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FULL PAPER

Nobuaki Ohtaka · Hayato Masuya · Shigeru Kaneko
Yuichi Yamaoka

Two *Ophiostoma* species associated with bark beetles in wave-regenerated *Abies veitchii* forests in Japan

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Abstract Two species of *Ophiostoma* were isolated from four bark beetles (i.e., *Cryphalus montatus*, *C. piceae*, *Dryocoetes hectographus*, and *Polygraphus proximus*) infesting *Abies veitchii* and from their galleries in the wave-regenerated forests in the central part of the main island (Honshu) of Japan. One of them is described here as a new species, *Ophiostoma subalpinum*, and the other is identified as *O. davidsonii*, newly reported in Japan. *Ophiostoma subalpinum* is characterized by short ostiolar hyphae, oblong or allantoid ascospores enclosed in a thin, hyaline sheath, and a *Pesotum* anamorph.

Key words *Ophiostoma davidsonii* · *Ophiostoma subalpinum* · Ophiostomatoid fungi · *Pesotum* · Wave regeneration

Introduction

Ophiostomatoid fungi (e.g., *Ophiostoma* Syd. & P. Syd., *Ceratocystis* Ellis & Halst., and *Ceratocystiopsis* H.P. Upadhyay & W.B. Kendr.) are commonly associated with bark beetles (Coleoptera: Scolytidae) that particularly infest conifers (Francke-Grosmann 1963; Paine et al. 1997). These fungi include economically important species that cause sap stain (Lagerberg et al. 1927; Gibbs 1993) or tree mortality (Harrington 1988; Brasier 1991).

From 1998 to 2000, we isolated several species of *Ophiostoma* from bark beetles infesting *Abies veitchii* Lindl. (Veitch fir, "Shirabe" in Japanese) in the course of the survey of fungi concerning the wave regeneration ("Shimagare" in Japanese) phenomenon at natural *Abies* forests in subalpine areas of the central part of the main island (Honshu) of Japan. From two collecting sites of wave-regenerated forests, two *Ophiostoma* species were isolated in high frequencies from bark beetles and their galleries in the trunks of adult *A. veitchii*: one was found to be a new species and other was identified as *O. davidsonii* (Olchow. & J. Reid) H. Solheim, which has been recorded only in Canada. The purpose of this article is to describe the morphological and cultural characteristics of these two *Ophiostoma*, proposing a new species.

Materials and methods

Sampling and isolation of fungi

Two collecting sites were chosen at central Honshu of Japan: Mt. Asahi, Oku-chichibu, Yamanashi Prefecture (35°52′N, 138°39′E) and Mt. Shimagare in Yatsugatake Mts., Nagano Prefecture (36°04′N, 138°20′E). Both sites were located in wave-regenerated forests dominated first by *A. veitchii* and second by *A. mariesii* Masters (Maries fir, "Oh-shirabiso" in Japanese). Both sites were at an elevation of 2400 m.

Mature *A. veitchii* infested by adult bark beetles, but having green needles and newly developed current-year shoots, were felled at two sites. On Mt. Asahi, one tree was felled each time on June 11 and July 23, 1998, on June 23 and July 29, 1999, and two trees on September 7, 2000. On Mt. Shimagare, two trees were felled on August 3, 1999. Then, the whole trunks of the trees were brought back to the laboratory for isolation after cutting them into 1-m-long logs.

N. Ohtaka (✉) · Y. Yamaoka
Laboratory of Plant Parasitic Mycology, Institute of Agriculture and Forestry, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan
Tel. +81-298-53-4707; Fax +81-298-53-4707
e-mail: ohtaka@bres.tsukuba.ac.jp

H. Masuya
Tohoku Research Center, Forestry and Forest Products Research Institute, Iwate, Japan

S. Kaneko
Forestry and Forest Products Research Institute, Ibaraki, Japan

Contribution no. 163, Laboratory of Plant Parasitic Mycology, Institute of Agriculture and Forestry, University of Tsukuba

Isolations were done from adult bark beetles and their galleries. Bark beetles collected from *A. veitchii* on Mt. Asahi were *Cryphalus montatus* Nobuchi and *Dryocoetes hectographus* Reitter and *Polygraphus proximus* Blandford, while those from Mt. Shimagare were *C. piceae* Ratzeburg and *D. hectographus*. *Cryphalus montatus* and *C. piceae* were dominantly collected, but *D. hectographus* and *P. proximus* were rare.

