A new *Leptographium* species from Russia

K. JACOBS[1], M. J. WINGFIELD[1], N. V. PASHENOVA[2] and V. P. VETROVA[2]

[1] *Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, 0002, Republic of South Africa.*
[2] *Sukachev Institute of Forest SB RAS; Akademgorodok, Krasnoyarsk, 660036, Russia.*

Received 1 October 1999; accepted 16 March 2000.

Species of *Leptographium* are well-known inhabitants of conifers in the Northern Hemisphere, in which they cause a blue-stain. They are also known to be associated with insects, especially bark beetles (*Coleoptera: Scolytidae*). Surveys of dying stands of Siberian fir (*Abies sibirica*) have resulted in the consistent isolation of an unknown *Leptographium* from the galleries of the fir sawyer beetle, *Monochamus urussovi* (*Coleoptera: Cerambycidae*). This fungus is responsible for the blue-stain in living trees. Comparison with known species of *Leptographium* led to the conclusion that it had not been previously described, and the name *Leptographium sibiricum* sp. nov. is introduced here.

INTRODUCTION

Species of *Leptographium* can generally be recognized by their mononematous conidiophores with pigmented stipes and complex conidiogenous apparatus. Single celled, hyaline conidia are produced through percurrent annellidic proliferation (Kendrick 1962). The conidiogenous cells are, furthermore, characterized by delayed secession of the conidia, giving the conidiogenous cells a sympodial appearance (van Wyk, Wingfield & Marasas 1988). The conidia accumulate in slimy masses at the apex of the conidiophores, making these fungi ideal for dispersal by insects.

