Mycoscience 38: 421–427, 1997

Amylostereum laevigatum associated with the Japanese horntail, *Urocerus japonicus*

Masanobu Tabata[1] and Yasuhisa Abe[2]

[1] Shikoku Research Center, Forestry and Forest Products Research Institute, 915, Asakura-tei, Kochi 780, Japan
[2] Forestry and Forest Products Research Institute, P. O. Box 16, Tsukuba, Ibaraki 305, Japan

Accepted for publication 30 October 1997

The fungus associated with the Japanese horntail, *Urocerus japonicus*, in Kochi, Kagawa and Ehime Prefectures was studied. Cultures isolated from the mycangia of 113 adult females of the horntail showed the same cultural characteristics. Four of basidiocarps found on felled logs of *Cryptomeria japonica* were identified as *Amylostereum laevigatum* based on morphological characteristics. This was the first record of *A. laevigatum* from Japan. The cultures isolated from the basidiocarps had the same cultural characteristics as those from the mycangia of *U. japonicus*. One mycangial isolate produced basidiocarps on artificially inoculated stem segments of *Cr. japonica* after a 6-mo incubation and was identified as *A. laevigatum*. One isolate from the basidiocarps of *A. laevigatum* and one from the mycangium of *U. japonicus* were artificially inoculated into five trees each of *Chamaecyparis obtusa* and *Cr. japonica*. The wood of all inoculated trees showed discoloration, with no difference in shape and pattern of discoloration between the two isolates. The inoculated fungi were reisolated from the areas of discoloration in the inoculated trees.

Key Words——*Amylostereum laevigatum*; Japanese horntail; symbiont; *Urocerus japonicus*; wood discoloration.

Of the five recorded species of *Amylostereum* (Chamuris, 1988), only *A. areolatum* (Fr.: Fr.) Boidin and *A. chailletii* (Pers.: Fr.) Boidin are known to be *Sirex* and *Urocerus* symbionts (Gaut, 1969, 1970; Sano et al., 1995).

When the female of *Urocerus japonicus* Smith (Japanese horntail) oviposits in the wood of host trees, *Chamaecyparis obtusa* (Sieb. et Zucc.) Endlicher and *Cryptomeria japonica* (L. f.) D. Don, the fungus is also inoculated into the wood of these trees together with eggs (Kanamitsu, 1978; Okuda, 1989; Sano, 1992). After inoculation, wood discoloration occurs (Okuda, 1989; Sano, 1992). When the eggs are deposited into the stem in several directions, stellate discoloration is formed in the cross section of the stem (Okuda, 1989; Sano, 1992). Discoloration in wood of *Ch. obtusa* and *Cr. japonica* extends up to 14–76 cm in the longitudinal direction, centered on the oviposition site (Nishiguchi et al., 1981; Okuda, 1985). Wood discoloration of *Ch. obtusa* and *Cr. japonica* caused by the Japanese horntail and *Amylostereum* sp. has become problematic at plantations in Shikoku, Kinki, Chugoku and other districts of Japan (Okuda, 1989; Sano, 1992; Suto, 1994).

Kanamitsu (1978) reported *A. chailletii* to be carried in the mycangia of females of *U. japonicus*, which is widely distributed in Japan (Takeuchi, 1962). Sano et al. (1995) reported the identification of the fungus isolated from the mycangia of horntails in Mie Prefecture by cultural characteristics. However, there have been no reports about identification of the fungus based on morphology of basidiocarps (teleomorph) induced from the cultures isolated from the mycangia. Studies are required to identify the symbionts exactly by teleomorph, as fungal species other than *A. areolatum* and *A. chailletii* may be associated with horntails. For these reasons, we studied the fungus in the mycangia of Japanese horntails that emerged from felled logs of *Ch. obtusa* and *Cr. japonica* in Kochi, Kagawa, and Ehime Prefectures, Shikoku District. The objective of this paper is to determine the species of the fungus isolated from the mycangia of *U. japonicus* by teleomorph and cultural characteristics. Furthermore, we examined the pathogenicity of isolates from horntail and basidiocarp by means of inoculation experiments.