Living beetles were collected from their galleries and individually placed onto 1% malt extract agar (MA) plates (10 g Difco malt extract, 15 g agar, and 1 l distilled water). Small pieces of wood (2 × 2 × 2 mm) were taken with a sterilized scalpel from the egg galleries constructed by the adult beetles and placed on 1% MA plates. After incubation, pure cultures were obtained by picking up hyphae or conidia on the plates with a sterilized tungsten needle and transferring these to plates with 2% MA (20 g malt extract, 15 g agar, and 1 l distilled water) and 1% Pablum agar (PA; 10 g Pablum mixed cereal, 15 g agar, and 1 l distilled water). All plates were incubated at 15°C in the dark. Where necessary, small pieces of autoclaved twigs or bark of *A. veitchii* were added onto the plates to promote perithecial production.

Morphological observations

Perithecial and conidiomatal structures were examined by a differential interference contrast (DIC) microscope (Leica DMLB) and a scanning electron microscope (SEM). For SEM observation, 8-mm-diameter agar disks were cut from the colonies with a sterilized scalpel and fixed in 3% glutaraldehyde overnight. These disks were then dehydrated in graded ethanol and ethanol-isoamylacetate series. The materials were subsequently critical point dried, coated with platinum-palladium at 25-nm-thickness, and examined using a Hitachi S-4200 scanning electron microscope operating at 15 kV.

Temperature for growth

The growth rate of the selected isolates was examined at 4°, 10°, 15°, 20°, 25°, and 30°C in the dark. A 4-mm-diameter mycelial disk from the actively growing culture was put in the center of 2% MA plates and incubated at different temperatures. Three replicates were prepared for each isolate. Average radial colony diameter was measured in three different directions in each plate after 1-week incubation, and growth rates were calculated as millimeters per day (mm/day).

Cycloheximide tolerance for growth

Cycloheximide tolerance was examined at 20°C using the method of Harrington (1981). The isolates were incubated on 2% MA plates containing 1 μg/ml cycloheximide. Growth rate at 20°C was calculated by three replicates and compared with that on the plates without cycloheximide.

Taxonomy

An undescribed *Ophiostoma* species and *O. davidsonii* are described using Japanese isolates and comparisons were made in the literature for these and related species. Description of the species was made using the cultures on autoclaved bark of *A. veitchii*. Color notations follow Rayner (1970).