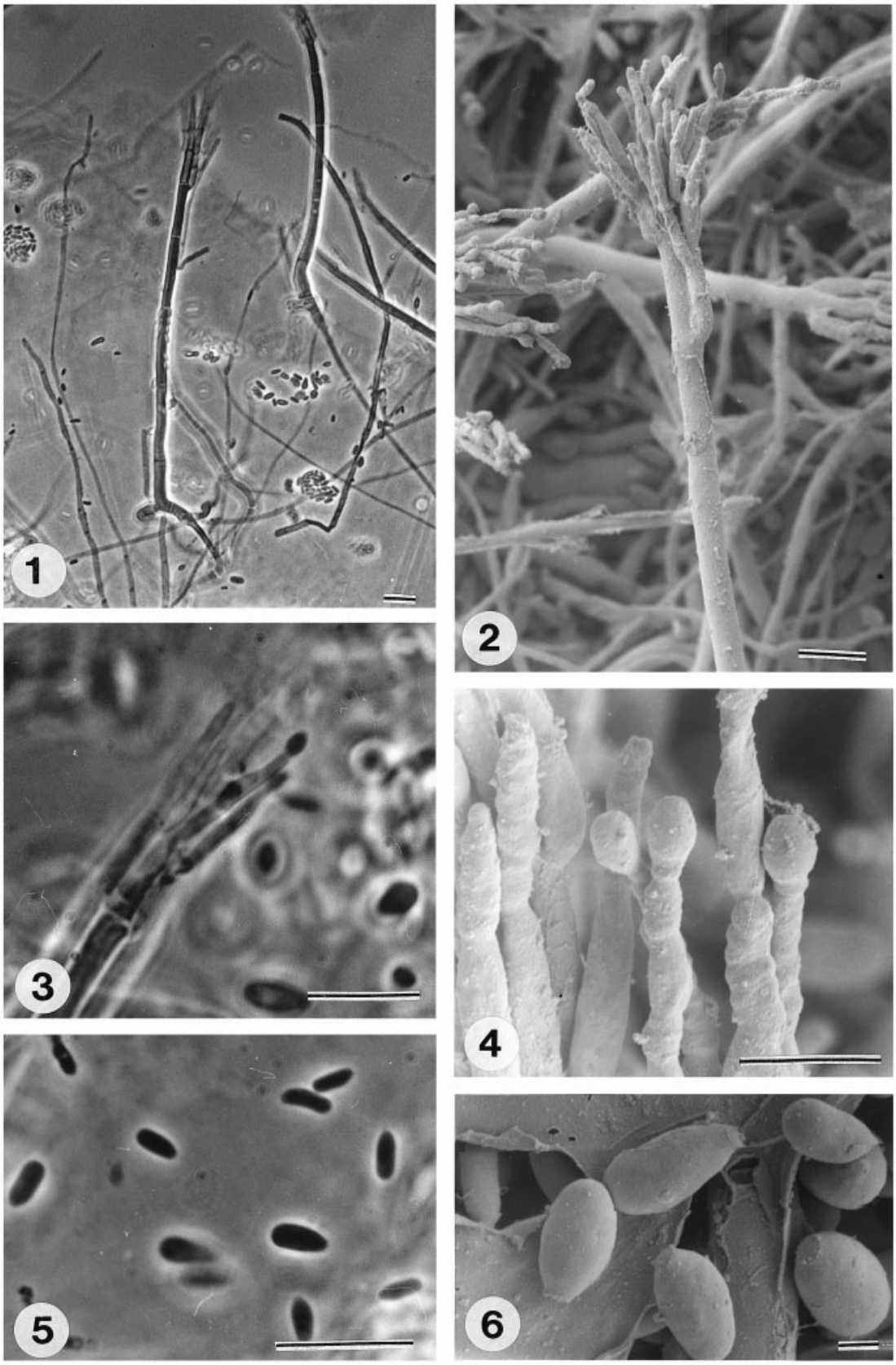
Most species in *Leptographium* are associated with insects, especially bark beetles (Solheim 1992*a*, *b*, 1995). The relationship between fungi and their insect vectors remains uncertain (Paine, Raffa & Harrington 1990, Hobson, Parmeter & Wood 1991, Lévieux *et al*. 1994, Raffa 1995, Wingfield, Harrington & Solheim 1995). In some cases it appears that the insects serve only as vectors of the fungi, which are essentially saprobic (Harrington 1988, 1993). Some evidence suggests that they play a role in tree death (Wingfield 1986) and in some cases they provide nutrition for the insects (Six & Paine 1996). In association with insects, species of *Leptographium* are known for their ability to cause blue-stain of lumber (Solheim & Långström 1991, Solheim 1992*a*, *b*, 1995). Furthermore, the three varieties of *L. wageneri* cause the serious, black stain root disease of conifers in the North Western United States (Cobb 1988, Harrington & Cobb 1984, Harrington 1993).

Species of *Leptographium* are generally known to inhabit conifers (Lagerberg *et al*. 1927, Kendrick 1962, Harrington 1988), although some exceptions are known (Davidson 1942, 1958, 1971, 1976, Jooste 1978, Weber *et al*. 1996). In the Northern Hemisphere several new species have recently been described from conifers (van der Westhuizen *et al*. 1995, Jacobs, Wingfield & Bergdahl 1997, Jacobs *et al*. 1998). In all cases, the species were found to be restricted to their relatively narrow niches. Surveys between 1988 and 1998 of dying *Abies sibirica* in Siberia have led to the consistent isolation of a *Leptographium* (Vetrova *et al*. 1992, Pashenova *et al*. 1994) from the galleries of the fir sawyer beetle *Monochamus urussovi* (*Coleoptera: Cerambycidae*). The aim of this study was to compare isolates of this species from Siberia with known species of *Leptographium* and establish its identity.

MATERIALS AND METHODS

A survey of dying *Abies sibirica* trees in Krasnoyarsk Territory (Central Siberia, Russia, 53–60° N, 90–94° E) resulted in the consistent isolation of an unknown species of *Leptographium* from the galleries of *M. urussovi*. Frequency of the *Leptographium* in *M. urussovi* galleries was 70–100% (Pashenova *et al*. 1995; 1998). Conidiophores of the fungus were found in all parts of *M. urussovi* galleries in trunks of Siberian fir. The ability of the *Leptographium* to develop in phloem and sapwood was confirmed by laboratory and field experiments (Pashenova *et al*. 1994).

