a wall-building ring (Fig. 2*E*). Furthermore, patterns of conidium development are analysed in terms of five stages of development, namely regeneration of the conidiogenous cell, proliferation of the cell, ontogeny of the new conidium, delimitation of the conidium and conidial secession.[35]



Figs 8–12. Scanning and transmission electron microscopy of the conidiogenous cells of a *Sporothrix* anamorph, *Knoxdaviesia proteae, Graphium olivaceapinii* and *Sporendocladia bactrospora*. Fig. 8. SEM of the conidiogenous cell of *Sporothrix* with the characteristic denticles at the apex (arrows). Fig. 9. TEM of a section through the conidiogenous cell of *K. proteae* in which conidia are formed by the apical wall-building process and well-developed periclinal thickening (arrows) is characteristic. Fig. 10. SEM of the conidiophore of *K. proteae* with distinct phialidic conidiogenous cells. Fig. 11. Section through the conidiogenous cell of *G. olivaceapinii* where delayed secession of conidia result in apparent sympodial development. Fig. 12. TEM of a section through the conidiogenous cell of *S. bactrospora* where cylindrical conidia, in true chains, are formed by ring wall building.

Phialidic conidium development

Until recently, the term phialide has been broadly applied and, in general, used to refer to conidiogenous cells, with or without collarettes and from which conidia formed endogenously.[37] Therefore, using this broad definition, anamorphs of *Ceratocystis s.l.* in genera such as *Chalara, Phialocephala, Phialographium* and *Knoxdaviesia* would be considered to have phialidic conidial development. There are, however, two clearly distinct patterns of conidial development amongst these so-called 'phialidic' species. Firstly, there are those species in which conidia develop through a ring wall-building process (Fig. 12). Here, conidia are produced in chains and the conidiogenous cells have deep-set tubular collarettes. In the terms of Minter, Kirk & Sutton,[36] these would be thallic phialides. The genus *Chalara* is the only anamorph of *Ceratocystis* in this group (Fig. 2*E*). *Chalara* species with thallic phialides and ring wall-building conidium development[36] are well defined. Acceptance of their unique nature provides additional support for separating *Ceratocystis s.s.* from *Ophiostoma.*

In the second group, conidia develop through an apical wall-building process and usually accumulate in a slimy mass at the apex of the phialide (Fig. 9). These are characterized by the accumulation of proliferation wall layers and thus have periclinal thickening in the phialide neck. In terms of Minter *et al.*,[35] they are 'holoblastic phialides'. Anamorphs of *Ceratocystis s.l.* belonging to this group are in the genera *Phialocephala, Phialographium* and *Knoxdaviesia* (Fig. 3*C*).

Early use of the broad definition of a phialide has resulted in considerable confusion. This is particularly true in the genus *Phialocephala* as defined by Kendrick.[4] *Phialocephala* has therefore come to include species with ring wall, as well as those with apical wall-building conidiogenous cells. In an attempt partially to resolve this problem, Wingfield, van Wyk and Wingfield[38] transferred species of *Phialocephala* with ring wall-building conidial development to *Sporendocladia* Arnaud: Nag Raj & Kendrick (Fig. 1*G*). Species remaining in *Phialocephala* apparently still represent a heterogeneous group that requires further study.

In *Ophiostoma*, there is only one species, *O. francke-grosmanniae* (Davidson) De Hoog & Scheffer, reported to have a mononematous anamorph with phialidic conidial development. Although optical microscopy clearly indicates the presence of phialides, electron microscopic studies[39] have shown that conidial development is more closely allied to that in *Leptographium* than *Phialocephala.* This anamorph would therefore best be accommodated in *Leptographium.* The only other mononematous anamorph of *Ceratocystis s.l.* that apparently has apical wall-building phialides is that of *Ceratocystiopsis proteae.* In this fungus, phialides are distinct, with proliferation wall layers accumulating at the apex of the phialide as periclinal thickening.[39] No evidence of percurrent proliferation of the conidiogenous cell above the collarette has been found in this unique fungus.

