RECLASSIFICATION OF VERTICICLADIELLA BASED ON CONIDIAL DEVELOPMENT

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The established method of distinguishing Leptographium, Verticicladiella and Phialocephala (the Leptographium complex) on the basis of annellidic, sympodial and phialidic conidial development, respectively, is challenged. Leptographium and Verticicladiella could not be differentiated with confidence using light microscopy whereas Phialocephala spp. examined were distinguishable from the latter genera. Scanning electron microscopy (SEM) confirmed that the conidiogenous cells of Phialocephala spp. do not elongate when producing a succession of conidia. Using SEM, Verticicladiella and Leptographium spp. were impossible to separate on the basis of conidial development. This was due to certain Leptographium and Verticicladiella spp. exhibiting both sympodial and annellidic (percurrent) proliferation on a single conidiophore or conidiogenous cell. The genus Verticicladiella is therefore reduced to synonymy with Leptographium.

The Leptographium complex includes the genera Leptographium Lagerberg & Melin, Verticicladiella Hughes and Phialocephala Kendrick (Kendrick, 1961, 1962). These fungi are characterized by dark, mononematous, penicillately-branched conidiophores with conidia produced in a slimy matrix (Hughes, 1953; Kendrick, 1961, 1962). They commonly occur on the surface of wood and many are associated with wood-infesting insects such as bark beetles (Coleoptera: Scolytidae) and weevils (Coleoptera: Curculionidae) (Goheen & Cobb, 1978; Upadhyay, 1981; Wingfield, 1983).

Leptographium, Verticicladiella and Phialocephala spp. are commonly recognized anamorphs of the genus Ceratocystis Ellis & Halst. sensu lato (De Hoog & Scheffer, 1984; Griffin, 1968; Hunt, 1956; Olchowecki & Reid, 1974; Upadhyay, 1981). The anamorph genera have been separated on the basis of conidial development (Hughes, 1953; Kendrick, 1961, 1962). Leptographium spp. are purportedly characterized by having conidiogenous cells which develop annellidically (percurrently). Conidia in Verticicladiella spp. develop sympodially whereas those of Phialocephala spp. develop phialidically (Hughes, 1953; Kendrick, 1961, 1962).

Using the mode of conidial development as the sole criterion by which to differentiate the three genera has resulted in confusion. Wingfield & Marasas (1983) identified a new species, Verticicladiella truncata, in which conidial development appeared to vary between sympodial and annellidic. Whether to assign this species to Leptographium or Verticicladiella was a problem. Kendrick (1980) emphasized this difficulty and noted that members of the Leptographium complex were similar both

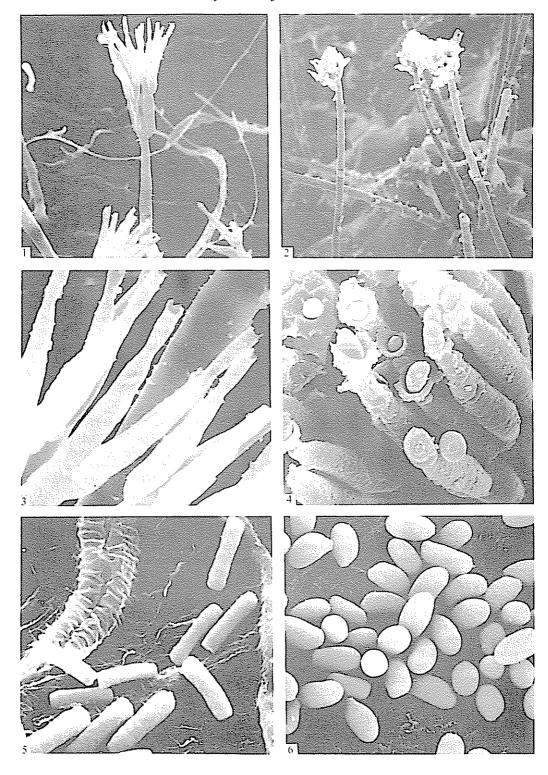
morphologically and ecologically and suggested that the genera required taxonomic revision.

This paper presents results of an examination of conidiogenous cell and conidial development in some species of *Leptographium*, *Verticicladiella* and *Phialocephala*. The acceptability of using conidial development to distinguish the genera is considered.