Spore masses were transferred from the apex of conidiophores to 2% malt extract (MEA) (20 g Biolab malt extract, 20 g Biolab agar and 1000 ml distilled water) plates amended



Figs 1–6. *Leptographium sibiricum* (PREM 56399). **Fig. 1.** Conidiophore with a dark olivaceous stipe and complex conidiogenous apparatus (Bar = 10 μm). **Fig. 2.** Complex conidiogenous apparatus (Bar = 10 μm). **Fig. 3.** Conidiogenous cells showing false sympodial conidiogenesis (Bar = 10 μm). **Fig. 4.** Conidiogenous cells showing false sympodial conidiogenesis (Bar = 5 μm). **Fig. 5.** Conidia (Bar = 10 μm). **Fig. 6.** Conidia (Bar = 1 μm).

with 0.5 g l^{-1} cycloheximide. Resulting colonies were transferred to clean 2% MEA plates and incubated at 25 °C until the onset of sporulation. Fungal structures for microscopic examination were mounted on glass slides in lactophenol. Fifty measurements of each relevant morphological structure were made and ranges and averages computed. Colours were determined with the aid of colour charts (Rayner 1970).

The optimal temperatures for growth of representative isolates (CMW 4484, CMW 4481) was determined by inoculating eight MEA plates for each temperature with 6 mm diameter agar disks taken from the actively growing margins of a fresh isolates. The plates were incubated at temperatures of 5–35 ° at 5 ° intervals. Colony diameters were measured on the fourth and the eight day after inoculation and the colony diameter computed as an average of eight readings.

For scanning electron microscopy (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 Jeol JSM 840 Scanning Electron microscope.

Cycloheximide tolerance of isolates (CMW 4484, CMW 4481) was determined by growing them on 2% MEA amended with 0.5 g l^{-1} cycloheximide. Dishes were incubated in the dark at 25 ° for 8 days and two colony diameters were measured. Five replicate plates were used and the growth rate (mm day^{-1}) was determined based on the average of 10 diameter readings.

RESULTS

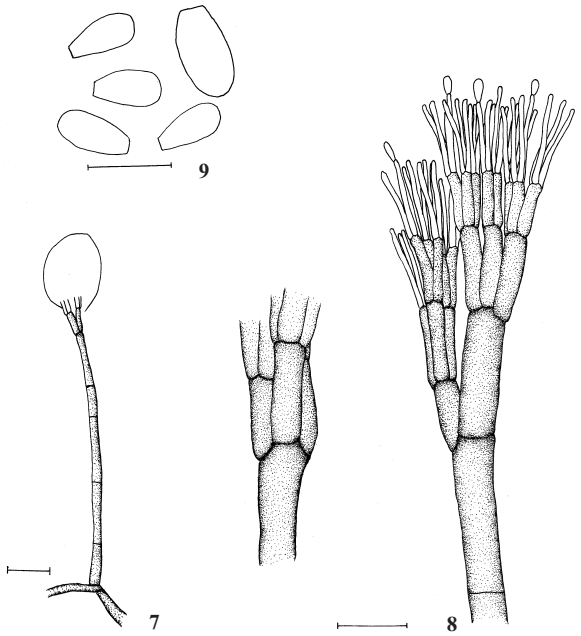
The *Leptographium* from *Abies sibirica* is characterized by short, light olivaceous conidiophores with up to three series of branches. It has an optimum growth temperature of 25 °C and can tolerate high concentrations of cycloheximide in culture. It is, furthermore, characterized by small oblong to obovoid conidia. Comparison with known species of *Leptographium* revealed that this species is new and it is, therefore, described as follows:

Leptographium sibiricum K. Jacobs & M. J. Wingf., **sp. nov**. (Figs 1–9)

Coloniae crescunt optime ad 25 °C. Conidiophora (109–)165(–238) µm longa, structurae rhizoidiformes absentes. Apparatus conidiogenus (26–)40(–56) µm longus, massa conidica exclusa, cum 2 vel 3 seriebus ramorum cylindricorum; ramis primariis 2 vel 3. Cellulae conidiogenae discretae, 2 vel 3 in quoque ramo, cylindricae, apicem versus parum attenuatae, (6–)13(–30) µm longae, (1–)2(–3) µm latae. Conidia oblonga, (2–)4(–6) × (1–)2(–3) µm.

Typus: **Russia**: Krasnoyarsk Territory, Taseevo, *ca* 57 ° N 94 ° E, isolated from egg chambers of *Monochamus urussovi* in the phloem of *Abies sibirica* damaged by the moth *Dendrolimus superans sibiricus*, July 1996, *V. P. Vetrova* (PREM 56399-holotypus).

Colonies with optimal growth at 25 °C on 2% MEA, reaching 31 mm diam in 7 days, no growth below 10 ° or above 35 °, able to withstand high concentrations of cycloheximide with a no reduction in growth on 0.5 g l^{-1} cycloheximide after 8 days at 25 ° in the dark. Colony dark olivaceous (19″f), margin smooth. Hyphae submerged or on top of solid medium with no aerial mycelia, light olivaceous to hyaline, smooth, not constricted at the septa, (2–)3(–7) µm. *Conidiophores* occurring singly, arising directly from the mycelium, erect, macronematous, mononematous, (109–)165(–238) µm long, rhizoid-like structures absent. Stipe light olivaceous, smooth, cylindrical, simple, 2–7-septate, (68–)128(–200) µm long (from first basal septum to below primary branches), 4.5–5.5 µm wide below primary branches, apical cell not swollen, (3–)5.5(–8) µm wide at base, basal cell not swollen. *Conidiogenous apparatus* (26–)40(–56) long, excluding the conidial mass, with 2 to 3 series of cylindrical branches; 2–3 primary branches, light olivaceous, smooth, cylindrical, aseptate, (8–)14(–25) µm long and (2–)4(–5) µm wide, secondary branches hyaline, light olivaceous, aseptate, (8–)11(–17) µm long, (2–)2.5(–3) µm wide, tertiary branches hyaline, aseptate, (5–)9(–12) µm long, (1–)2(–3) µm wide. *Conidiogenous cells* discrete, 2–3 per branch, cylindrical, tapering slightly at the apex, (6–)13(–20) µm long and (1–)2(–3) µm wide. Conidium development occurring through replacement wall building with holoblastic ontogeny and percurrent proliferation and delayed secession giving a false impression of sympodial proliferation (Minter, Kirk & Sutton 1982, 1983, van Wyk *et al*. 1988). *Conidia* oblong, (2–)4(–6) × (1–)2(–3) µm, conidia accumulating in slimy droplets at the apex of conidiogenous apparatus.



Figs 7–9. *Leptographium sibiricum* (CMW 4484). **Fig. 7.** Habit sketch of the conidiophore, Bar = 50 µm. **Fig. 8.** Conidiogenous apparatus, Bar = 10 µm. **Fig. 9.** Conidia, Bar = 10 µm.

Specimens examined: **Russia**: Krasnoyarsk Territory, Taseevo, *ca* 57° N 94° E, isolated from egg chambers of *M. urussovi* in the phloem of *A. sibirica* damaged by the Siberian moth (*Dendrolimus superans sibiricus*), July 1996; *V. P. Vetrova*, (CMW 4481; = DEG 30/96), Yartzevo, *ca* 60° N 90° E, isolated from a larval gallery of *M. urussovi* in phloem of *Abies sibirica*, Aug. 1993. *V. P. Vetrova*, (CMW

4484; = DEG 27/94), Taseevo, *ca* 57° N 94° E, isolated from pupal chambers of *M. urussovi* in sapwood damaged by the Siberian moth, Jul. 1996, *V. P. Vetrova*, (CMW4487; = DEG 06/96).