Numerous *Ophiostoma* species have synnematous anamorphs apparently with apical wall building and phialidic conidial development. On the grounds of their phialidic development, these have been described in, or assigned to, the genus *Phialographium* In a recent study of the purported *Phialographium* anamorph of *Ophiostoma cucullatum* Solheim, evidence of percurrent, sympodial and phialidic conidial development was found.[40] This led Wingfield *et al.*[9] to examine conidium development in additional anamorphs of *Ophiostoma* in *Phialographium, Graphium* and *Pesotum.* These authors concluded that the three genera cannot be reliably separated on the basis of conidial development, and reduced *Pesotum* and *Phialographium* to synonymy with *Graphium.*

Percurrent conidium development

For almost three decades, *Leptographium* and *Verticicladiella* were separated on the basis of their percurrent and sympodial conidium development, respectively. In the description of *Verticicladiella truncata* Wingfield and Marasas, scanning electron microscopy was used to examine conidium ontogeny.[41] Although conidium development appeared distinctly sympodial, annellations were also apparently present on the conidiogenous cells (Fig. 1*E*). This led to a more detailed study of conidium development in additional species of *Verticicladiella* and *Leptographium.*[42] Conclusions drawn from the latter study were that annellidic as well as apparent sympodial development (Fig. 11) can occur in single species of *Leptographium* and *Verticicladiella.* This then provided justification for reducing *Verticicladiella* to synonymy with *Leptographium.*[42]

The apparent occurrence of both annellidic and sympodial conidial development on single conidiogenous cells of *Leptographium* has remained confusing. Furthermore, there appear to be distinct differences in the extent of proliferation and size of the conidium base amongst species of *Leptographium.* For this reason, van Wyk, Wingfield and Marasas[43] attempted to interpret patterns of conidium development further in a number of *Leptographium* species showing differences in conidiogenous cell morphology.

A number of interesting conclusions were made from the study of van Wyk *et al.*[43] Firstly, where conidia are large, the outer wall layers of conidiogenous cells remaining after conidial secession can be flared. In the absence of further extensive proliferation, they can appear to be phialides. Further, synchronization of conidial development appears to have a marked effect on the morphology of the conidiogenous cell. Therefore, where conidial secession is delayed and overlaps the onset of proliferation, conidia remain attached at the sides of the conidiogenous cells. This then creates an illusion of sympodial development in conidiogenous cells that actually proliferate percurrently.

Conidial development in *Graphium* anamorphs of *Ophiostoma* appears to be identical to that found in *Leptographium.*[29] We therefore doubt whether sympodial development of conidiogenous cells occurs at all in these genera. Similarly, preliminary studies of conidium development in species of *Hyalorhinocladiella* (authors, unpublished) suggest that they produce conidia percurrently and give only illusory appearance of developing sympodially.

Sympodial conidium development

Although we believe that sympodial development is absent from species of *Leptographium* and *Graphium*, this pattern of development is present and obvious in *Sporothrix.* In this genus, a single conidium is produced from a conidiogenous locus and, at secession, a distinct denticle remains (Fig. 8). Regeneration and proliferation result in a new conidiogenous locus adjacent to, but removed from, the previous one (Fig. 2*A*).

When considering conidium development in *Sporothrix*, an interesting point to note is that many *Graphium* species with percurrent conidial development have synanamorphs in *Sporothrix.*[3,11] This suggests to us that the underlying mode of conidial development in the two genera is probably similar and this remains a matter that deserves careful study.

Conclusions

The mode of conidium development has been a particularly significant taxonomic criterion in anamorphs of *Ceratocystis s.l.* Application of this character has led to the establishment of an excessive number of names for anamorphs, particularly of *Ophiostoma*. Re-evaluation of conidium development as a taxonomic character is now leading to a condensation of anamorph genera used in this group of fungi.

Two essentially different forms of conidium development can be applied to *Ceratocystis s.l.* These are ring wall building, which occurs only in anamorphs of *Ceratocystis s.s.*, and apical wall building, which applies to the numerous anamorphs of *Ophiostoma* (including *Ceratocystiopsis*). In the latter group, there appear to be three distinct, although probably related forms of conidium development. These include: (i) phialidic development, where repeated conidiation results in periclinal thickening at the apex of the conidiogenous cell; (ii) percurrent proliferation, where conidium development leaves annellations or scars on the conidiogenous cell (here delayed secession of conidia can lead to the illusion that these cells have proliferated sympodially); and (iii) sympodial development where, after secession, each conidium leaves a distinct denticle on the conidiogenous cell.

