Ophiostoma europhioides and *Ceratocystis pseudoeurophioides*, synonyms of *O. piceaperdum*

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Accepted 14 May 1999.

Ophiostoma piceaperdum and *O. europhioides* are well-known, first described from conifers in Canada. They have been considered to be synonymous. After studying the type material, as well as a collection of isolates of *O. piceaperdum* and *O. europhioides*, we have concluded that they cannot be distinguished from each other, so we support the synonymy of *O. europhioides* and *O. piceaperdum* and provide a description for the *Leptographium* anamorph of *O. piceaperdum*. *Ceratocystis pseudoeurophioides* has previously been distinguished from *O. europhioides* based on differences in anamorph morphology. This species has also been reduced to synonymy with *O. penicillatum*, which was reported to have cucullate ascospores. Later descriptions of *O. penicillatum* reported it to have allantoid ascospores. We conclude that *C. pseudoeurophioides* cannot be distinguished from *O. piceaperdum* and is, therefore, reduced to synonymy with that species.

Ophiostoma is an economically important group of fungi, best known for an ability to cause diseases of trees (Gibbs, 1978; Brasier, 1991). Many species cause considerable economic losses due to sapstain of lumber (Solheim, 1986; Gibbs, 1993). Most are effectively dispersed by insects, especially bark beetles (Coleoptera: Scolytidae) (Münch, 1907; Lagerberg, Lundberg & Melin, 1927; Leach, Orr & Christensen, 1934; Upadhyay, 1981). This accounts for the extensive damage they can cause to plantation and forest trees (Solheim, 1986, 1992*a*, *b*).

Ophiostoma spp. are characterized by dark, flask-shaped ascocarps with ascospores that accumulate in slimy masses at the tips of ascocarp necks (Upadhyay, 1993; Wingfield, Seifert & Webber, 1993). Their anamorphs are found in many different genera including *Leptographium*, *Graphium*, *Sporothrix* and *Hyalorhinocladiella* (Mouton, Wingfield & Van Wyk, 1993, 1994; Wingfield *et al*., 1993). Most of these anamorphs are characterized by conidia that accumulate in mucilaginous masses at the apices of conidiophores, facilitating insect dispersal.

Ophiostoma piceaperdum (Rumbold) Arx was first described from sapwood of *Picea glauca* (Moench) Voss., associated with blue-stain and infestation by the bark beetle *Dendroctonus piceaperda* Hopkins (Rumbold, 1936). Rumbold (1936) found that this fungus resembled the recently described *Ceratostomella penicillata* (= *O. penicillatum*) Grosmann. She could, however, distinguish the two species by the smaller conidia and conidiophores in *O. piceaperdum*.

Ophiostoma europhioides (E. F. Wright & Cain) H. Solheim was described as *Ceratocystis europhioides* from Canada by Wright & Cain (1961) from *Picea* and *Pinus* spp. Wright & Cain (1961) noted the similarity with *O. penicillatum*, but could separate them because the allantoid ascospores and conidia of *O. penicillatum* (Grosmann, 1931, 1932) were unlike the cucullate ascospores and ellipsoid to obovoid conidia of *O. europhioides* (Wright & Cain, 1961).

Upadhyay (1981) treated *O. piceaperdum* and *O. europhioides* as synonyms. So did Hutchson & Reid (1988) in their survey of ophiostomatoid fungi from New Zealand. Solheim (1986), however, treated the two species as different in his study of ophiostomatoid fungi from Norway spruce; as did Harrington (1988) in a review and Yamaoka *et al*. (1997) in a survey of ophiostomatoid fungi associated with *Ips typographus* f. *japonicus* in Japan.

Original descriptions of ascospore shapes suggest that *O. piceaperdum* and *O. europhioides* are distinct (Rumbold, 1936; Wright & Cain, 1961). Isolates of *O. piceaperdum* have been described as having ellipsoidal ascospores, while ascospores of *O. europhioides* are cucullate. Ascospores of *O. piceaperdum* were not illustrated by Rumbold (1936). The importance of this fungus as an agent of blue-stain and its occurrence in various parts of the world has prompted us to reconsider its taxonomy. Olchowecki & Reid (1974) described *O. pseudo-europhioides* from spruce (*Picea* spp.) in Canada. The fungus can be distinguished from *O. europhioides* by apparently different anamorphs. *Ophiostoma pseudoeurophioides* was described as having a *Verticicladiella* anamorph and *O. europhioides* a *Leptographium* anamorph. In his monograph of *Ceratocystis* and *Ceratocystiopsis*, Upadhyay (1981) treated *O. pseudoeurophioides* as a synonym of *O. penicillatum*, and reported the anamorph