Materials and Methods

Isolation from horntails Approximately 1,000 logs (7–17 cm in diam, 1–2 m long) of *Ch. obtusa* and *Cr. japonica*, which appeared to have been attacked in the previous year by the horntail, were collected from 21 plantations in Kochi, Kagawa and Ehime Prefectures (Table 1). The logs were brought into outdoor cages at the Shikoku Research Center of the Forestry and Forest Products Research Institute during the months of April and May in 1993, 1994, 1995 and 1996. Newly emerged horntails were caught, and only the females were put in the freezer at −20°C for 15–30 min to paralyze them before dissection under a stereoscopic microscope for removal of their mycangia. Fungi taken from the mycangia were mounted in lactophenol and observed under a light microscope.

Mycangia were also excised individually from horn-

Table 1. Origin of the Japanese horntail, *Urocerus japonicus*, used to isolate the fungi from the mycangia.

Locality of collection	Date of collection	Tree species	Number of emerged horntails		Number of isolates
			Male	Female	
Hirota[d], Ehime[a]	April 1996	*Cr. japonica*	5	1	1
Tsushima[c], Ehime[a]	May 1994	*Cr. japonica*	6	0	0
Ayauta[c], Kagawa[a]	May 1994	*Ch. obtusa*	0	1	1
Ookawa[c], Kagawa[a]	May 1994	*Ch. obtusa*	6	2	2
Oonohara[c], Kagawa[a]	May 1994	*Ch. obtusa*	3	0	0
Ikegawa[c], Kochi[a]	April 1996	*Cr. japonica*	0	2	2
Kitagawa[d], Kochi[a]	April 1994	*Cr. japonica*	0	5	5
Motoyama[c], Kochi[a]	April 1995	*Cr. japonica*	0	19	19
Ookawa[d], Kochi[a]	April 1996	*Cr. japonica*	3	1	1
Oonomi[d], Kochi[a]	April 1995	*Cr. japonica*	6	0	0
Ootoyo1[c], Kochi[a]	May 1994	*Cr. japonica*	27	50	50
Ootoyo2[c], Kochi[a]	April 1995	*Cr. japonica*	0	4	4
Ootoyo3[c], Kochi[a]	April 1996	*Ch. obtusa*	0	1	1
Sakawa1[c], Kochi[a]	May 1993	*Cr. japonica*	10	1	1
Sakawa2[c], Kochi[a]	May 1996	*Ch. obtusa*	0	5	5
Susaki[b], Kochi[a]	April 1994	*Ch. obtusa*	0	3	3
Taishoo[c], Kochi[a]	April 1996	*Ch. obtusa*	5	1	1
Tosa1[c], Kochi[a]	April 1994	*Cr. japonica*	6	0	0
Tosa2[c], Kochi[a]	May 1996	*Cr. japonica*	0	4	4
Tosayamada[c], Kochi[a]	May 1996	*Cr. japonica*	0	9	9
Umaji[d], Kochi[a]	April 1994	*Cr. japonica*	5	4	4
Total			82	113	113

a) Prefecture; b) city; c) town; d) village.

tails with sterilized forceps and put on potato-dextrose agar (PDA) in Petri plates. The Petri plates were incubated at 20°C for 4–7 d and mycelia growing from mycangia were isolated. All the cultures used are stored at the Shikoku Research Center of the Forestry and Forest Products Research Institute.

Examination of basidiocarps on the felled logs Basidiocarps occurring on four felled logs were collected at four *Cr. japonica* plantations in Kochi Prefecture, on 16 Nov. and 3 Dec. 1994 at Ootoyo Town, on 11 May 1995 at Niyodo Village, and on 20 Nov. 1996 at Ookawa Village. The basidiocarps were examined morphologically and cultures were isolated from basidiospores. All the isolates used are stored at the Shikoku Research Center of the Forestry and Forest Products Research Institute.

Cultural characteristics A total of 113 cultures (Table 1) isolated from mycangia of individual female horntails and 3 cultures (FD-4, 115, 127, Table 2) isolated from the basidiospores of the three basidiocarps were grown on PDA in Petri plates at 25°C, and their cultural characteristics were recorded and assigned according to the key pattern of Stalpers (1978).

The effect of temperature on mycelial growth was studied for four isolates (FD-1–4, Table 2) using 9-cm Petri plates containing 20 ml of PDA. A 4-mm plug cut from the colony of the test fungus on PDA was placed centrally on each plate. Inoculated plates were incubated at a test temperature from 0 to 35°C at intervals of

Table 2. Origin of 6 *Amylostereum laevigatum* isolates used to study the mycelial growth response to temperature and cultural characteristics.