MATERIALS AND METHODS

The following isolates of *Phialocephala*, were examined: *P. bactrospora* Kendrick (Kendrick, 1961) ATCC44606; *P. dimorphospora* Kendrick (Kendrick, 1961) DAOM165556A; *P. fusca* Kendrick (Kendrick, 1963) DAOM67995, DAOM 74598; *P. humicola* Jong & Davis (Jong & Davis, 1972) ATCC38881.

Isolates of Leptographium examined included the Leptographium anamorph of Ceratocystis brevicollis Davidson (Davidson, 1958) isolate COLO465 supplied by T. E. Hinds, U.S. Forest Service, Fort Collins, CO80526. U.S.A.; L. lundbergii Lagerberg & Melin (Lagerberg, Lundberg & Melin, 1927) ATCC2235, CBS352.29, DAOM75265; L. pyrinum Davidson (Davidson, 1978) ATCC34943; L. reconditum Jooste (Jooste, 1978) isolate 1244 supplied by Dr W. Jooste, Potchefstroom University for C.H.E., Potchefstroom 2520, South Africa; L. terebrantis Barras & Perry (Barras & Perry, 1971) two isolates, CMW9 and CMW11 (author's culture collection) from a previous study (Wingfield, 1983) and one isolate, CMW47 supplied by Dr T. C. Harrington, Department of Plant Pathology, University of New Hampshire, Durham, NH 03824, U.S.A.



The following Verticicladiella spp. were examined: V. abietina (Pk) Hughes (Hughes, 1953) DAOM37980 and isolate C13189 supplied by Dr T. C. Harrington; V. antibiotica Kendrick (Kendrick, 1962) DAOM84338; Verticicladiella anamorph of Ceratocystis aureum (Robis.-Jeff. & Davidson) Upadhyay (Robison-Jeffrey & Davidson, 1968; Upadhyay, 1981) ATCC16936; V. brachiata Kendrick (Kendrick, 1962) DAOM34360; Verticicladiella anamorph of Ceratocystiopsis crassivaginata (Griffin) Upadhyay (Griffin, 1968; Upadhyay, 1981) isolates COLO486 and COLO498 supplied by T. E. Hinds; V. dryocoetidis Kendrick & Molnar (Kendrick & Molnar, 1965) isolate COLO565 supplied by T. E. Hinds; the Verticicladiella anamorph of Ceratocystis huntii Robis .-Jeff. (Robison-Jeffrey & Grinchenko, 1964) isolate COLO468 supplied by T. E. Hinds; V. penicillata (Grosm.) Kendrick (Kendrick, 1962) CBS140.36, DAOM63691; V. procera Kendrick (Kendrick, 1962) isolate CMW3 supplied by A. Lackner, North Carolina State University, Raleigh NC 27607. U.S.A.; CMW10 from a previous study (Wingfield, 1983) PREM45701, 45704 also examined by Wingfield & Marasas (1983) and DAOM33940; Verticicladiella anamorph of Cera-& Davidson) robusta (Robis.-Jeff. tocystis Upadhyay (Robison-Jeffrey & Davidson, 1968; Upadhyay, 1981) isolate COLO452 supplied by T. E. Hinds; V. serpens (Goid.) Kendrick (Goidanich, 1936; Kendrick, 1962; Wingfield & Marasas, 1981) CBS141.36, CBS641.76, DAOM17660; PREM45442; V. truncata Wingfield & Marasas (Wingfield & Marasas, 1983) PREM45677, PREM45696, PREM45700, PREM45896; V. wageneri Kendrick (Harrington, 1982; Kendrick, 1962) isolates CAD-46, CAS-3, CAS-15 supplied by Dr T. C. Harrington.

In addition to general examination of the fungilisted above, a number of species in each of the genera were selected for more critical examination. These included L. lundbergii (ATCC2235); L. pyrinum (ATCC 34943); L. terebrantis CMW9; the Verticicladiella anamorph of Ceratocystis huntii (isolate COLO468); V. procera DAOM33940; V. truncata (PREM45698); P. fusca (DAOM74598) and P. bactrospora (ATCC44606). Cultures were maintained at 24 °C on 2 % malt extract agar (20 g Difco malt extract; 20 g Difco Bacto agar; 1000 ml water) in Petri dishes.