to be a *Verticicladiella*. He also reported cucullate ascospores for *O. penicillatum*, in contrast to the allantoid ascospores reported for the neotype of this species by Solheim (1986). Wingfield (1985) reduced *Verticicladiella* to synonymy with *Leptographium*, thus eliminating the only obvious difference between *O. europhioides* and *O. pseudoeurophioides*. Harrington (1988) also treated these species as synonyms in his monographic study of species in *Leptographium*. In view of the confused taxonomy of *O. europhioides*, *O. piceaperdum* and *O. pseudoeurophioides*, this study was undertaken to review their status.

MATERIALS AND METHODS

Material for examination included all available herbarium specimens of *O. piceaperdum*, *O. europhioides* and *O. pseudoeurophioides*. In addition, isolates of *O. europhioides* and *O. piceaperdum*, were obtained from a variety of culture collections and from various colleagues. Characterization of isolates was done on fungal structures produced on 2% malt extract agar (MEA, 20 g Biolab malt extract, 20 g Biolab agar and 1000 ml distilled water). For microscopy, relevant structures were mounted in lactophenol on glass slides. Herbarium specimens were examined by placing a drop of 1% KOH on the dried tissue. After 5 min, small pieces of fungal tissue were removed and mounted in lactophenol on glass slides. Fifty measurements of each relevant morphological structure were made and ranges and means computed. Colours were determined using the charts of Rayner (1970).

Available isolates of the fungi under consideration were examined using SEM. Small blocks of agar cut from sporulating colonies were fixed in 3% glutaraldehyde and 0.5% osmium tetroxide in a 0.1 M phosphate buffer, dehydrated in a graded acetone series and critical-point dried. Specimens were mounted and coated with gold palladium alloy and examined using a JSM 6400 scanning electron microscope.

The optimal growth temperatures for two representative isolates of *O. europhioides* and *O. piceaperdum* (CBS 366.75 and CMW 2811) were determined by inoculating eight MEA plates with 6 mm diam. agar discs taken from the actively growing margins of fresh isolates. The plates were incubated at temperatures in the range 5–20 °C at 5° intervals and 20–30 °C at 2.5° intervals. Colony diameters were measured after 8 d and growth was computed as means from eight readings. Cycloheximide tolerance of these two isolates was determined on MEA plates (eight per isolate) amended with 0.5 g l^{-1} cycloheximide. The plates were incubated at 25 °C and colony diameters were measured on the eighth day.

RESULTS

Type specimens of *O. europhioides* (TRTC 45762, TRTC 36263, WIN(M) 71-18) and *O. piceaperdum* (BPI 595980, BPI 595981, BPI 595982), included both anamorph and teleomorph structures. Both species produced dark, olivaceous colonies and optimal growth occurred at 25 °C. Conidiophores developed abundantly on the surface of the mycelium in groups of 2–7. *Ophiostoma piceaperdum* and *O. europhioides*, have mean stipe lengths of 50–300 µm, and the conidiophores are characterized by the absence of rhizoid-like structures at the base. Both species have conidiophores with 2–3 primary branches and 3–4 series of branches. The conidia of *O. piceaperdum* and *O. europhioides* are ellipsoidal to obovoid with truncate ends and rounded apices. Conidia were also found to be of similar length, in the range 3–9 µm (Table 1).