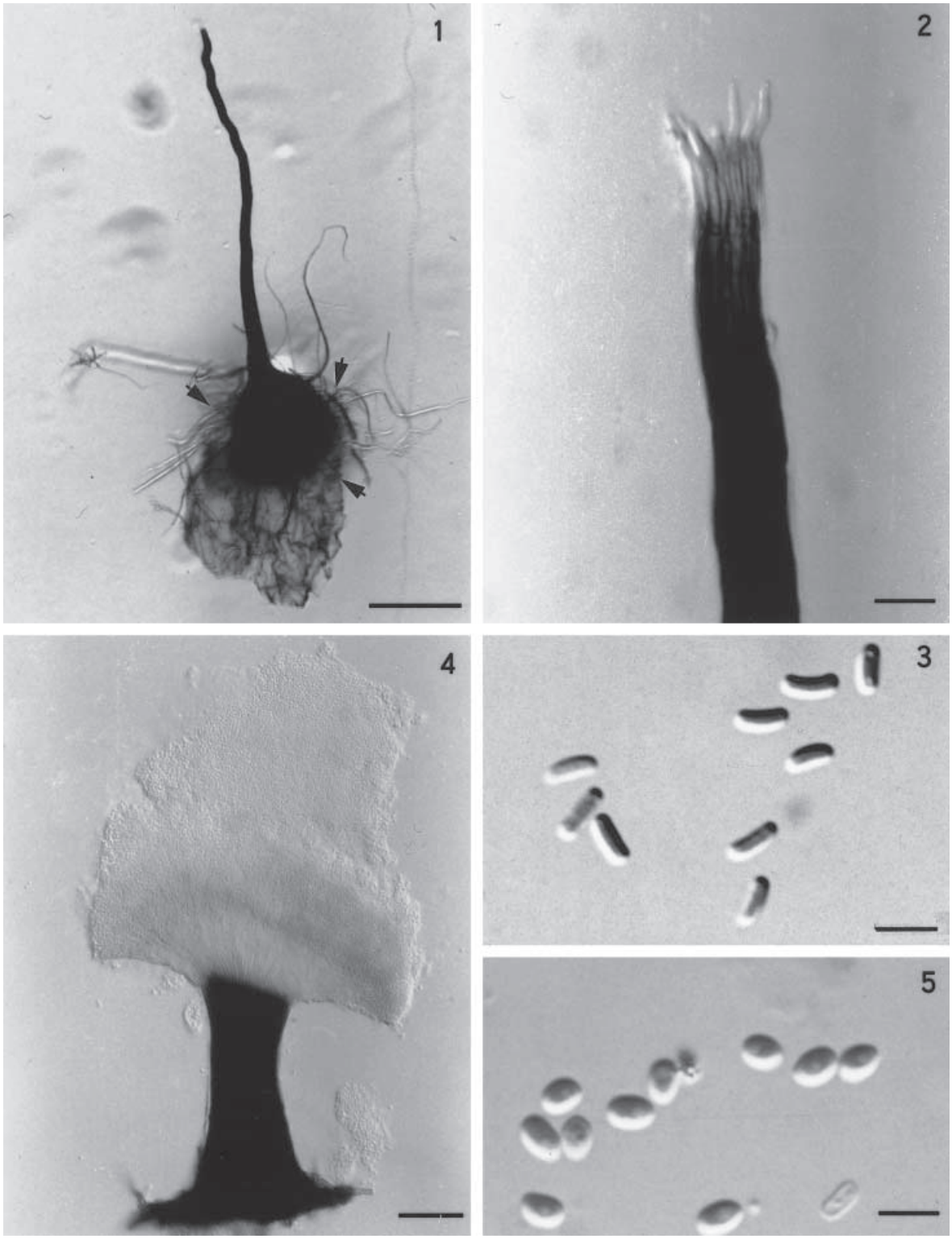
Ophiostoma subalpinum Ohtaka & Masuya, sp. nov.
Figs. 1–5, 11

Anamorphosis: *Pesotum* sp.

Perithecia superficialia, basi nigro-brunnea, globosa vel subglobosa, 85–195 μm diam, appendicibus fuscis hyphoideisque ornata; colla nigro-brunnea, cylindracea, recta vel curvata, sursum gradatim attenuata, 355–650 μm longa hyphis ostiolaribus inclusa, ad basim 23–40 μm lata, ad apicem 9–17 μm lata; hyphae ostiolares 4–8 divergentes, bubalino-flavae vel hyalinae, aseptatae, 5–16 μm longae. Asci deliquescentes, non visi. Ascosporae hyalinae, unicellulares, oblongae, aspectu laterali allantoideae videntur, frontali ellipsoideae, vertice globosae, aliquando vagina tenui hyalina cinctae, 3.0–4.0 × 1.5–2.0 μm, ad apicem collorum in guttulam aggregatae. Synnemata 185–340 μm longa, ad basim olivaceo-nigra. Cellulae conidiogenae cylindraceae, terminales, annellidicae, 1.0–1.7 μm latae, 9–14 μm longae. Conidia hyalina, aseptata, ellipsoidea vel ovidea, 2.7–4.2 × 1.7–2.5 μm, in muco aggregata.