Fungi were examined using light and scanning electron microscopy (SEM). Agar discs bearing

conidiophores were fixed in 2.5% glutaraldehyde and osmium tetroxide in a 0.1 M phosphate buffer, dehydrated in a graded acetone series, critical point dried, coated with gold palladium and examined using a Phillips scanning electron microscope.

RESULTS

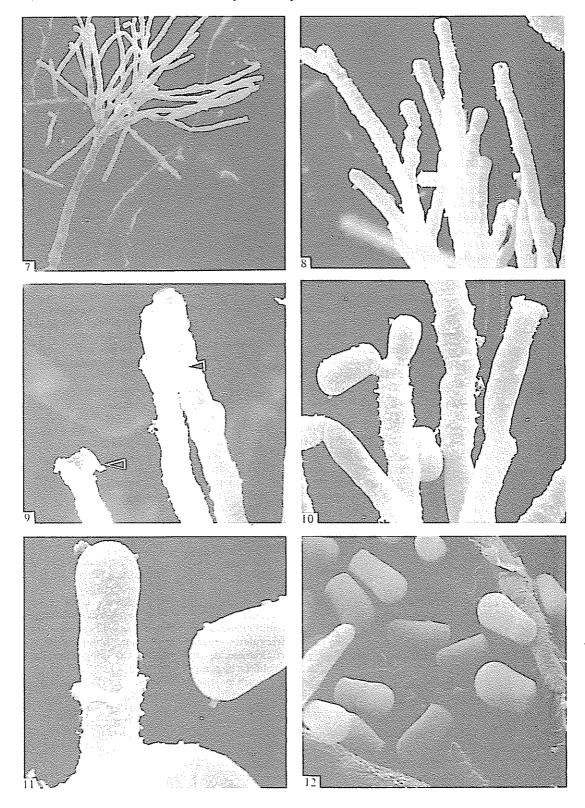
Using SEM, conidiogenous cells in *P. bactrospora* and *P. fusca* were phialidic with well-developed collarettes (Figs 1-4). Conidia were elongate with parallel walls and only slightly constricted at the point of attachment in *P. bactrospora* (Fig. 5), and pyriform with distinctly constricted points of attachment in *P. fusca* (Fig. 6).

Conidiogenous cells in *L. lundbergii* had proliferated, extending in length during successive production of conidia (Figs 7–11). Progressive development of conidia resulted in scars encircling the conidiogenous cells suggesting that the proliferation was percurrent. Some conidiogenous cells appeared to have resumed vegetative growth after production of a series of conidia (Figs 9–11). This sometimes resulted in displaced fungus wall tissue similar to a collarette below the point of resumed growth (Figs 10–11). In addition to the presence of encircling scars, apparent sympodial proliferation was observed in some conidiogenous cells (Figs 8, 10). Conidia in *L. lundbergii* were broadly truncate (Fig. 12).

Ceratocystis huntii and L. terebrantis both had distinct encircling scars on the conidiogenous cells and were similar to each other (Figs 13–15, 18–20). Sympodial conidiogenous cell development with conidia produced successively on alternate sides of the conidiogenous cells (Figs 14, 19) was also apparent. In some cases, development resulted in the presence of 'collarettes' similar to those observed in L. lundbergii at the apices of conidiogenous cells (Figs 15, 20). Conidia in C. huntii and L. terebrantis were obtuse, had points of attachment less broadly truncate than those in L. lundbergii and were often observed to be budding (Figs 16, 17, 20, 22).

Encircling scars resulting from successive production of conidia in *L. pyrinum* were evident on conidiogenous cells (Figs 23, 24). These scars were irregularly spaced and often oblique on the conidiogenous cell walls. Conidiogenous cells proliferated sympodially (Figs 24, 25) and many of the scars on the conidiogenous cells appeared to have resulted from secession of successively

Figs. 1–6. Phialocephala fusca and P. bactrospora. Figs 1, 3, 5, Conidiophores (\times 730), conidogenous cells (\times 3300) and conidia (\times 5600) of P. bactrospora. Figs 2, 4, 6, Conidiophores (\times 730), conidiogenous cells (\times 5600) and conidia (\times 5600) of P. fusca.



produced conidia (Fig. 24). Conidia in *L. pyrinum* were more broadly truncate than those in *G. huntii* and *L. terebrantis* and most similar in size and shape to those in *L. lundbergii* (Fig. 26).