Through application of the condensed view of conidium development presented here, the number of anamorph genera applied to *Ophiostoma* can be considerably reduced. *Graphium, Leptographium, Sporothrix, Hyalorhinocladiella* and *Knoxdaviesia* are well-defined anamorphs of this group. Although it is perhaps idealistic, these genera might be reserved for anamorphs of *Ophiostoma*. Genera such as *Allescheriella, Graphilbum, Hyalopesotum, Graphiocladiella* and *Pachnodium* deserve further consideration before they are placed with confidence amongst the anamorphs of *Ophiostoma*.

We are most grateful to B.D. Wingfield and Z.A. Pretorius for critical reviews of the manuscript. Financial support of the Foundation for Research Development is gratefully acknowledged.

Received 5 October 1992; accepted 21 January 1993.

1. Münch E. (1907). Die Blaufaüle des Naldelholzes. *Naturw. Z. Land-u. Forst.* 5, 531–573.
2. Hughes S.J. (1953). Conidiophores, conidia and classification. *Can. J. Bot.* **31**, 577–659.
3. Upadhyay H.P. (1981). *A monograph of* Ceratocystis *and* Ceratocystiopsis. University of Georgia Press, Athens.
4. Wingfield M.J., van Wyk P.S. and Marasas W.F.O. (1988) *Ceratocystiopsis proteae* sp. nov. with a new anamorph genus. *Mycologia* 80, 23–30.
5. Bretz T.W. (1952). The ascigerous stage of the oak wilt fungus. *Phytopathology* 42, 435–437.
6. Davidson R.W. (1935). Fungi causing stain in logs and lumber in the southern states, including five new species. *J. agric. Res.* 50, 789–807.
7. Davidson R.W. (1944). Two American hardwood species of *Endoconidiophora* described as new. *Mycologia* 36, 300–306.
8. Melin E. and Nannfeldt J.A. (1934). Researches into the blueing of ground woodpulp. *Svenska SkogvsFör. Tidskr.* 32, 397–616.
9. Bakshi B.K. (1951). Studies on four species of *Ceratocystis*, with a discussion of fungi causing sapstain in Britain. *CMI mycol. Pap.* 35, 1–16.
10. Hunt J. (1956). Taxonomy of the genus *Ceratocystis. Lloydia* 19, 1–58.
11. De Hoog G.S. (1974). The genera *Blastobotrys, Sporothrix, Calcarisporium* and *Calcarisporiella* gen. nov. *Stud. Mycol.* 7, 1–88.
12. Jewell T.R. (1974). A quantitative study of cellulose distribution in *Ceratocystis* and *Europhium. Mycologia* 66, 139–146.
13. Rosinski M.A. and Campana R.J. (1964). Chemical analysis of the cell wall of *Ceratocystis ulmi. Mycologia* 56, 738–744.
14. Smith M.J., Patik C.M. and Rosinski M.A. (1967). A comparison of cellulose production in the genus *Ceratocystis. Mycologia* 59, 965–969.
15. Spencer J.F.T. and Gorin P.A.J. (1971). Systematics of the genera *Ceratocystis* and *Graphium*. Proton magnetic resonance spectra of the mannose-containing polysaccharides as an aid in classification. *Mycologia* **63**, 387–402.
16. Weijman A.C.M. and de Hoog G.S. (1975). On the subdivision of the genus *Ceratocystis. Antonie van Leeuwenhoek* 41, 353–360.
17. Harrington T.C. (1981). Cycloheximide sensitivity as a taxonomic character in *Ceratocystis. Mycologia* 73, 1123–1129.
18. Goidánich G. (1936). Il genere di Ascomiceti *Grosmannia* G.Goid. *Boll. Staz. Patol. veg. Roma* 16, 26–60.
19. Grosmann H. (1932). Über die systematischen Beziehungen der Gaftung *Leptographium* Lagerberg et Melin zur Gattung *Ceratostomella* Sacc. Nebst einigen Bemerkungen über *Scopularia* venusta Preuss und *Hantzschia phycomyces* Awd. *Hedwigia* 72, 183–194.
20. Molnar A.C. (1965). Pathogenic fungi associated with a bark beetle on alpine fir. *Can. J. Bot.* 43, 563–570.