Isolate	Locality of collection	Date of collection	Origin
FD-1	Sakawa[b], Kochi[a]	5 Jul. 1993	Mycangium of *U. japonicus*
FD-2	Ootoyo[b], Kochi[a]	11 Aug. 1994	Mycangium of *U. japonicus*
FD-3	Tosayamada[b], Kochi[a]	3 Aug. 1994	Mycangium of *U. japonicus*
FD-4	Ootoyo[b], Kochi[a]	10 Dec. 1994	Basidiospores of *A. laevigatum*
FD-115	Ootoyo[b], Kochi[a]	10 May 1996	Basidiospores of *A. laevigatum*
FD-127	Ookawa[c], Kochi[a]	29 May 1996	Basidiospores of *A. laevigatum*

a) Prefecture; b) town; c) village.

5°C with ten replicates for each temperature. Colony size was measured along two diam at right angles every 2 d and radial growth of mycelium was calculated.

Inoculation to stem segments The logs (3-5 cm in diam) from fresh *Cr. japonica* stems were cut into segments of 11–12 cm in length, and four holes (ca. 2.5 mm in diam and ca. 1 cm long) were drilled in each segment. Four stem segments were put into plastic bags singly and autoclaved at 121°C for 1 h. Sterilized toothpicks (ca. 2 mm in diam and ca. 1 cm long) were put on PDA plates inoculated with a mycangial isolate (FD-2) and incubated at 25°C in darkness for 3 wk. Cultured toothpicks were aseptically put into the holes of segments with sterilized forceps. Inoculation was performed on 20 February 1995. The plastic bags were sealed and placed at the corner of the laboratory to the production of fruit bodies.

Inoculation of trees Five to seven yr-old trees of *Ch. obtusa* (4.0–6.0 m high, 4–7 cm in diam at breast height) and 5 yr-old trees of *Cr. japonica* (4.1–5.0 m high, 4–6 cm in diam at breast height) were used. They were planted at the Shikoku Research Center of the Forestry and Forest Products Research Institute. One isolate from the mycangium of a Japanese horntail (FD-1) and one from a basidiocarp (FD-4) were used for inoculation. Toothpicks cultured as described above were used as inocula. Three holes (ca. 2.5 mm in diam and ca. 1 cm long) were drilled at the height of 1.2 m in the stem of each tree. Cultured toothpicks (FD-1, 4) and a sterilized toothpick (control) were put into the holes and covered with plastic film (Parafilm) and adhensive tape. Five trees each of the two tree species were inoculated on 29 July 1996. Inoculated trees were cut down and examined 1 mo after inoculation. The maximum extent of discoloration in the wood was measured in the longitudinal, tangential, and radial directions, and results were expressed as the range and average extent of discoloration of 15 inoculation points in five trees. Three inoculated trees each of *Ch. obtusa* and *Cr. japonica* were used for isolation of the infecting fungus. Three to nine pieces of wood (3 × 4 × 3 mm) were taken from the areas of discoloration, treated with 70% ethanol solution for 30 min and sodium hypochlorite solution (about 1% available chlorine) for 2 min, then washed with sterilized water (twice), placed on PDA in Petri plates and incubated at 20°C in darkness for 3 wk.

Results

The fungus associated with horntails and felled logs A total of 82 adult males and 113 adult females of *U. japonicus* emerged from the collected logs during the period from mid-July to early September in 1993, 1994, 1995 and 1996 (Table 1). The mycangia (Fig. 1) of the adult females (Fig. 2) were filled with a mass of hyphal fragments (Fig. 7). The hyphal fragments were hyaline in color, 12.5–280 μm long and 2.5–8 μm wide. They consisted of one to six cells and had clamp connections at the septum. Mycelia were isolated from all the adult females, yielding a total of 113 cultures (mycangial isolates) (Table 1). All cultures had the same mycelial growth, the same color of colony, the same hyphal system, and hyphae with clamp connections. Colonies were white to creamy-brown and produced cottony to pelliculate mycelia on PDA (Fig. 8a).

Basidiocarps of the genus *Amylostereum* were found among the collected basidiocarps formed on the bark of four *Cr. japonica* logs. They were pale brown and strictly resupinate. Basidiospores measured 7–10 × 3–4 μm. The fungus was identified as *A. laevigatum* based on morphological characteristics. Three cultures (basidiospore isolates) were isolated successfully from the basidiospores of the three collected basidiocarps of *A. laevigatum*. Basidiospore isolates had almost the same cultural characteristics as the mycangial isolates. The morphological and cultural characteristics of the fungus were as follows.