Perithecia mostly formed on autoclaved barks of *A. veitchii*, rarely formed on MA/PA; basal part-blackish brown (1''''m), globose to subglobose, 85–195 μm in diameter, ornamented with cinnamon-brown (15'k) hyphal appendages (Fig. 1); necks blackish-brown, nearly cylindrical or tapered, straight or curved, 355–650 μm long including ostiolar hyphae, 23–40 μm wide at the base, 9–17 μm wide at the tip; ostiolar hyphae 4–8, divergent, buff-yellow (19d) or hyaline, aseptate, 5–16 μm long (Fig. 2). Asci deliquescent, not seen. Ascospores hyaline, aseptate, oblong, or allantoid in side view (Fig. 3), ellipsoidal in face view, globose in end view, enclosed in a thin, hyaline sheath, 3.0–4.0 × 1.5–2.0 μm, aggregating in a droplet at the tip of the necks. Synnemata (Fig. 4) rarely formed, composed of a robust stipe and a subspherical capitulum, simple or rarely branched, olivaceous-black (21''''m) at base, gradually becoming hyaline toward apex, 185–340 μm long including hyaline capitulum, 60–180 μm wide at base, tapering to 35–80 μm wide near the apex, and flaring to 90–210 μm wide at a capitulum (Fig. 4). Conidiophores unbranched or scarcely branched. Conidiogenous cells cylindrical, terminal, annellidic, 9–14 μm long, 1.0–1.7 μm wide (see Fig. 11). Conidia hyaline, aseptate, ellipsoidal, or ovoid (Fig. 5), 2.7–4.2 × 1.7–2.5 μm, aggregated in a slimy mass. *Hyalodendron*-like *Sporothrix* synanamorph absent.

Colonies on 2% MA cinnamon (15''); submerged vegetative hyphae cinnamon-brown, branched, septate, interwoven, 1.7–3.5 μm in diameter. Growth rate of colonies on 2% MA 3.6–4.3 (average, 3.9) mm/day at 20°C. Optimal growth on 2% MA at 20°C, and no growth at 4° and 30°C. Resistant



Figs. 1–5. *Ophiostoma subalpinum* MAFF 410923, DIC. **1** Perithecium with hyphal appendages (*arrows*). **2** Tip of perithecial neck. **3** Ascospores. **4** Synnema of *Pesotum* anamorph. **5** Conidia. *Bars* **1** 100 μm; **2** 10 μm; **3**, **5** 5 μm; **4** 50 μm

to cycloheximide with approximately 80% reduction in growth on 2% MA with 1 μg/ml cycloheximide at 20°C.

Holotype: TFM:FPH 7521, dried culture of MAFF 410923 grown on 2% MA with autoclaved bark of *A. veitchii*, isolated by N. Ohtaka, August 2, 1999, from a drop of ascospores obtained from *Abies veitchii* infested by *Cryphalus montatus*, Mt. Asahi, Yamanashi Prefecture, Japan.

Isotype: TSH-C1501 (Mycological herbarium, Institute of Agriculture and Forestry, University of Tsukuba, Japan).

Table 1. Comparison of *Ophiostoma subalpinum* with related species

Characters	Unit	Species		
		O. subalpinum	*O. piceae*[a]	*O. torticiliata*[b]
Perithecial base	Width (μm)	85–195	80–225 (–280)	150–250
Perithecial neck	Length (μm)	355–650	500–2000	(400–) 700–1500
Ostiolar hyphae	Length (μm)	5–16	10–25 (–40)	Up to 135
	Number	4–8	15–25	No data
Ascospores	Size (μm)[c]	3–4 × 1.5–2	2–5 × 1.5–2	2.5–3.5 × 1–1.5
	Shape	Oblong or allantoid	Oblong, lunate, or allantoid	Lunate or orange section shaped
Genus name of anamorph		*Pesotum*	*Pesotum*, *Sporothrix*	*Pesotum*
Synnemata	Length (μm)	185–340	470–1200 (–1500)[d]	Up to 1200
Conidia	Size (μm)	2.7–4.2 × 1.7–2.5	2.5–6 × 1–2.5[d]	2.5–4 × 1–2
	Shape	Ellipsoidal or ovoid	Ellipsoidal, oblong, or allantoid[d]	Clavate, ovoid, or oblong
Host		*Abies veitchii*	Various	*Populus balsamifera*