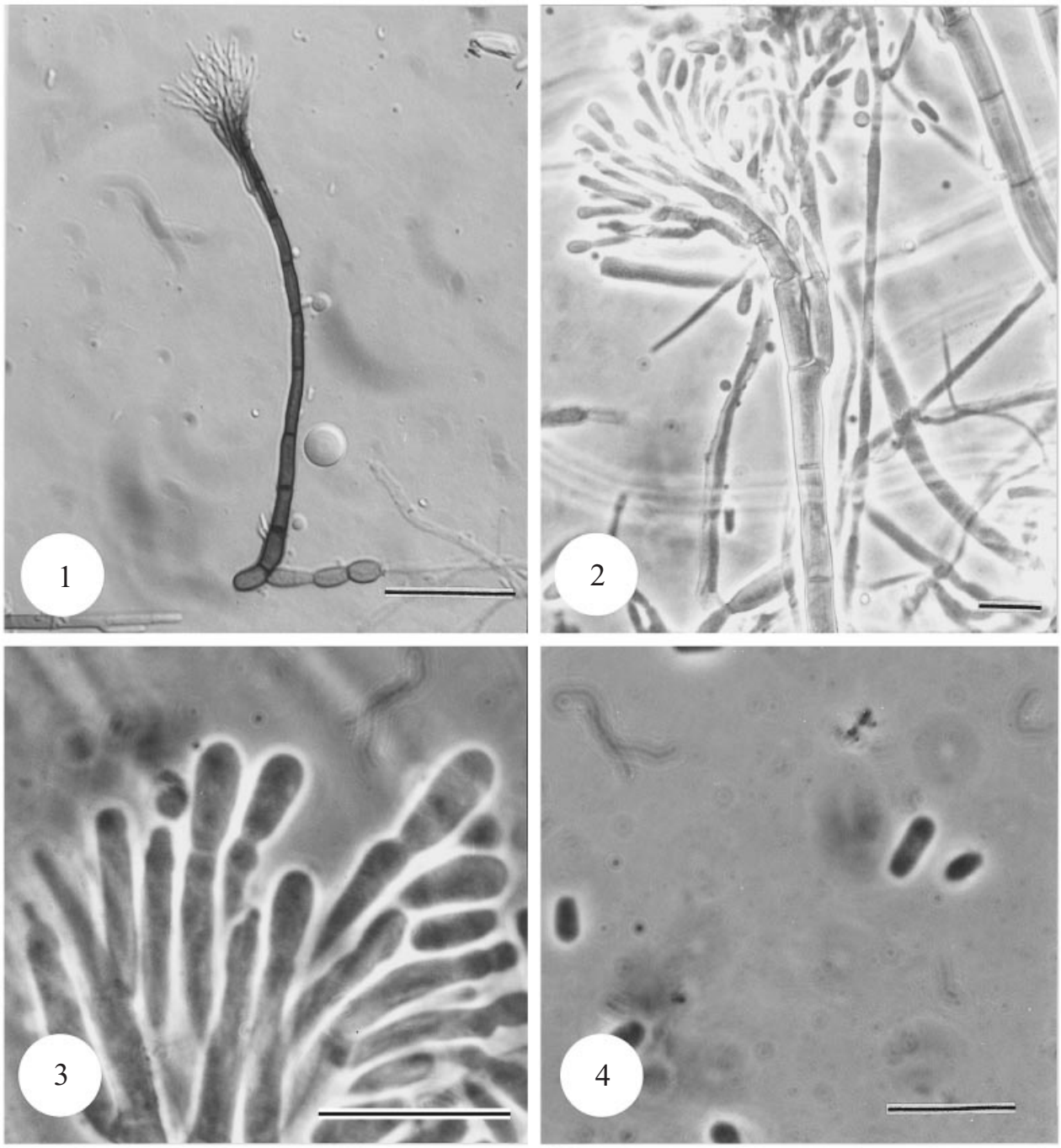
No distinction could be made between the teleomorph structures of *O. piceaperdum* and *O. europhioides* in cultures. Perithecia of both species had neck lengths in the range 250–1130 µm, and the apices of the necks were characterized by the absence of ostiolar hyphae. Ascospores were distinctly cucullate in both species, and their sizes were in the range 4–6 µm long (Table 1).

Ophiostoma piceaperdum and *O. europhioides* cannot be distinguished on morphology and are, therefore, considered to be synonyms. No anamorph names were provided in the descriptions of either *O. piceaperdum* or *O. europhioides*, although it was noted that a *Leptographium* anamorph was present (Rumbold, 1936; Wright & Cain, 1961). Given the fact

Table 1. Comparison of *Ophiostoma piceaperdum, O. europhioides* and *O. pseudoeurophioides**.