Description

Amylostereum laevigatum (Fr.) Boid., Rev. Mycol. **23**: 345. 1958. Figs. 3, 9–11

Basidiocarps strictly resupinate, attached tightly to the substrate, forming patches 3 to 15 cm in extent, 75–300 μm thick (Fig. 9), hymenial surface smooth, pale brown, sometimes cracked when dry. Hyphal system monomitic, generative hyphae hyaline, thin to thick-walled with clamps, 3–4 μm wide. Cystidia present in the surface and inside of the hymenium, pale brown, thick-walled, clavate with acute or somewhat rounded edge, encrusted with granular matter, 23–50 × 3–7 μm, 11–25 × 3–7 μm in encrusted part (Fig. 11). Basidia subclavate to subcylindrical (Fig. 10a), 35–40 × 5–5.5 μm with 4-sterigmata. Basidiospores ellipsoid to cylindrical, (6.5–)7–10 × 3–4 μm, hyaline, smooth, thin-walled, and amyloid (Fig. 10b).

Cultural characteristics: Colonies cottony, finally pelliculate, white to yellowish-brown on PDA (Fig. 8b) and with offensive odor. Reverse pale brown. Cystidia pale brown, thick-walled, clavate, with acute or somewhat rounded edge, encrusted with granular matter, 28–88 × 3–6 μm. Hyphae hyaline with clamps, thin-walled. Marginal hyphae 2–5.5 μm wide. Aerial hyphae 1–4 μm wide. Key patterns of the culture were: 1, 2, 3, 6, 13, 21, (22), 24, 30, (31), (35), (36), 38, 39, 44, 45, 48, (51), 52, 53, (54), (58), (60), 72, (83), 90, 94.

Specimen examined: SFM1; Ootoyo; Kochi; on bark of felled log of *Cr. japonica*; 16 Nov. 1994. SFM2; Ootoyo; Kochi; on bark of felled log of *Cr. japonica*; 3 Dec. 1994. SFM3; Niyodo; Kochi; on bark of felled log of *Cr. japonica*; 11 May 1995. SFM4; Ookawa; Kochi; on bark of felled log of *Cr. japonica*; 20 Nov. 1996. The specimens are stored at the Shikoku Research Center of the Forestry and Forest Products Research Institute.

Mycelial growth of mycangial isolates and a basidiospore isolate Figure 12 shows the effect of temperature on mycelial growth of the fungi from the mycangia of Japanese horntails (FD-1–3) and from the basidiospores of a collected basidiocarp of *A. laevigatum* (FD-4). Mycelial growth occurred at temperatures between 5°C and 30°C in the four isolates. Maximum mycelial growth occurred at 20°C in FD-1 and 2 and at 25°C in