Conidial development in *V. truncata* (Figs 27–30) was most like that observed in *Leptographium* spp. Conidiogenous cells commonly had encircling scars (Figs 27–30). However, sympodial proliferation of the conidiogenous cells was also observed (Figs 30, 31). In some cases conidiogenous cells appeared to proliferate vegetatively before resumption of continuous conidial production (Figs 29, 30). Conidia in *V. truncata* were broadly truncate and commonly observed to be budding (Figs 31, 32).

In *V. procera*, proliferation of the conidiogenous cells was less pronounced than in *V. truncata* or the *Leptographium* spp. examined (Figs 33–35). Conidiogenous cells appeared to proliferate sympodially with less proliferation than that observed in conidiogenous cells of *V. truncata* (Fig. 30). This apparently resulted in tightly packed scars remaining after conidial secession (Fig. 35). Conidia in *V. procera* were less strongly truncate than those of *V. truncata* or *Leptographium* spp. (Fig. 36).

When these fungi were examined using light microscopy, Phialocephala spp. were easily recognizable from other members of the Leptographium complex due to the presence of well-developed collarettes and the absence of extensive proliferation of the conidiogenous cells (Figs 36, 37). The means of conidiogenous cell development following conidial production in Leptographium spp. and Verticicladiella spp. were more difficult to determine (Figs 38-41). In species such as V. truncata, conidiogenous loci appeared to be distinctly sympodial in some conidiogenous cells and progressively percurrent in others. In all Verticicladiella spp. and Leptographium spp. conidiogenous cells elongated during progressive development. This elongation due to proliferation was, however, least obvious in V, procera.

DISCUSSION

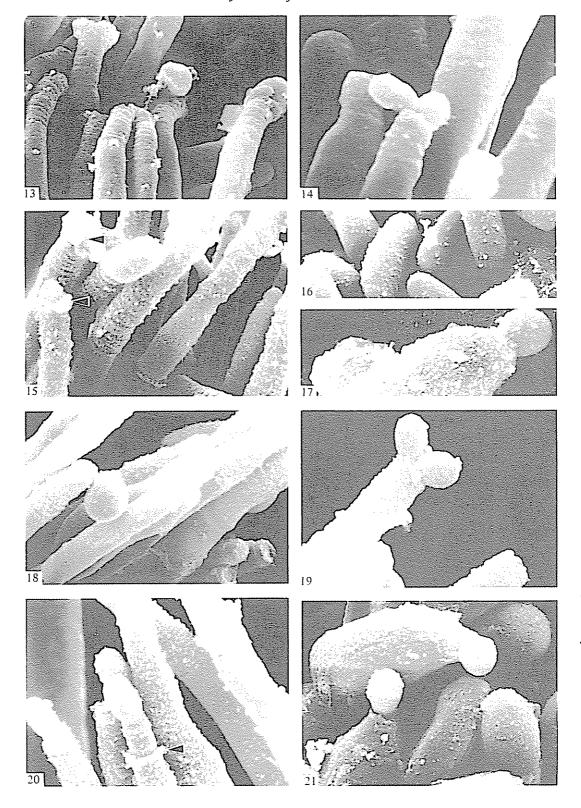
Previously experienced difficulties in distinguishing between *Leptographium* and *Verticicladiella* based on their alleged annellidic and sympodial 'conidial development' (Wingfield & Marasas, 1983) were reaffirmed here. By definition, *L. lundbergii*, the type species of the genus (Lagerberg *et al.*, 1927)