	O. piceaperdum	*O. europhioides*	*O. pseudoeurophioides*
Host	*Picea glauca, P. abies*	*Picea abies; P. glauca; P. mariana; P. jezoensis; Pinus glauca; P. resinosa; P. strobus; P. sylvestris; P. banksiana; Pseudotsuga mensiezii*	*Picea mariana*
Associated insect	*Dendroctonus piceaperda*	*Dendroctonus rufipennis; D. valens; Dryocoetus* sp.; *Hylurgops palliatus; Ips typographus; Pityogenes chalcographus*	None reported
Distribution	U.S.A.	Canada, USA	Canada
Anamorph	*Leptographium*	*Leptographium*	*Leptographium*
Rhizoids	Absent	Absent	Absent
Conidiophore length	140–300 µm	60–300 µm	150–500 µm
Conidium shape	Obovoid	Obovoid	Obovoid
Conidium size	3–11 µm	3.2–8.5 µm	2.5–5
Perithecium neck length	110–950 µm	256–1128 µm	300–850 µm
Perithecium base size	90–350 µm	136–360 µm	150–300 µm
Ascospore shape	Cucullate (Rumbold reported ellipsoid ascospores)	Cucullate	Cucullate
Ascospore size	3.6–5.6 µm	2.8–5.5 µm	4.5–5 × 2–2.5 µm

* Data and information in this table are derived from publications of Rumbold (1936) (*O. piceaperdum*), Wright & Cain (1961) (*O. europhioides*) and Olchowecki & Reid (1974) (*O. pseudoeurophioides*).



Figs 1–4. Light micrographs of the conidiophore and conidia of *L. piceaperdum* (CMW 660) (Bars = 10 µm). **Fig. 1.** Conidiophore. **Fig. 2.** Conidiogenous apparatus. **Fig. 3.** Conidiogenous cells. **Fig. 4.** Conidia.

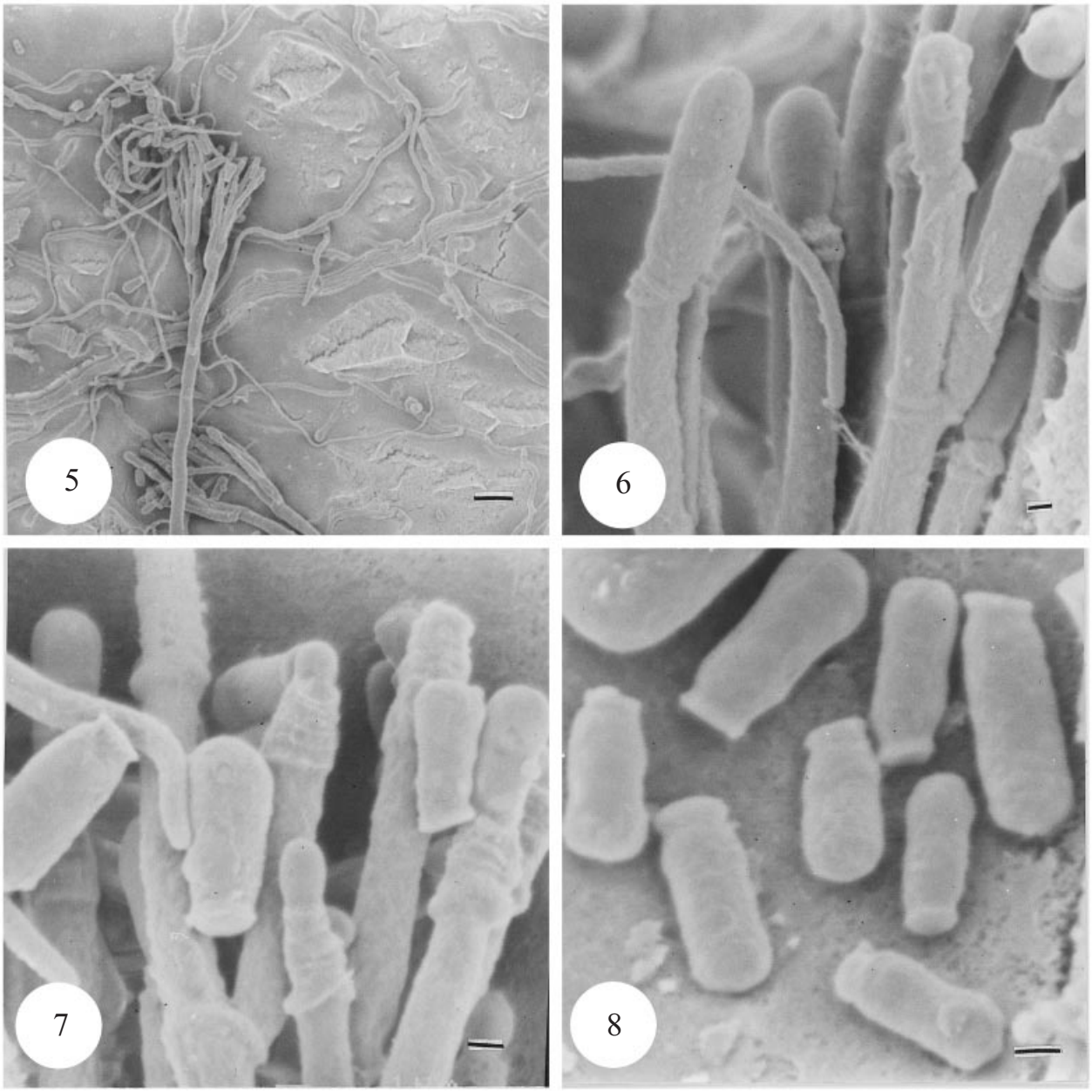
that this fungus occurs commonly in the absence of the teleomorph, we provide a name for its *Leptographium* anamorph. A short Latin diagnosis for the anamorph of *O. piceaperdum* was provided by Rumbold (1936) and an additional Latin description is thus not required. The following emended description is provided to avoid further confusion.