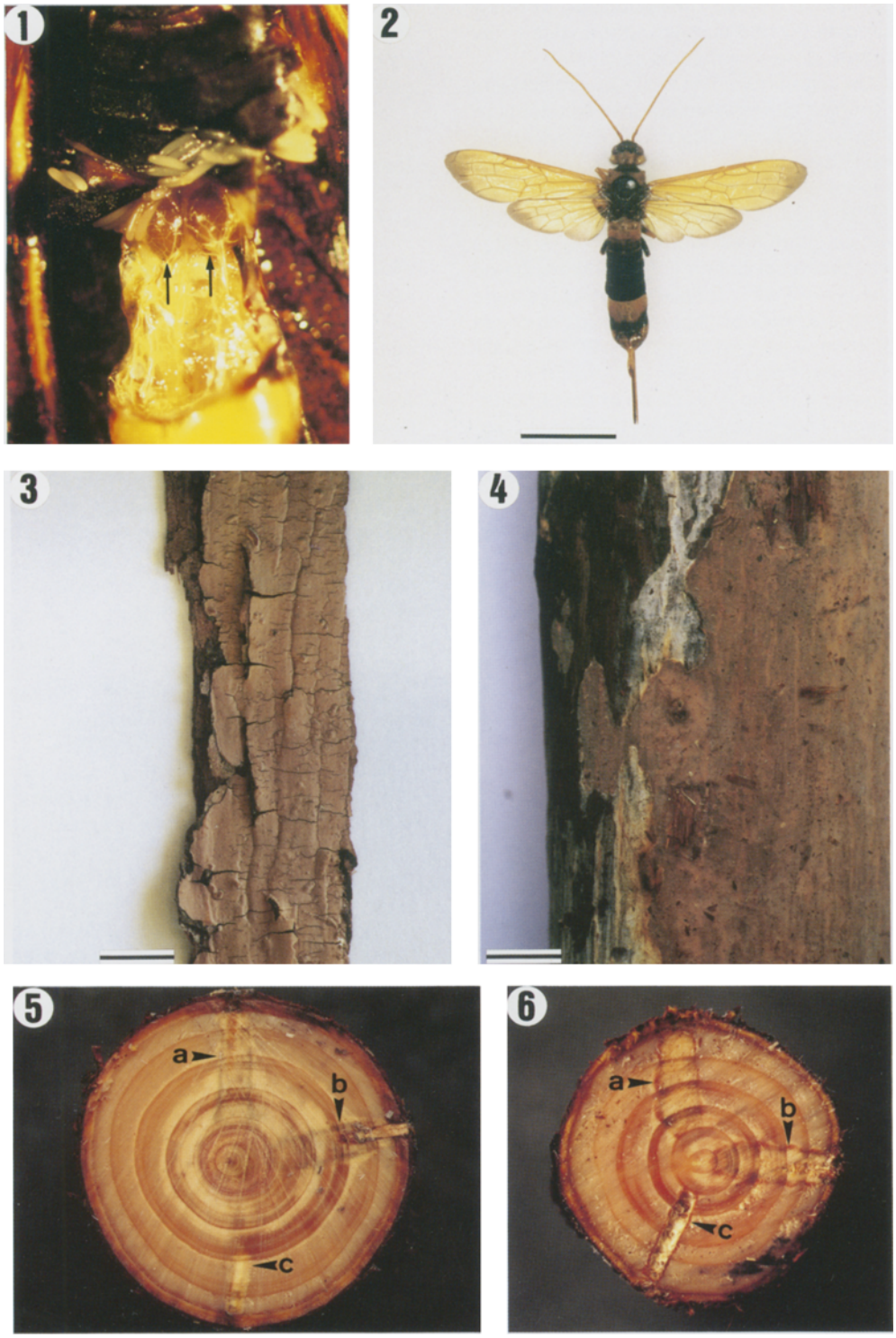

Fig. 1. Anatomy of abdomen of *Urocerus japonicus*; arrows show the mycangia.
Fig. 2. Adult female of *U. japonicus*. Scale bar = 1 cm.
Fig. 3. Basidiocarp of *Amylostereum laevigatum* on *Cryptomeria japonica* bark collected in the field (SFM3). Scale bar = 1 cm.
Fig. 4. Basidiocarp produced on the stem segment of *Cr. japonica* artificially inoculated with mycangial isolate (FD-2). Scale bar = 1 cm.
Fig. 5. Wood discoloration in the cross section of the stem of *Chamaecyparis obtusa* inoculated with the fungus from the mycangia of *U. japonicus* (a) and the fungus from the basidiospores of *A. laevigatum* (b), and a sterilized toothpick (c).
Fig. 6. Wood discoloration in the cross section of the stem of *Cr. japonica* inoculated with the fungus from the mycangia of *U. japonicus* (a) and the fungus from the basidiospores of *A. laevigatum* (b), and a sterilized toothpick (c).