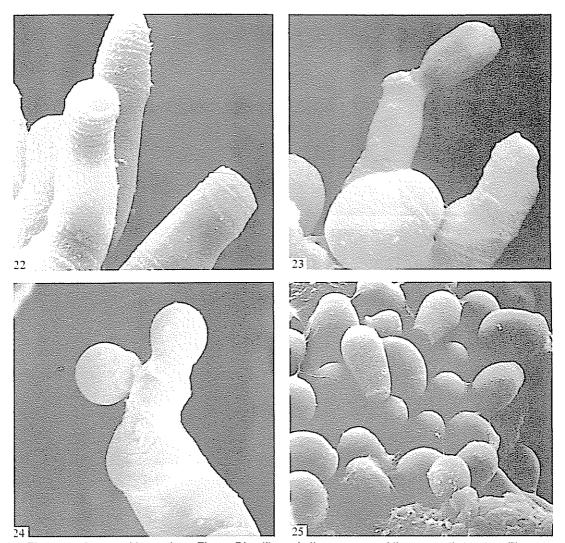
should have distinctly annellidic conidiogenous cells with ring-like encircling scars (remains of the outer conidiogenous cell wall) left at the apex of the conidiogenous cell after secession (Hughes, 1953). Scanning electron micrographs of conidiogenous cells in L. lundbergii show, however, that sympodial proliferation resulting in geniculate conidiogenous cells as well as percurrent proliferation of conidiogenous cells occur in this fungus. Examination of other Leptographium spp. (L. terebrantis, L. pyrinum and C. huntii) also suggest that conidial development in these species is associated with percurrent as well as sympodial conidiogenous cells. Ultrastructural studies on the development of the conidia are necessary to determine unequivocally that both enteroblastic and holoblastic proliferation of the conidiogenous cells occur in these genera.

Although sympodial proliferation of conidiogenous cells in *V. truncata* appeared to be more common than in *Leptographium* spp., evidence of percurrent proliferation in this fungus was however also apparent. Proliferation of conidiogenous cells in *V. procera* was apparently sympodial, however, without as much extension in length of the conidiogenous cells as was observed in *V. truncata* or *Leptographium* spp.

Because both sympodial and percurrent development occurred in species of Leptographium and Verticicladiella, it must be concluded that separation of these genera solely on this basis is impossible. Other genera have also been reported to exhibit both annellidic and sympodial ontogeny. Some of these include the coelomycetes Seimatosporium kriegerianum (Bresadola) Morgan-Jones & Sutton (Sutton, 1964) and Ajrekarella polychaetriae Kamat & Kalani (Sutton, 1967), and some anamorphs of the Ascomycete genera Diatrype Fr., Diatrypella (Ces. & de Nor.) Sacc., Eutypa Tul. (Glawe & Rogers, 1982 a, b) and Monographella Petrak (Samuels & Hallett, 1983). Many anamorphs of the Rhytismataceae also exhibit variation between sympodial, annellidic and phialidic development (D. Minter, pers. comm.). In contrast, however, Zhang, Kendrick & Brubacher (1983) emphasized the stability of annellidic and sympodial proliferation as taxonomic characters in Sporidesmiella Kirk although Kirk (1982) had considered the taxa concerned to be varieties of the same species. Minter, Kirk & Sutton (1982, 1983) have provided a new view of Deuteromycete development which predicts that species proliferating both

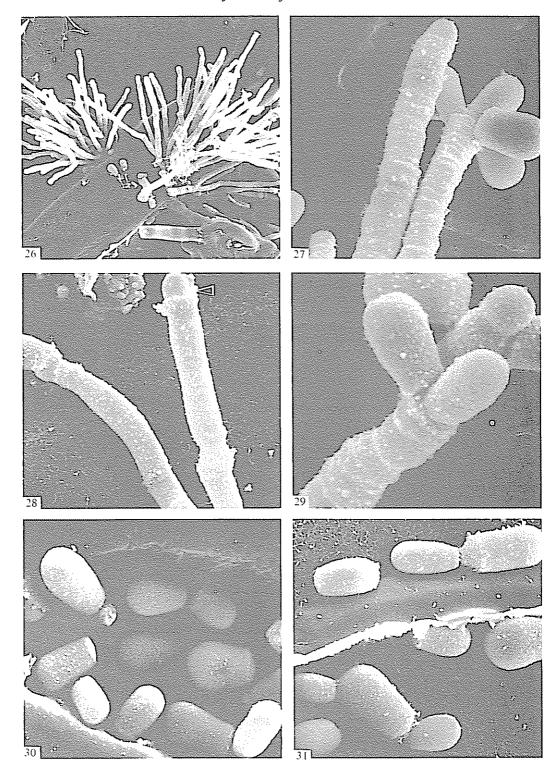
Figs 7–12. Leptographium lundbergii. Fig. 7. Conidiophores showing extensive proliferation of conidiogenous cells (×730). Fig. 8. Conidiogenous cells with percurrent and sympodial proliferation (×3300). Fig. 9. Displacement of outer cell wall layers to form collarettes (arrow) on conidiogenous cells (×5600). Fig. 10. Sympodial proliferation of conidiogenous cells (×5600). Fig. 11. Extension of conidiogenous cell after period of successive conidium production (×11300). Fig. 12. Conidia with truncate bases (×5600).