Leptographium piceaperdum K. Jacobs & M. J. Wingf., **sp. nov.**

Diagnosis in lingua Latina est in Rumbold (*J. Agric. Res.* **52**: 436, 1936).

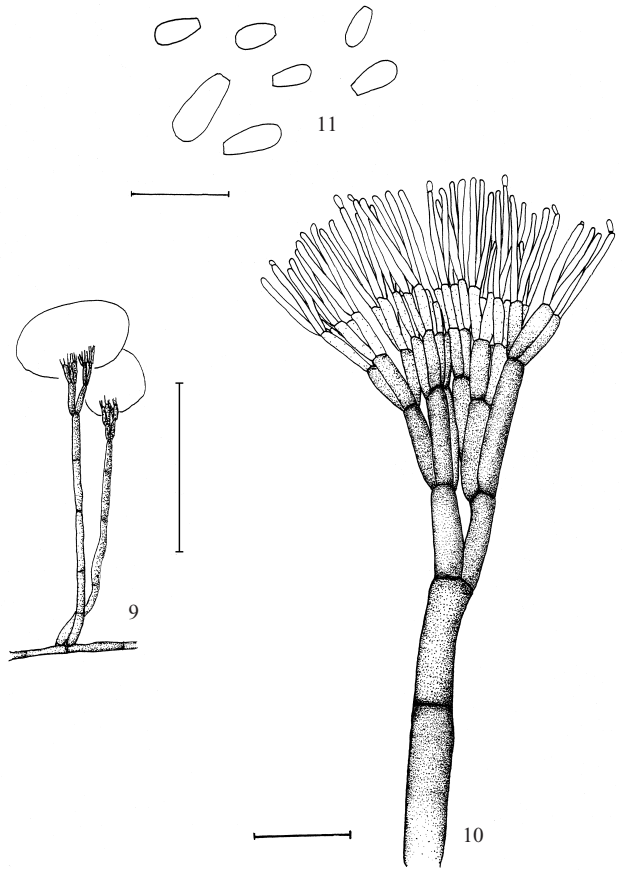
Typus: **Canada**: Nova Scotia, ex *Picea glauca*, *C. T. Rumbold* (BPI 59581-fungus anamorphis holotypus).

Colonies with optimal growth at 25 °C on 2% MEA, reaching 34 mm diam after 8 d. No growth below 5 °C or above 30 °C. Able to withstand high concentrations of cycloheximide with no reduction in growth on 0.5 g l^{-1} cycloheximide after 4 d at 20 °C in the dark. Colonies dark olive (21″ m) with smooth margins. Hyphae submerged on solid medium with little aerial mycelia, hyaline to light olivaceous (21″k), smooth, occasionally roughened by granular deposits, straight, not constricted at the septa, 1.5–6 (mean = 4) µm diam. *Conidio-*



Figs 5–8. SEM of a conidiophore and conidia of *L. piceaperdum* (CMW 660). **Fig. 5.** Conidiophore (Bar = 10 μm). **Figs 6, 7.** Conidiogenous cells (Bar = 1 μm). **Fig. 8.** Conidia (Bar = 1 μm).