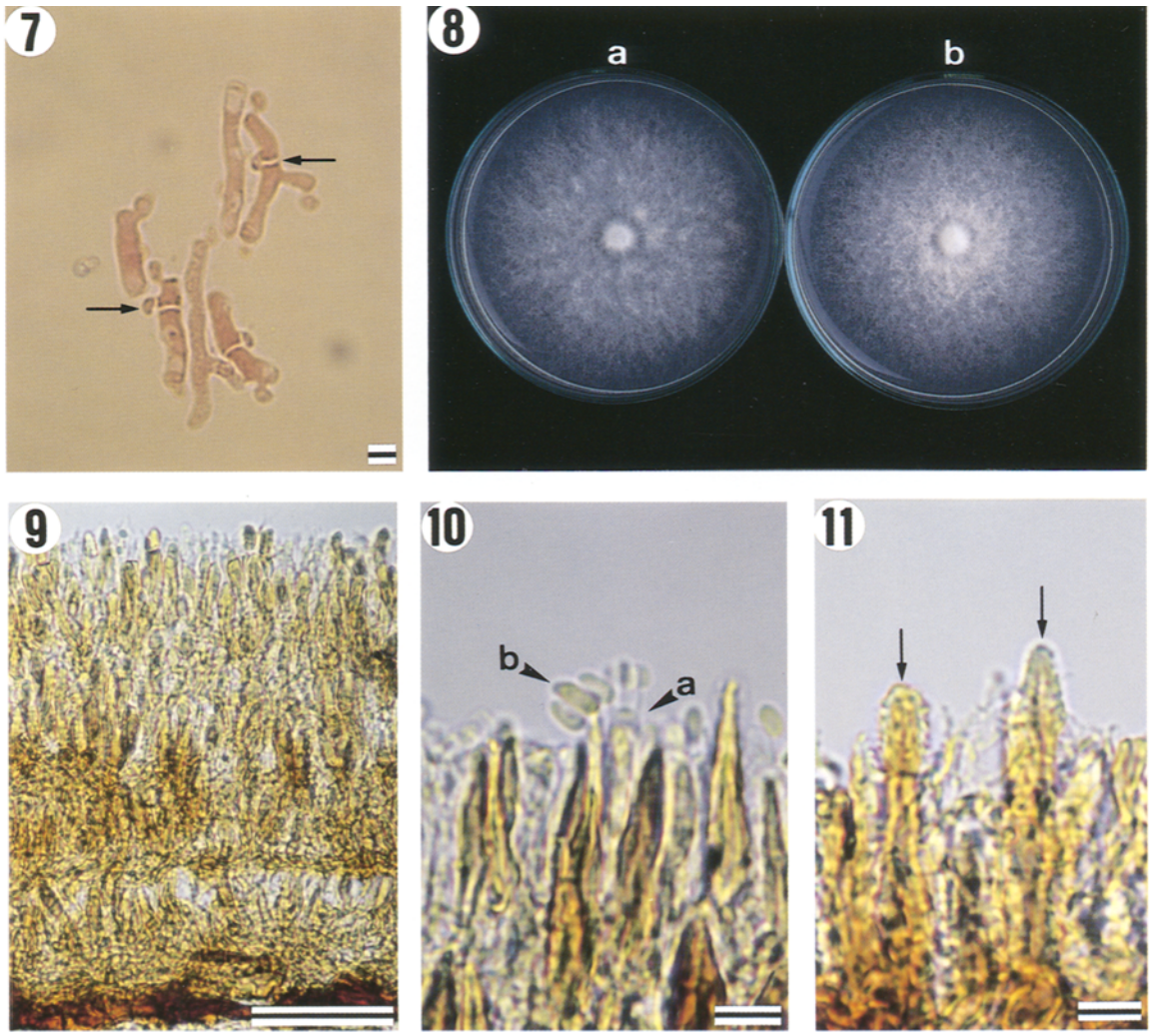

Fig. 7. Hyphal fragments with clamp connections (arrows) stored in the mycangia of *U. japonicus*. Scale bar = 5 μm.
Fig. 8. Culture derived from the mycangia of *U. japonicus* (FD-2, a); culture from *A. laevigatum* collected on a *Cr. japonica* log (FD-4, b).
Both cultures were grown on PDA at 25°C in darkness for 1 wk.
Figs. 9–11. *Amylostereum laevigatum* collected on *Cr. japonica* log, SFM3.
9. Section of the basidiocarp. 10. Basidium (a) and basidiospores (b). 11. Cystidia (arrows). Scale bars: 9 = 50 μm; 10, 11 = 10 μm.

FD-3 and 4. The pattern of growth was same for the four isolates.

Inoculation to the stem segments Fruit bodies were produced on stem segments 6 mo after the inoculation of isolate FD-2. They were strictly resupinate, attached tightly to the substrate and formed patches 1–10 cm in extent, 75–225 μm thick. Hymenial surface was smooth and pale brown (Fig. 4).

Basidiospores produced on stem segments measured 6.5–9 × 3–3.5 μm, and microscopic characteristics of basidiocarps were almost identical with those of the specimens (SFM1-4).