All cultures are maintained in the culture collection of the Forestry and Agricultural Biotechnology Institute (UP), Pretoria.

DISCUSSION

Leptographium sibiricum has short delicate conidiophores similar to those found in *L. brachiatum*, *L. elegans*, *L. antibioticum* and the *Leptographium* anamorphs of *Ophiostoma grandifoliae* and *O. leptographioides* (Davidson 1942, Kendrick 1962, Davidson 1976, Wingfield, Crous & Tzean 1994). It can, however, be distinguished from these species on various morphological characters. *L. sibiricum* and *L. antibioticum* are both characterized by short conidiophores, although those of *L. antibioticum* can be slightly longer (Table 1). Furthermore, both species have oblong to obovoid conidia of equal length. These species can be distinguished by the number of primary branches of the conidiophores. *L. sibiricum* has two or three branches, whereas *L. antibioticum* can have up to five primary branches. These species can also be distinguished ecologically; *L. antibioticum* has been isolated from pine and spruce in North America and is not known to be associated with any insects (Kendrick 1962, Mielke 1979, Harrington 1988). In contrast, *L. sibiricum* appears to be consistently associated with the siberian fir sawyer beetle on fir in Siberia.

Leptographium sibiricum is morphologically similar to *L. brachiatum*, which has conidiophores of a similar length. They also have conidia of a similar shape and size (Table 1). These species can be distinguished by the presence of rhizoids in *L. brachiatum* and their absence in *L. sibiricum*. The lateral branches on the conidiophores, one of the most obvious characters of *L. brachiatum*, are absent in *L. sibiricum*. As in the case of *L. antibioticum*, *L. brachiatum* originates from spruce in North America and is not associated with insects (Kendrick 1962), while *L. sibiricum* originates from fir and is associated with insects.

Leptographium sibiricum and *L. elegans* are morphologically similar and cannot be distinguished based on conidiophore length, conidium shape and size or the number of primary conidiophore branches. Both species are characterized by the absence of rhizoids. However, these species can be distinguished by the presence of a *Sporothrix* synanamorph in *L. elegans*, and the absence of these structures in *L. sibiricum*. Furthermore, these species also differ in host specificity and insect association. *L. elegans* occurs on *Chamaecyparis formosensis* wood and has not been associated with insect activity (Wingfield *et al*. 1994).

Leptographium sibiricum, *Ophiostoma grandifoliae* and *O. leptographioides* cannot be distinguished on conidiophore length or conidial shape (Davidson 1942, 1976). However, the conidia of *O. leptographioides* are almost twice as long ((4–)6(–12) µm) as those of *O. grandifoliae* ((2.5–)3.5(–4) µm) and *L. sibiricum* ((2–)4(–6) µm). *O. leptographioides* and *O. grandifoliae* are characterized by rhizoids at the bases of the conidiophores, in contrast to *L. sibiricum* where they are absent. Both *O. grandifoliae* and *O. leptographioides* have been isolated from non-coniferous hosts (Davidson 1942, 1976), while *L. sibiricum* is only known to occur on *Abies sibiricus*. Also, *L. sibiricum* is consistently associated with an insect, while *O. grandifoliae* and *O. leptographioides* have no known insect associates (Davidson 1942, 1976).