21. Shaw G.C. and Hubert E.E. (1952). A review of the *Leptographium–Scopularia–Hantzschia* nomenclature. *Mycologia* 44, 693–704.
22. Kendrick W.B. (1961). The *Leptographium* complex. *Phialocephala* gen. nov. *Can. J. Bot.* 39, 1079–1085.
23. Kendrick W.B. (1962). The *Leptographium* complex. *Verticicladiella* Hughes. *Can. J. Bot.* 40, 771–797.
24. Kendrick W.B. (1963). The *Leptographium* complex. *Penicillium repens* C.& E. *Can. J. Bot.* 41, 573–577.
25. Kendrick W.B. (1963). The *Leptographium* complex. Two new species of *Phialocephala. Can. J. Bot.* 41, 1015–1023.
26. Kendrick W.B. (1964). The *Leptographium* complex. *Hantzschia* Auerswald. *Can. J. Bot.* 42, 1291–1295.
27. Crane J.L. and Schoknecht, J.D. (1973). Conidiogenesis in *Ceratocystis ulmi, Ceratocystis piceae* and *Graphium penicillioides. Am. J. Bot.* 60, 346–354.
28. Upadhyay H.P. and Kendrick W.B. (1974). A new *Graphium*-like genus (conidial state of *Ceratocystis*). *Mycologia* 66, 181–183.
29. Wingfield M.J., Kendrick W.B. and van Wyk P.S. (1991). Analysis of conidium ontogeny in anamorphs of *Ophiostoma: Pesotum* and *Phialographium* are synonyms of *Graphium. Mycol. Res.* 95, 1328–1333.
30. Upadhyay H.P. and Kendrick W.B. (1975). Prodromus for a revision of *Ceratocystis* (Microascales, Ascomycetes) and its conidial states. *Mycologia* 67, 798–805.
31. Mouton M., Wingfield M.J. and van Wyk P.S. (1993). Conidium development in the *Knoxdaviesia* anamorph of *Ceratocystiopsis proteae. Mycotaxon* 46, 363–370.
32. Samson R.A. (1974). *Paecilomyces* and some allied hyphomycetes. *St. Mycol.* 6, 1–119.
33. De Hoog G.S. and Scheffer R.J. (1984). *Ceratocystis* versus *Ophiostoma*: a reappraisal. *Mycologia* 76, 292–299.
34. Wingfield M.J. (1993). Problems in delineating the genus *Ceratocystiopsis.* In Ceratocystis *and* Ophiostoma: *Taxonomy, Ecology and Pathogenicity*, ed. M.J. Wingfield, K.A. Seifert and J.F. Webber, pp. 19–23. (in press).
35. Minter D.W., Kirk P.M. and Sutton B.C. (1982). Holoblastic phialides. *Trans. Br. mycol. Soc.* 79, 75–93.
36. Minter D.W., Kirk P.M. and Sutton B.C. (1983). Thallic phialides. *Trans. Br. mycol. Soc.* 80, 39–66.
37. Minter D.W., Sutton B.C. and Brady B.L. (1983). What are phialides anyway? *Trans. Br. mycol. Soc.* 81, 109–120.
38. Wingfield M.J., van Wyk P.S. and Wingfield B.D. (1987). Reclassification of *Phialocephala* based on conidial development. *Trans. Br. mycol. Soc.* 89, 509–520.
39. Mouton M., Wingfield M.J. and van Wyk P.S. (1993). Identification of the anamorph of *Ophiostoma francke-grosmanniae. Mycologia* 84, 857–862.
40. Wingfield M.J., van Wyk P.S. and van Wyk P.W.J. (1989). Conidial development in the anamorph of *Ophiostoma cucullatum. Mycol. Res.* 93, 91–95.
41. Wingfield M.J. and Marasas W.F.O. (1983). Some *Verticicladiella* species, including *V. truncata* sp. nov., associated with root diseases of pine in New Zealand and South Africa. *Trans. Br. mycol. Soc.* 80, 231–236.
42. Wingfield M.J. (1985). Reclassification of *Verticicladiella* based on conidial development. *Trans. Br. mycol. Soc.* 85, 81–93.
43. Van Wyk P.S., Wingfield M.J. and Marasas W.F.O. (1988). Differences in synchronization of stages in the development of *Leptographium* conidia. Trans. Br. mycol. Soc. 90, 451–456.
44. Malloch D. (1974). *Sphaeronaemella helvellae. Fungi Can.* No. 53.
45. Robinson-Jeffrey R.C. and Davidson R.W. (1968). Tree new species with *Verticicladiella* imperfect states on blue-stained pine. *Can. J. Bot.* 46, 1523–1527.