Inoculation of trees Wood discoloration occurred in all trees inoculated with isolates (Figs. 5, 6). Discoloration was reddish brown to pale brown, being paler in *Ch. obtusa* than *Cr. japonica*, spindle-form in the cross section, and ovariform in the longitudinal section. Table 3 shows the extent of discoloration in *Ch. obtusa* and *Cr. japonica* one month after inoculation. In the longitudinal direction, the average discoloration in *Ch. obtusa* was more than twice that in *Cr. japonica*, and the maximal discoloration in wood inoculated with the basidiospore isolate reached 28.5 cm and 15.7 cm, respectively. There was no difference in the pattern or extent of discoloration between the basidiospore isolate and the mycangial isolate in trees of the same species. The inoculated fungi were reisolated from the areas of discoloration of all the inoculated trees but not from controls. *Pestalotiopsis* sp. was also isolated from the areas of discoloration of the inoculated trees and all controls.

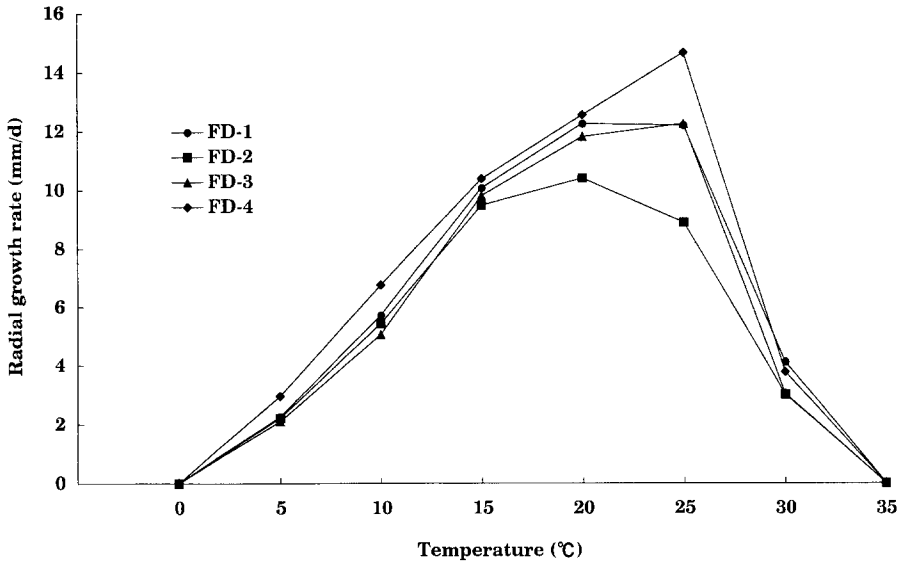

Fig. 12. Effect of temperature on mycelial growth of three isolates from the mycangia of *Urocerus japonicus* (FD-1–3) and one isolate from the basidiospores of *Amylostereum laevigatum* (FD-4).

Table 3. Extent of discoloration in wood of *Chamaecyparis obtusa* and *Cryptomeria japonica* inoculated with *Amylostereum laevigatum* isolates.

Inoculum	Tree species	Longitudinal direction (cm)		Tangential direction (cm)		Radial direction (cm)	
		Range of discoloration	Average	Range of discoloration	Average	Range of discoloration	Average
FD-1	*Ch. obtusa*	12.4–23.3	19.6	0.5–0.8	0.6	1.6–2.4	2.1
FD-4	*Ch. obtusa*	14.0–28.5	19.5	0.4–0.7	0.6	1.6–2.4	2.0
Control	*Ch. obtusa*	0.7– 1.5	1.1	0.2–0.3	0.2	0.8–1.7	1.2
FD-1	*Cr. japonica*	6.2–10.3	7.6	0.4–0.6	0.4	1.4–2.2	1.8
FD-4	*Cr. japonica*	5.1–15.7	9.8	0.4–0.5	0.5	1.2–2.3	1.8
Control	*Cr. japonica*	0.9– 2.8	1.4	0.2–0.3	0.3	1.1–1.8	1.3

Discussion

All the mycangial isolates from 113 adult females of the Japanese horntail produced the same colonies and had the same microscopic characteristics, suggesting that a single species of fungus is associated with the horntail in Kochi, Kagawa and Ehime Prefectures in Shikoku District. The cultural characteristics of mycangial isolates coincided closely with those of basidiospore isolates. The basidiocarps collected on the felled logs of *Cr. japonica* in the field and those produced on the *Cr. japonica* stem segments in the laboratory were both resupinate and had monomitic hyphal system. The basidiocarps collected on the felled logs were slightly larger, but their morphological characteristics accorded closely with those of basidiocarps produced on the stem segments. There was little difference in the size of basidiospores between the basidiocarps of mycangial isolates and those of a basidiospore isolate. Thus, the fungus isolated from the mycangia of *U. japonicus* is conspecific with the one producing basidiocarps on the felled logs of *Cr. japonica*.