The fir sawyer beetle appears to be the main vector of *L. sibiricum* in Central Siberia. This beetle is one of the most destructive xylophages in Europe and Asia. Its distribution extends from Finland and Poland in the west to the Russian shore of the Pacific Ocean, excluding Chukotka and Kamchatka, in the east. The southern boundary of the area corresponds with a zone of conifer forests in the European part of Russia and runs to the northern regions of Kazakhstan, Mongolia, China and Korea in Asia (Isaev *et al*. 1988). Kasnoyarsk Territory, where our collections were made, is at the centre of *M. urussovi*'s distribution. The fir sawyer beetle mainly inhabits dark coniferous forests (taiga), and although it can infest many conifers belonging to the *Pinaceae*, the

Table 1. Characteristics of *L. sibiricum* compared with those of morphologically similar species.

	L. sibiricum	*L. antibioticum*	*L. brachiatum*	*L. elegans*	*O. grandifoliae*	*O. leptographioides*
Substrate	*Abies sibirica*	*Pinus contorta, P. monticola, Abies lasiocarpa, Thuja plicata*[a]	*Pseudotsuga menziesii, Picea mariana*[b]	*Chamaecyparis formosensis*[c]	*Fagus grandifolae*[d]	*Quercus*[e]
Insect association	*Monochamus urrussovi*	Not known	Not known	Not known	Not known	Not known
Conidiophore length	(109–)165(–238) µm	(110–)223(–407) µm	(73–)116(–186) µm	(102–)234(–432) µm	(80–)179(–397) µm	(77–)140(–237) µm
Conidium shape	oblong to obovoid	oblong to obovoid	oblong to obovoid	oblong	obovoid	oblong to obovoid
Conidium size	(2–)4(–6) µm	(2.5–)4(–5) µm	(3–)4(–5.5) µm	(3–)4(–5) µm	(2.5–)3.5(–4) µm	(4–)6(–12) µm
Teleomorph	absent	absent	absent	absent	*Ophiostoma*	*Ophiostoma*
Rhizoids	absent	present	present	absent	present	present
Primary branches	2–3	2–5	2	2–3	2–3	2–3
Lateral branches	absent	absent	present	absent	absent	absent

[a] Kendrick (1962), Mielke (1979) and Harrington (1988).
[b] Kendrick (1962).
[c] Wingfield, Crous & Tzean (1994).
[d] Davidson (1976).
[e] Davidson (1942).

Siberian fir is the main host plant of the beetle within Siberia (Isaev *et al*. 1988). The role of *L. sibiricum* in the life-cycle of the beetle is not known, although it does contribute to blue-stain of the trees.

The first sawyer beetle breeds in the trunks of fir trees. Female beetles lay eggs in the phloem of the trunk, and the larvae bore galleries in the phloem, sapwood and heartwood. Pupal chambers are in the sapwood near to surface of trunk. Upon leaving the pupal chamber, juvenile (imago stage) beetles undergo maturation feeding in the crowns of trees. While feeding, the beetles injure the branches. Therefore, additional feeding on the crowns results in the desiccation of branches and weakened trees. The weakened trees then become susceptible to stem colonization by the beetles. It has been suggested that fungi, carried by *M. urussovi*, might play the main role in the desiccation of branches (Isaev *et al*. 1988).

Despite the constant association between *L. sibiricum* and the fir sawyer beetle, *L. sibiricum* was not found in branches injured by juvenile beetles when this material was collected in the forests. It appears that *L. sibiricum* is inoculated into the phloem of Siberian fir during oviposition. This results in the development of lesions 40–60 mm across, 2–3 times greater than the control, after wound inoculations (Vetrova *et al*. 1992, 1999, Pashenova *et al*. 1994). Very little is known about the biology of *L. sibiricum*. The fungus appears too be inoculated into stressed trees during oviposition. Phoretic mites or some other secondary vectors might transmit *L. sibiricum* to trees. Such an association has been suggested for species of *Ophiostoma* found in the galleries of *Monochamus* species in North America (Wingfield & Blanchette 1983). Additional studies on the pathogenicity and insect associates of *L. sibiricum* are required.

ACKNOWLEDGEMENTS

We thank the National Research Foundation (NRF), and members of the Tree Pathology Co-operative Programme (TPCP) for financial support. We acknowledge Hugh Glen for providing the Latin diagnosis.