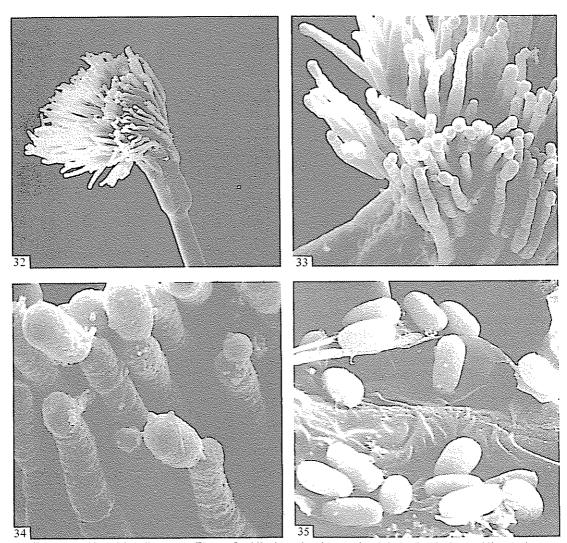




Figs 22–25. Leptographium pyrinum. Fig. 22. Ring-like encircling scars on conidiogenous cells (\times 5600). Fig. 23. Conidial secession showing scars on outer wall layer and sympodial development of conidiogenous cell (\times 5600). Fig. 24. Sympodial proliferation of conidiogenous cell (\times 5600). Fig. 25. Conidia with broadly truncate bases (\times 3600).

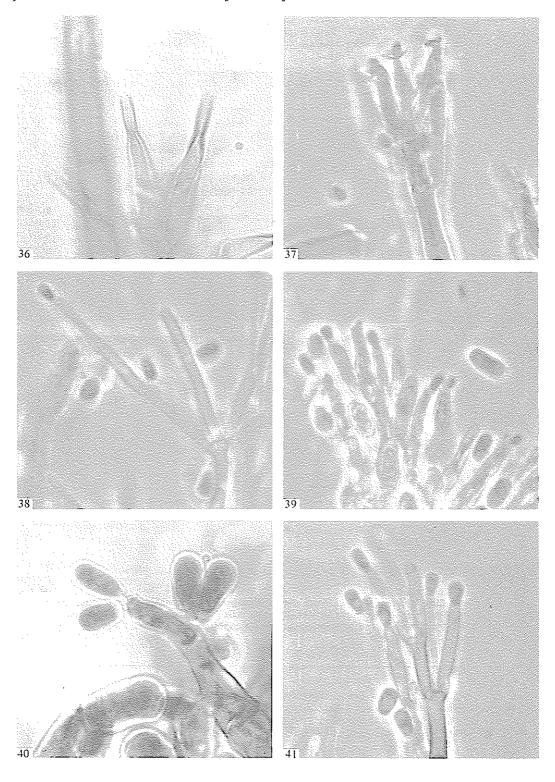
Figs 13–21. Ceratocystis huntii and Leptographium terebrantis. Figs 13–17. Ceratocystis huntii Fig. 13. Conidogenous cells showing ring like encircling scars (\times 5600). Fig. 14. Conidiogenous cells with apparent sympodial development (\times 5600). Fig. 15. Displaced outer wall tissue (arrows) of conidogenous cells (\times 5600). Fig. 16. Conidia (\times 5600). Fig. 17. Conidia budding (\times 5600). Figs 18–21. L. terebrantis. Fig. 18. Conidiogenous cells with encircling scars (\times 5600). Fig. 19. Sympodial proliferation of conidiogenous cell (\times 5600). Fig. 20. Displacement of outer cell wall tissue (arrow) during proliferation of conidiogenous cell (\times 5600). Fig. 20. Budding conidia (\times 5600).