[a] Combined data from the present paper, Hunt (1956), and Upadhyay (1981)
[b] Combined data from Olchowecki and Reid (1974) and Upadhyay (1981)
[c] Including sheath
[d] Data of *Pesotum* synanamorph

Etymology: Refers to the distributing zone of the fungus.

Additional specimens examined: TSH-C1502, dried culture of MAFF 410924, isolated by N. Ohtaka, June 26, 1999, from a drop of ascospores obtained from *A. veitchii* infested by *C. montatus*, Mt. Asahi, Yamanashi Prefecture, Japan; TSH-C1503, dried culture of MAFF 410925, isolated by N. Ohtaka, August 7, 1999, from a drop of ascospores obtained from *A. veitchii* infested by *C. piceae*, Mt. Shimagare, Nagano Prefecture, Japan.

Morphological characteristics of *O. subalpinum* were similar to those of *O. piceae* and *O. torticiliata* (Olchow. & J. Reid) Seifert & G. Okada (Olchowecki and Reid 1974). These three species are characterized by divergent ostiolar hyphae, oblong or curved ascospores, and *Pesotum* anamorphs. Table 1 shows the comparisons of the main characteristics of *O. subalpinum*, *O. piceae*, and *O. torticiliata*. We examined several cultures and dried specimens (indicated with *) of *O. piceae* isolated in Japan (MAFF 41055, 410667, 410668, 410669; TSH-C29*, 33*) and Europe (no. 15866 from Dr. T. Kowalski, Poland; four isolates from Dr. K. Przybyl, Poland) for comparative study.