REFERENCES

Cobb, F. W. (1988) *Leptographium wageneri*, cause of black-stain root disease: a review of its discovery, occurrence and biology with emphasis on pinyon and ponderosa pine. In *Leptographium Root Diseases on Conifers*: 41–62. American Phytopathological Society, St Paul, MN.

Davidson, R. W. (1942) Some additional species of *Ceratostomella* in the United States. *Mycologia* **34**: 650–662.

Davidson, R. W. (1958) Additional species of *Ophiostomataceae* from Colorado. *Mycologia* **50**: 661–670.

Davidson, R. W. (1971) New species of *Ceratocystis*. *Mycologia* **63**: 5–15.

Davidson, R. W. (1976) Sapwood staining fungi from two tree species. *Memoirs of the New York Botanical Garden* **28**: 45–49.

Harrington, T. C. (1988) *Leptographium* species, their distributions, hosts and insect vectors. In *Leptographium Root Diseases on Conifers*: 1–39. American Phytopathological Society, St Paul, MN.

Harrington, T. C. (1993) Diseases of conifers caused by species of *Ophiostoma* and *Leptographium*. In *Ceratocystis and Ophiostoma: taxonomy, ecology and pathogenicity* (M. J. Wingfield, K. A. Seifert & J. F. Webber, eds). American Phytopathological Society, St Paul, MN.

Harrington, T. C. & Cobb, F. W. (1984) Host specialization of three morphological variants of *Verticicladiella wageneri*. *Phytopathology* **74**: 286–290.

Hobson, K. R., Parmeter, J. R. & Wood, D. L. (1991) Bluestain fungi and the xylem occlusion enigma. In *Proceedings of the North American Forest Insect Work Conference* (D. C. Allen & L. P. Abrahamson, eds): 156–157.

Isaev, A. S., Rozhkov, A. S. & Kiselev, V. V. (1988) [Fir Sawyer beetle *Monochamus urussovi* (Fisch.).] Nauka, Novosibirsk [in Russian.]

Jacobs, K., Wingfield, M. J. & Bergdahl, D. (1997) A new species of *Ophiostoma* from North America, similar to *Ophiostoma penicillatum*. *Canadian Journal of Botany* **75**: 1315–1322.

Jacobs, K., Wingfield, M. J., Wingfield, B. D. & Yamaoka, Y. (1988) Comparison of *Ophiostoma huntii* and *O. europhioides* and description of *O. aenigmaticum* sp. nov. *Mycological Research* **102**: 289–294.

Jooste, W. J. (1978) *Leptographium reconditum* sp. nov. and observations on conidiogenesis in *Verticladiella*. *Transactions of the British Mycological Society* **70**: 152–155.

Kendrick, W. B. (1962) The *Leptographium* complex. *Verticicladiella* S. Hughes. *Canadian Journal of Botany* **40**: 771–797.

Lagerberg, T., Lundberg, G. & Melin, E. (1927) Biological and practical researches into blueing in pine and spruce. *Svenska Skogsvårdsföreningens Tidskrift* **25**: 145–272, 561–691.

Lévieux, J., Piou, D., Cassier, P., André, M. & Guillaumin, D. (1994) Association of phytopathogenic fungi for the scots pine (*Pinus sylvestris* L.) with the European pine weevil *Hylobius abietis* (L.) (*Col., Curculionidae*). *The Canadian Entomologist* **126**: 929–936.

Mielke, M E. (1979) *Verticicladiella species and associated root stain and decay fungi isolated from symptomatic Northern Rocky Mountain conifers*. MSc thesis, University of Idaho, Moscow.

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.

Paine, T. D., Raffa, K. F. & Harrington, T. C. (1990) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* **42**: 179–206.