Figs 32–36. Verticicladiella procera. Fig. 32. Conidiophore showing restricted elongation during conidiogenesis (×730). Fig. 33. Sympodial development of conidiogenous cells (×5600). Fig. 34. Conidiogenous cells showing sympodial proliferation and scars marking areas of conidium development (×11300). Fig. 35. Conidia (×5600).

Figs 26–31. *Verticicladiella truncata*. Fig. 26. Conidiophores (\times 3300). Fig. 27. Conidiogenous cells with scars left after seccession of conidia (\times 5600). Fig. 28. Elongating conidiogenous cell showing displacement (arrow) of outer wall tissue (\times 5600). Fig. 29. Apparent sympodial development of conidiogenous cell (\times 11300). Fig. 30. Conidia with truncate bases (\times 5600). Fig. 31. Budding conidia (\times 5600).



enteroblastically and holoblastically (sympodially and percurrently), are more common than was previously thought. The present work confirms this prediction.

Conidial development in Leptographium spp. and Verticicladiella spp. could be described in terms of the five developmental stages suggested by Minter et al. (1982) in the following way. The first conidium is produced holoblastically and delimited by a septum (conidium ontogeny and conidium delimitation). Thereafter the conidium secedes (secession) and the conidiogenous cell proliferates enteroblastically percurrently or holoblastically sympodially (proliferation). The second conidium is formed holoblastically involving all walls of the adjacent proliferation (regeneration).

Conidial development in *V. procera* was different from that observed in *V. truncata* and *Leptographium* spp. Conidiogenous cells appeared to have proliferated sympodially although the resulting geniculate conidiogenous cell was not as obvious as some of those observed in *V. truncata* and *Leptographium* spp. This was apparently due to a more limited proliferation of the conidiogenous cells in *V. procera*. The extent of proliferation of conidiogenous cells in species of *Verticicladiella* and *Leptographium* may become a useful taxonomic character at the species level.

Conidial development and shape in the two Phialocephala spp. examined here suggests that this genus is not homogeneous and that P. bactrospora is distinctly different (cylindrical conidia with truncate ends and long cylindrical collarettes) from P. fusca. Phialocephala bactrospora is more similar to a Chalara spp. and conidiogenous cells suggest that conidia are being produced by ring wall building (Minter et al., 1983; Minter, pers. comm.). By comparison, the conidia of P. fusca in the collarettes suggests that development is by replacement wall building (Minter et al., 1983). Phialocephala bactrospora may thus be related to Ceratocystis spp. with Chalara type anamorphs whereas P. fusca is closer to the Leptographium/ Verticicladiella types (Minter, pers. comm.). A more detailed examination of conidial development in Phialocephala is required to establish whether this genus should be separated from Leptographium and Verticicladiella.

The genera Graphium Corda, Pesotum Crane &

Schoknecht and *Phialographium* Upadhyay & Kendrick, are synnematous homologues of *Leptographium*, *Verticicladiella* and *Phialocephala* respectively (Crane & Schoknecht, 1973; Upadhyay & Kendrick, 1974). Observations on the mononematous species in this study could apply to their synnematous homologues. Conidiogenous cell proliferation in *Graphium* spp. (annellidic) and *Pesotum* spp. (sympodial) might be sufficiently similar to warrant consolidation of these genera.

Kendrick (1980) noted the morphological similarity between Leptographium, Verticicladiella and Phialocephala spp. and questioned whether the separation of these genera based on conidial ontogeny is justified. The results of this study, however, suggest that *Phialocephala* can be distinguished from Leptographium and Verticicladiella using light microscopy. Although conidial development in many Phialocephala spp. may not be conceptually different from conidial ontogeny in Leptographium and Verticicladiella spp., it is considered reasonable to leave the genus Phialocephala intact at present. The separation of Verticicladiella spp. and Leptographium spp. solely on the basis of sympodial and annellidic conidium development can clearly not be justified. Verticicladiella spp. should therefore be assigned to the genus Leptographium. The following synonomy is proposed:

LEPTOGRAPHIUM Lagerberg & Melin, Sv. Skogsvardsf. Tidskr. 25: 257 (1927).