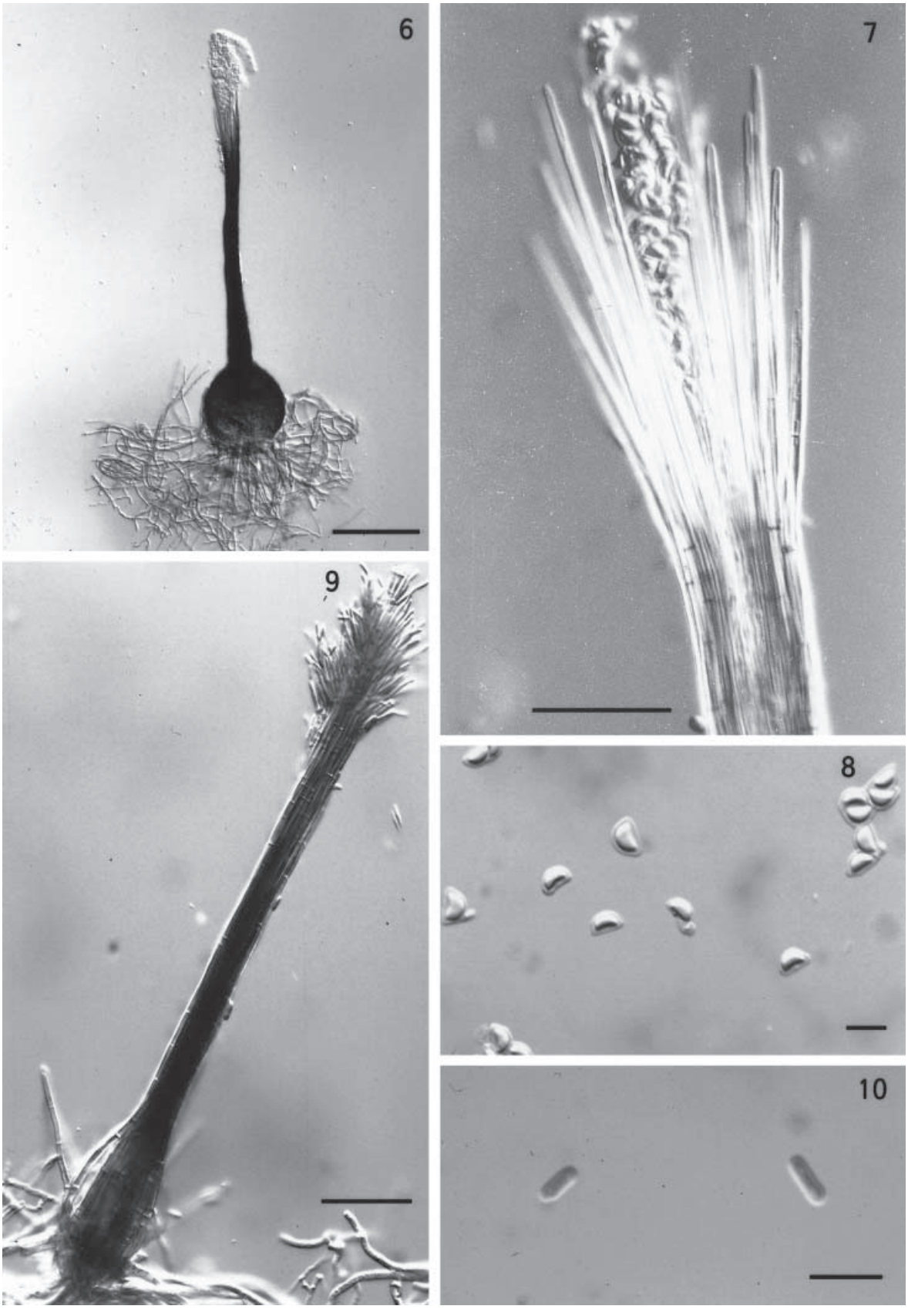
Ophiostoma subalpinum can be distinguished from the two related species by the following characteristics. Ostiolar hyphae of *O. subalpinum* are relatively shorter and their number is smaller than those of the other two species. Particularly, the ostiolar hyphae of *O. torticiliata* are apparently longer than those of *O. subalpinum*. Perithecial necks of *O. subalpinum* are shorter than those of the other two species. Ascospores of *O. subalpinum* are oblong or allantoid, whereas those of *O. torticiliata* are lunate or orange section shaped and have more distinct sheaths (Olchowecki and Reid 1974; Upadhyay 1981).

Morphological characteristics of the anamorphic states also serve as one of the keys to distinguish these species. Conidial formation of *O. subalpinum* on media (MA and PA with autoclaved bark of *A. veitchii*) is less abundant, while that of *O. piceae* in our experiments and *O. torticiliata* (Olchowecki and Reid 1974) is abundant. Synnemata of the *Pesotum* anamorph of *O. subalpinum* are distinctly shorter than those of the other two species. The *O. piceae* complex consists of morphologically and phylogenetically related species; i.e., *O. piceae* s. str., *O. canum* (Münch) Syd. & P. Syd., *O. floccosum* Math.-Kaarik, *O. setosum* Uzunovic et al., *O. querci* (Georgév.) Nannf., *O. catonianum* (Goid.) Goid., *O. ulmi* (Buisman) Nannf., *O. novo-ulmi* Brasier, and *O. himal-ulmi* Brasier & M. D. Mehrotra (Harrington et al. 2001). All the members of the *O. piceae* complex have *Hyalodendron*-like *Sporothrix* synanamorphs but *O. subalpinum* does not. The existence of the *Sporothrix* synanamorph is a remarkable feature for distinguishing the *O. piceae* complex from *O. subalpinum*.