phores occurring singly or in groups of 2–7, arising directly from the mycelium with smaller conidiophores on aerial mycelia, erect, macronematous, mononematous, 140–300 (mean = 204) μm long, rhizoid-like structures absent (Figs 1, 5, 9). Stipe light olivaceous (21″k), smooth, cylindrical, simple, 3–8 septate, 70–195 (mean = 121) μm long (from first basal septum to below primary branches), 5–9 (mean = 6) μm wide below primary branches, apical cell not swollen; 6–12.5 (mean = 8) μm wide at base, basal cell not swollen. *Conidiogenous* apparatus 55–120 (mean = 84) μm long, excluding the conidial mass, with 2–5 series of cylindrical branches, 2–3 primary branches, light olivaceous (21″k), smooth, cylindrical, 0–1 septate 15.5–39 (mean = 21.0) μm long and 3–8 (mean = 5) μm wide, secondary branches light olivaceous (21″k), aseptate, 11–23 (mean = 12) μm long, 2–6 (mean = 4) μm wide, tertiary branches light olivaceous (21″k), aseptate, 9–22 (mean = 15) μm long, 2–5 (mean = 3) μm wide, quaternary branches, hyaline to light olivaceous (21″k), aseptate, 7–16 (mean = 11.5) μm long, 2–3 (mean = 2.5) μm wide (Figs 2, 10). *Conidiogenous cells* discrete, 2–3 per branch, cylindrical, tapering slightly at the apex, 11–26 (mean = 17.5) μm long and 1.5–3 (mean = 2) μm wide. Conidium development occurring through replacement wall building with holoblastic ontogeny, percurrent proliferation and delayed secession giving the false impression of sympodial proliferation (Minter *et al.*, 1982, 1983; Van Wyk, Wingfield and Marasas, 1988) (Figs 3, 6, 7). *Conidia* light grey olivaceous (19‴), aseptate, obovoid to ellipsoid with truncated ends and rounded apices, 3–9 × 1–3 (mean = 5 × 2) μm (Figs 4, 8, 11). Conidia accumulating in slimy droplets at the apex of conidiogenous apparatus, hyaline at first, becoming cream coloured (19′f) with age.



Figs 9–11. Conidiophores and conidia of *L. piceaperdum* (CMW 660). **Fig. 9.** Conidiophore without rhizoids (Bar = 100 µm). Conidiogenous apparatus (Bar = 10 µm). **Fig. 11.** Conidia (Bar = 10 µm).

Specimens examined

Herbarium types: *Ophiostoma piceaperdum*: Canada, Nova Scotia, St Peters, Cape Breton, *Picea glauca, C. T. Rumbold*, June 1930, BPI 595981; (holotype); Canada, Nova Scotia, St Peters, Cape Breton, *P. glauca, R. E. Balch*, June 1930, BPI 595980; Canada, Nova Scotia, St Peters, Cape Breton, *Picea glauca, R. E. Balch*, June 1930, BPI 595982; *Ophiostoma europhioides*: Canada, Ontario, Shabotik River, Algoma district, *P. mariana, R. F. Cain*, 20 June 1961, TRTC 45762; Canada, Ontario, Challenen Lake, Sudbury district, *P. mariana, R. F. Cain, J. Reid & W. Obust*, 20 June 1961, TRTC 36263; Canada, Ontario, Shabotik River, Algoma district, *P. mariana, R. F. Cain*, 20 June 1961, MFB 7439; Canada, Ontario, Shabotik River, Algoma district, *P. mariana, R. F. Cain*, 20 June 1961, MFB 7439; Canada, Manitoba, Sandilands Forest Reserve, *P. mariana, A. Olchowecki*, 20 June 1961, WIN(M) 71-18; *O. pseudoeurophioides*: Canada, Sandilands, Forest Reserve, *P. mariana, A. Olchowecki*, 24 Apr., 1971 WIN(M) 71-13.

Cultures: *O. piceaperdum*: *P. abies, A. M. Hallakesela*, CMW 660 (same as CBS 366.75); *O. europhioides*: USA, Nippletop Mountain, *P. rubens, T. C. Harrington*, 1987, CMW 281 (= C274); *E. F. Wright*, CMW 479 (= CBS 444-69); Austria, Nasswald, *P. abies, T. Kiristis*, 1993, CMW 3314.