Pashenova, N. V., Vidryakova, G. A. & Vetrova, V. P. (1994) [Phytopathogenic micromycetes associated with black fir sawyer]. *Lesovedenie* **3**: 39–47. [In Russian.]

Pashenova, N. V., Vetrova, V. P., Matrenina, R. M. & Aphanasova, E. N. (1995) The blue-stain fungi associated with aggressive xylophagous insects on conifers in Middle Siberia (Russia). In *Bark Beetles, Blue-stain Fungi, and conifer Defence System, Proceedings IUFRO S7.01 Symp., 31 July–2 Aug., 1995*: Aktuelt fra Scogforsk, Ås.

Pashenova, N. V., Vishnyakova, Z. V. & Vetrova, V. P. (1998) Structural changes of bark and wood mycobiota in conifers after damage by Siberian moth and xylophagous pests. *Lesovedenie* **4**: 11–19. [In Russian.]

Raffa, K. F. (1995) Bark beetles, fungi, trees and humans: Four perspectives, four agendas. In *Proceedings of a Symposium held at the Norwegian Forest Research Institute* (E. Christiansen, ed.): 7–9. Ås.

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

Six, D. L. & Paine, T. D. (1996) *Leptographium pyrinum* is a mycangial fungus of *Dendroctonus adjunctus*. *Mycologia* **88**: 739–744.

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

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

Solheim, H. (1995) Blue-stain fungi associated with the spruce beetles *Dendroctonus rufipennis*. In *Proceedings of a symposium held at the Norwegian Forest Research Institute* (E. Christiansen, ed): 43. Ås.

Solheim, H. & Långström, B. (1991) Blue-strain fungi associated with *Tomicus piniperda* in Sweden and preliminary observations on their pathogenicity. *Annals of Scientific Forestry* **48**: 149–156.

van der Westhuizen, K., Wingfield, M. J., Yamaoka, Y., Kemp, G. H. J. & Crous, P. W. (1995) A new species of *Ophiostoma* with a *Leptographium* anamorph from Larch in Japan. *Mycological Research* **99**: 1334–1338.

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

Vetrova, V. P., Pashenova, N. V. & Grodnitsky, D. L. (1992) [Response of Siberian fir to inoculation with fungi-simbionts of black fir sawyer]. *Lesovedenie* **3**: 24–32. [In Russian.]

Vetrova, V. P., Stasova, V. V. & Pashenova, N. V. (1999) Effect of defoliation on resistance response of *Abies sibirica* Ledeb. to inoculation with blue stain-fungi. In *Physiology and Genetics of Tree–Phytophage Interactions, Proceedings IUFRO S7.01 Symp., 31 Aug.–5 Sept., 1997*: 287–297. INRA, Paris.

Weber, G., Spaaij, F. & Wingfield, M. J. (1996) *Leptographium costaricense* sp. nov., a new species from roots of *Talauma sambuensis*. *Mycological Research* **100**: 732–736.

Wingfield, M. J. (1986) Pathogenicity of *Leptographium procerum* and *L. terebrantis* on *Pinus strobus* seedlings and established trees. *European Journal of Forest Pathology* **16**: 299–308.

Wingfield, M. J. & Blanchette, R. A. (1983) The pine-wood nematode, *Bursaphelenchus xylophilus*, in Minnesota and Wisconsin: insect associates and transmission studies. *Canadian Journal of Forest Research* **13**: 1068–1976.

Wingfield, M. J., Crous, P. W. & Tzean, S. S. (1994) *Leptographium elegans*: a new species from Japan. *Mycological Research* **98**: 781–785.

Wingfield, M. J., Harrington, T. C. & Solheim, H. (1995) Do conifer bark beetles require fungi to kill trees? In *Bark Beetles, Blue-stain Fungi, and Conifer Defence System, Proceedings IUFRO S7.01 Symp., 31 July–2 Aug., 1995* (E. Christiansen, ed.): 6. Ås.

Corresponding Editor: P. M. Kirk