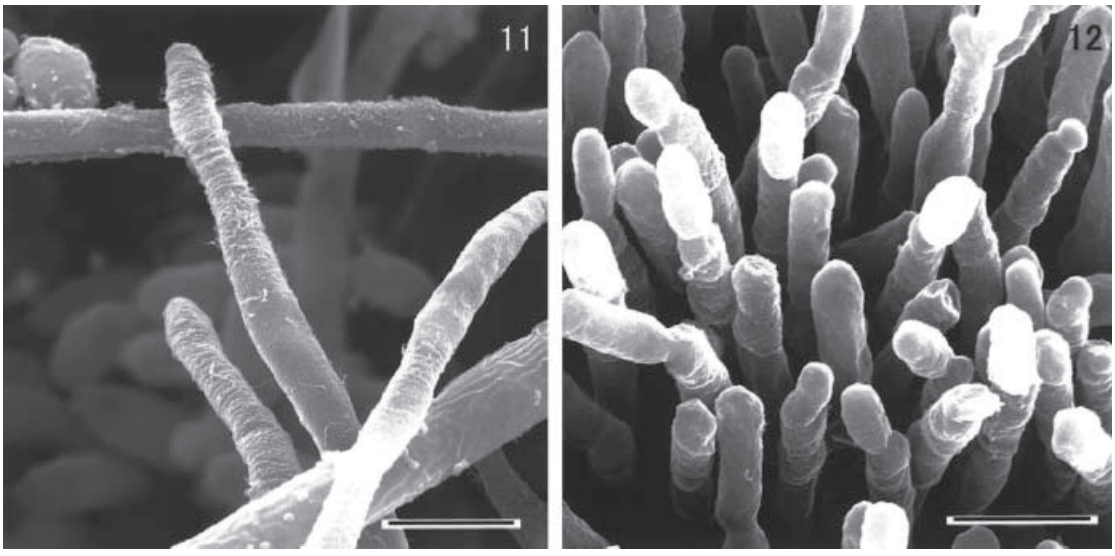
Ophiostoma subalpinum was isolated at the highest frequency from all bark beetle species examined and their galleries in the wood of *A. veitchii* at both sites.

Ophiostoma davidsonii (Olchow. & J. Reid) H. Solheim, Nord. J. Bot. 6: 203, 1986. Figs. 6–10, 12
≡*Ceratocystis davidsonii* Olchow. & J. Reid, Can. J. Bot. 52: 1698, 1974. Anamorph: *Pesotum* sp.

Perithecia superficial on autoclaved *A. veitchii* barks; basal part yellowish-olive (23''k) to olive (21''m), globose to subglobose, 85–145 μm in diameter (Fig. 6); necks yellowish-olive, straight, 220–290 μm long including ostiolar hyphae, expanding into ostiolar hyphae (Figs. 6, 7); ostiolar hyphae yellowish-olive at the base, light olive-gray (23''''d) to hyaline at the tip, tapered, septate, 60–100 μm long (Fig. 7). Asci deliquescent, not seen. Ascospores hyaline, aseptate, orange section shaped to hemispherical in side view, ellipsoidal in face view, globose in end view, enclosed in a nearly uniform hyaline sheath, 4.5–6.5 × 2.0–3.5 μm (Fig. 8). Synnemata 140–280 μm long including a capitulum, 10–28 μm wide at base (Fig. 9). Conidiophores unbranched or scarcely branched. Conidiogenous cells cylindrical, terminal, annellidic, 5–12 μm long, 1.5–3.0 μm wide (Fig. 12). Conidia hyaline, aseptate, oblong, 2.8–4.0 × 1.0–2.0 μm,



Figs. 6–10. *Ophiostoma davidsonii* MAFF 410926, DIC. **6** Perithecium. **7** Tip of perithecial neck. **8** Ascospores. **9** Synnema of *Pesotum* anamorph. **10** Conidia. *Bars* **6** 100 μm; **7**, **9** 20 μm; **8**, **10** 5 μm



Figs. 11, 12. Scanning electron photomicrographs of conidiogenous cells and conidia of *Ophiostoma subalpinum* and *O. davidsonii.* **11** *Ophiostoma subalpinum* MAFF 410923. **12** *Ophiostoma davidsonii* MAFF 410926. *Bars* **11** 20 μm; **12** 10 μm

aggregated in a slimy mass (Fig. 10). Colony on 2% MA olive to olive-gray (23''''b).