DISCUSSION

Ophiostoma piceaperdum and *O. europhioides* are indistinguishable based on morphological data. In the original description, however, the ascospores of *O. europhioides* were described as cucullate (Wright & Cain, 1961), whereas those of *O. piceaperdum* were noted as being allantoid (Rumbold, 1936). Examination of the herbarium type material, revealed that these species are both characterized by cucullate ascospores. The reason for this discrepancy is most probably because Rumbold (1936) did not describe the sheaths surrounding the ascospores that give the spores their cucullate appearance. Both species displayed *Leptographium* anamorphs with obovoid conidia that could not be distinguished from each other. Thus, morphological comparisons of the type specimens failed to distinguish between *O. europhioides* and *O. piceaperdum*, and from these observations we conclude that *O. piceaperdum* and *O. europhioides* are identical and thus support the synonymy proposed by Upadhyay (1981).

Ophiostoma piceaperdum and *O. europhioides* have both been considered to be similar to *O. penicillatum* (Rumbold, 1936; Wright & Cain, 1961; Griffin, 1968). *O. piceaperdum* can, however, easily be distinguished from *O. penicillatum* based on ascospore and conidial morphology. *Ophiostoma penicillatum* is characterized by the presence of curved ascospores and large, allantoid conidia. This is in contrast to the cucullate ascospores and obovoid conidia of *O. piceaperdum* (Grosmann, 1931, 1932; Rumbold, 1936; Wright & Cain, 1961).

The synonymy of *C. pseudoeurophioides* with *O. penicillatum*, proposed by Upadhyay (1981) is rejected. *Ceratocystis pseudoeurophioides* has been distinguished from *O. europhioides* based on the presence of a *Verticicladiella* state in the former species and a *Leptographium* state in the latter. When Wingfield (1985) synonymized *Verticicladiella* with *Leptographium*, this distinction became redundant. Examination of the type specimen [(WIN)M 71-13] and the original description of *C. pseudoeurophioides* (Olchowecki & Reid, 1974), revealed that this species cannot be distinguished from *O. piceaperdum* and we, therefore, propose the following synonymy:

Ophiostoma piceaperdum (Rumbold) Arx, *Antonie van Leeuwenhoek* **18**: 211 (1952).

Ceratostomella piceaperda Rumbold, *J. Agric. Res.* **52**: 436, (1936).

Grosmannia piceaperda (Rumbold) Goid. *R. Staz. Pat. Veg. Bol. Rome* **16**: 255 (1936).

Ceratocystis piceaperda (Rumbold) C. Moreau, *Rev. Mycol. Suppl.* Col. **17**: 22 (1952).

Ophiostoma europhioides (E. F. Wright & Cain) H. Solheim, *Nord. J. Bot.* **6**: 203 (1986).

Ceratocystis europhioides E. F. Wright & Cain, *Can. J. Bot.* **39**: 1222 (1961).

Ceratocystis pseudoeurophioides Olchow. & J. Reid, *Can. J. Bot.* **52**: 1700 (1974).

ACKNOWLEDGEMENTS

We thank colleagues, culture collections and herbaria noted in the text for kindly providing material for examination. We also thank the National Research Foundation (NRF), and members of the Tree Pathology Cooperative Programme for financial support, and Professor David. L. Hawksworth for nomenclatural advice.

REFERENCES

Brasier, C. M. (1991). *Ophiostoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia* **115**, 151–161.

Gibbs, J. N. (1978). Intercontinental epidemiology of Dutch elm disease. *Annual Review of Phytopathology* **16**, 287–307.

Gibbs, J. N. (1993). The biology of ophiostomatoid fungi causing sapstain in trees and freshly cut logs. In Ceratocystis *and* Ophiostoma*: Taxonomy, Ecology and Pathogenicity* (ed. M. J. Wingfield, K. A. Seifert & J. F. Webber), pp. 153–160. American Phytopathological Society Press, St Paul, Minnesota.

Goidanich, G. (1936). Il genera di Ascomiceti "Grosmann" G. Goid. *Bollettino della R. Statione di Patologia Vegetale-Roma*, N.S. **16**, 26–60.

Griffin, H. D. (1968). The genus *Ceratocystis* in Ontario. *Canadian Journal of Botany* **46**, 689–718.

Grosmann, H. (1931). Contributions to the knowledge concerning the life partnership between bark beetles and fungi. *Zeitschrift für Parasitenkunde* **3**, 56–102.

Grosmann, H. (1932). Uber die systematischen Beziehungen der Gattung *Leptographium* Lagerberg & Melin zur Gattung *Ceratostomella* Sacc. *Hedwigia* **72**, 183–193.

Harrington, T. C. (1988). *Leptographium* species, their distributions, hosts, and insect vectors. In *Leptographium Root Diseases on Conifers* (ed. T. C. Harrington & F. W. Cobb, Jr), pp. 1–39. American Phytopathological Society Press: St Paul, Minnesota.