Verticicladiella Hughes, Can. J. Bot. 31: 653 (1953).

The generic circumscription of *Leptographium* should be amended to include conidiogenous cells which develop enteroblastically (percurrent, annellidic) and holoblastically (sympodial).

Incorporation of the Verticicladiella spp. in Leptographium requires a number of new combinations. Of these, five species have been described as Verticicladiella anamorphs of Ceratocystis spp. after publication of a Verticicladiella monograph by Kendrick (1962). These include V. aurea, V. crassivaginata, V. grandifoliae Davidson, V. huntii and V. robusta. With the exception of V. grandifoliae, isolates of all these fungi have been examined. Assignment of the anamorph of C. grandifoliae to Verticicladiella by Davidson (1976)

Figs 36-41. Light micrographs of conidiogenous cells of *Verticicladiella* spp. Leptographium spp. and *Phialocephala* spp. Fig. 36. Phialides of *P. bactrospora* (\times 1750). Fig. 37. Phialides of *P. fusca* \times 1750). Fig. 38. Apparent sympodial proliferation in *L. lundbergii* \times 1750). Fig. 39. Sympodial and annellidic development in *L. terebrantis* (\times 1750). Fig. 40. Sympodial proliferation in *L. pyrinum* (\times 1750). Fig. 41. Apparent annellidic development in *V. truncata* \times 1750).

was reconfirmed by Upadhyay (1981). The following species previously in *Verticial adiella* are included in *Leptographium* as amended:

Leptographium abietinum (Peck) Wingfield, comb.nov.

Sporocybe abietina Peck, New York State Museum Rept 31: 45 (1879).

Verticicladiella abietina (Peck) Hughes, Can. J. Bot. 31: 653 (1953).

Leptographium antibioticum (Kendrick) Wingfield, comb.nov.

Verticicladiella antibiotica Kendrick, Can. J. Bot. 40: 781 (1962).

Leptographium aureum (Robis.-Jeff. & Davids.) Wingfield, comb.nov.

Verticicladiella aurea Robis.-Jeff. & Davids., Can. J. Bot. 46: 1525 (1968).

Leptographium brachiatum (Kendrick) Wingfield, comb.nov.

Verticicladiella brachiata Kendrick, Can. J. Bot. 40: 786 (1962).

Leptographium crassivaginatum (Griffin) Wingfield, comb.nov.

Verticicladiella crassivaginata Griffin, Can. J. Bot. 46: 701 (1968).

Leptographium dryocoetidis (Kendrick & Molnar) Wingfield, comb.nov.

Verticicladiella dryocoetidis Kendrick & Molnar, Can. J. Bot. 43: 39 (1965).

Leptographium grandifoliae (Davidson) Wingfield, comb.nov.

Verticicladiella grandifoliae Davidson, Mem. New. York Bot. Gard. 28: 45 (1976).

Leptographium huntii (Robis.-Jeff.) Wingfield, comb.nov.

Verticicladiella huntii Robis.-Jeff., Can. J. Bot. 40: 528 (1964).

Leptographium Penicillatum Grosm., Zeitschr.f. Parasitenkunde 3: 94 (1931).

Verticicladiella penicillata (Grosm.) Kendrick, Can. 7. Bot. 40: 776 (1962).

Leptographium procerum (Kendrick) Wingfield, comb.nov.

Verticicladiella procera Kendrick, Can. J. Bot. 40: 783 (1962).

Leptographium robustum (Robis.-Jeff. & Davids.) Wingfield, comb.nov.

Verticicladiella robusta Robis.-Jeff. & Davids., Can. J. Bot. 46: 1525 (1968).

Leptographium serpens (Goid.) Wingfield, comb.nov.

Scopularia serpens Goid., Boll. Staz. Patol. Vegetale 16: 42 (1936). Verticicladiella serpens (Goid.) Kendrick, Can. J. Bot. 40: 781 (1962).

Leptographium truncatum (Wingfield & Marasas) Wingfield, comb.nov.

Verticicladiella truncata Wingfield & Marasas, Trans. Br. Mycol. Soc. 80: 232 (1983).

Leptographium wageneri (Kendrick) Wingfield, comb.nov.

Verticicladiella wageneri Kendrick, Can. J. Bot. 40: 793 (1962).

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