Specimens examined: TSH-C1504 and 1505, dried culture of MAFF 410926 and 410927, respectively, isolated by N. Ohtaka, September 9, 2000, from a drop of ascospores obtained from *A. veitchii* infested by *Dryocoetes hectographus*, Mt. Asahi, Yamanashi Prefecture, Japan; TSH-C1506, dried culture of MAFF 410928, isolated by N. Ohtaka, August 7, 1999, from a drop of ascospores obtained from *A. veitchii* infested by *D. hectographus*, Mt. Shimagare, Nagano Prefecture, Japan.

Morphological characteristics of our isolates coincided with the original description of *O. davidsonii* (Olchowecki and Reid 1974) except for the size of the perithecial base. The perithecial bases of our isolates were larger (up to 145 μm in diameter) than those in the original description (60–90 μm in diameter). Comparison of our isolates with the type specimen of *O. davidsonii* (WIN (M) 71–30) reached the same conclusion. All other morphological characteristics fitted the type specimen well, and the perithecial size overlapped between our isolates and the type specimen. Therefore, we identify our isolates as *O. davidsonii*, which has been recorded on *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in Canada.

Ophiostoma davidsonii resembles *O. brevicolla* (R.W. Davidson) de Hoog & R.J. Sheff., *O. cucullatum* H. Solheim, *O. olivaceum* Math.-Kaarik, and *O. sagmatospora* (E.F. Wright & Cain) H. Solheim in perithecial characteristics. These species have ostiolar hyphae that are fused laterally and separated at the apex of the necks. These five species are mainly distinguishable on the basis of the morphology of the ascospores (Solheim 1986; Yamaoka et al. 1997). The ascospores of *O. brevicolla* and *O. davidsonii* are surrounded by uniform sheaths appearing orange section shaped to hemispherical, whereas those of *O. sagmatospora* and *O. olivaceum* are reniform and surrounded by a hatshaped sheath with distinct brims. In addition, ascospores of *O. cucullatum* are lunate with obtuse ends, surrounded by a thick hyaline sheath, and are cucullate in side view. Ascospores of *O. brevicolla* and *O. davidsonii* are similar, but these two species can be clearly distinguished based on the anamorphs; namely, *O. brevicolla* has the *Leptographium* anamorph in contrast to *Pesotum* anamorph in *O. davidsonii*.

Ophiostoma davidsonii was mainly isolated from *Dryocoetes hectographus* and their galleries, but it was rarely isolated from *Cryphalus montatus*, *C. piceae*, and *Polygraphus proximus* in this study. This result may indicate the close association between *O. davidsonii* and the beetle *D. hectographus*. Farris (1969) reported the presence of mycangia in *D. confusus* Sw. Further study is needed to clarify whether *D. hectographus* has mycangia.

There is no report of ophiostomatoid fungi isolated from *A. veitchii* and *A. mariesii* except our study. From *Abies sachalinensis* (Fr. Schm.) Masters (Sakhalin fir, "Todo-matsu" in Japanese) and bark beetles infesting them in Hokkaido, Japan, Aoshima (1965) recorded five *Ophiostoma* and *Ceratocystis* species: i.e., *O. albidum* Math.-Kaarik, *O. floccosum*, *O. piceae*, *O. pluriannulata* (Hedgc.) Syd., & P. Syd., and *C. polygrapha* Aoshima nom. nud. (without Latin description, should be treated as *Ophiostoma*). *Ophiostoma subalpinum* and *O. davidsonii* differ from these five species reported in Aoshima (1965).

Several ophiostomatoid fungi associated with bark beetles are known for their ability to kill host trees under suitable conditions (Raffa and Berryman 1983; Solheim and Långström 1991; Harrington 1993). However, pathogenicities of *O. subalpinum* and *O. davidsonii* have not been confirmed. Further work is needed to clarify the pathogenicity of these two *Ophiostoma* species by inoculation experiments.

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