Hutchson, L. J. & Reid, J. (1988). Taxonomy of some potential wood-staining fungi from New Zealand. 1. Ophiostomataceae. *New Zealand Journal of Botany* **26**, 63–81.

Lagerberg, T., Lundberg, G. & Melin, E. (1927). Biological and practical researches into blueing in pine and spruce. *Svenska Skogsvardsforeningens Tidskrift* **25**, 145–272.

Leach, L. G., Orr, L. W. & Christensen, C. (1934). The interrelationships of bark beetles and blue-staining fungi in felled Norway pine timber. *Journal of Agricultural Research* **49**, 315–341.

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

Minter, D. W., Kirk, P. M. & Sutton, B. C. (1983). Thallic phialides. *Transactions of the British Mycological Society* **80**, 39–66.

Moreau, C. (1952). Coexistence des formes *Thielaviopsis* et *Graphium* chez une souche de *Ceratocystis major* (Van Beyma) nov. comb. *Revue de Mycologie, Supplement Colonial* **17**, 17–25.

Mouton, M., Wingfield, M. J. & Van Wyk, P. S. (1993). Conidium development in the synnematous anamorphs of *Ophiostoma*. *Mycotaxon* **67**, 371–379.

Mouton, M., Wingfield, M. J. & Van Wyk, P. S. (1994). Conidium development in anamorphs of *Ceratocystis sensu lato*: a review. *South African Journal of Science* **90**, 293–298.

Münch, E. (1907). Die Blaufaule des Nadelhoizes. *Naturwissenshaftliche Zeitschrift für forest* **5**, 531–573.

Olchowecki, A. & Reid, J. (1974). The genus *Ceratocystis* in Manitoba. *Canadian Journal of Botany* **52**, 1675–1711.

Rayner, R. W. (1970). *A Mycological Colour Chart*. Commonwealth Mycological Institute and British Mycological Society, Kew.

Rumbold, C. T. (1936). Three blue-staining fungi including two new species associated with bark beetles. *Journal of Agricultural Research* **52**, 419–436.

Solheim, H. (1986). Species of *Ophiostomataceae* isolated from *Picea abies* infested by the bark beetle *Ips typographus*. *Nordic Journal of Botany* **6**, 119–207.

Solheim, H. (1992*a*). The early stages of fungal invasion in Norway spruce infested by the bark beetles *Ips typographus*. *Canadian Journal of Botany* **70**, 1–5.

Solheim, H. (1992*b*). Fungal succession in sapwood of Norway spruce infested by the bark beetle *Ips typographus*. *European Journal of Forest Pathology* **22**, 136–148.

Upadhyay, H. P. (1981). *A Monograph of Ceratocystis and Ceratocystiopsis*. University of Georgia Press: Athens.

Upadhyay, H. P. (1993). Classification of the ophiostomatoid fungi. In *Ceratocystis and Ophiostoma: taxonomy, ecology and pathogenicity* (ed. M. J. Wingfield, K. A. Seifert & J. F. Webber), pp. 7–13. American Phytopathological Society Press, St Paul, Minnesota.

Van Wyk, P., Wingfield, M. J. & Marasas, W. F. O. (1988). Differences in synchronization of stages of conidial development in *Leptographium* species. *Transactions of the British Mycological Society* **90**, 451–456.

Von Arx, J. A. (1952). Ueber die Ascomycetengattungen *Ceratostomella* Sacc., *Ophiostoma* Syd. und *Rostrella* Zimmerman. *Antonie van Leeuwenhoek* **42**, 201–213.

Wingfield, M. J. (1985). Reclassification of *Verticicladiella* based on conidial development. *Transactions of the British Mycological Society* **85**, 81–93.

Wingfield, M. J., Seifert, K. A. & Webber, J. F. (1993). Ceratocystis *and* Ophiostoma*: Taxonomy, Ecology and Pathogenicity*. American Phytopathological Society Press: St Paul, Minnesota.

Wright, E. F. & Cain, R. F. (1961). New species of the genus *Ceratocystis*. *Canadian Journal of Botany* **39**, 1215–1230.

Yamaoka, Y., Wingfield, M. J., Takahashi, I. & Solheim, H. (1997). Ophiostomatoid fungi associated with the spruce bark beetle *Ips typographus* f. *japonicus* in Japan. *Mycological Research* **101**, 1215–1227.