Amylostereum laevigatum is different from *A. chailletii*, which is known as a symbiont of *Sirex* and *Urocerus* species (Gaut, 1969, 1970). Eriksson and Ryvarden (1973), Breitenbach and Kränzlin (1986), and Chamuris (1988) state that the basidiocarps of *A. chailletii* are resupinate to effuso-reflexed with a narrow margin and that the hyphal system is dimitic. Reported basidiospore sizes of *A. chailletii* are 6–7.5 × 2.5–3 μm (Eriksson and Ryvarden, 1973), 5.5–7 × 2.5–3 μm (Breitenbach and Kränzlin, 1986), and 5–8 × 2–3.5 (–4) μm (Chamuris, 1988). The size of basidiospores of basidiocarps collected on the felled logs and produced on the stem segments in this study partially overlaps with that of *A. chailletii*, but *A. laevigatum* has a monomitic hyphal system and its basidiocarps never become reflexed. From these facts, *A. laevigatum* was concluded to be the symbiotic fungus of the Japanese horntail in Kochi, Kagawa and Ehime Prefectures of Shikoku District. The fungus is distributed in Canada, France, Norway, Sweden, Switzerland and USA (Boidin and Lanquetin, 1984; Breitenbach and Kränzlin, 1986; Eriksson and Ryvarden, 1973; Ginns and Lefebvre, 1993). It has never been recorded as a symbiont of *Sirex* or *Urocerus* species but is known to occur on the hosts of *Abies*, *Juniperus*, *Taxus*, and *Thuja* (Boidin and Lanquetin,

1984; Breitenbach and Kränzlin,1986; Eriksson and Ryvarden, 1973; Ginns and Lefebvre, 1993). In Japan, Kitajima (1938) and Hayashi (1974) have stated that the fungus occurs on the bark of *Ch. obtusa*. The former records only the scientific name of the fungus but gives no concrete description. Therefore, we were unable to confirm whether it is *A. laevigatum* or not. The latter give a full description of the fungus. We examined the specimen (10335-F, TFM) in more detail and found that it was a different species. This is the first report on *A. laevigatum* associated with the horntail in the world and the first record of *A. laevigatum* from Japan.

Francke-Grosmann (1939), Stillwell (1966), and Terashita (1970) reported that the mycangia of *Sirex cyaneus* Fab., *S. juvencus* L., *S. nitobei* Matsumura, *S. noctilio* Fab., *Urocerus albicornis* Fab. and *U. gigas* L. were filled with arthrospores. However, we found the fungus in the mycangia of *U. japonicus* to be present as hyphal fragments, in which cells were not separate but joined by clamp connections.

Sano et al. (1995) examined the fungus from the mycangia of *U. japonicus* in Mie Prefecture in the Kinki District of Japan and reported it to be as *A. chailletii*. The finding of different fungal species associated with the same species of horntail conflicts with the report of Gaut (1970), who showed that the same horntail species were always associated with the same fungal species, irrespective of geographical distribution. Therefore, further studies are required to clarify the species of fungus associated with the Japanese horntail in different districts of Japan.

Inoculation of isolates from a mycangium and a basidiocarp resulted in wood discoloration in all inoculated trees of *Ch. obtusa* and *Cr. japonica*. The discoloration reached 28.5 cm longitudinally, 0.8 cm tangentially, and 2.4 cm radially. From this result, it was able to show the damage of wood discoloration again. No difference in wood discoloration was found between the two isolates inoculated on trees of the same species. However, the extent of discoloration was larger in *Ch. obtusa* than in *Cr. japonica*, especially in the longitudinal direction. The results were in close accord with those reported by Sano et al. (1995) and Suto (1994).

Acknowledgements——The authors are grateful to Mr. H. Miyata, Kochi Prefectural Forest Experiment Station, Mr. M. Ookubo, Kagawa Forest Center, and Mr. K. Inoue, Ehime Prefectural Forest Experiment Station for help in collecting the felled logs of *Chamaecyparis obtusa* and *Cryptomeria japonica*.

Literature cited

Boiden, J. 1958. Hétérobasidiomycètes saprophytes et Homobasidiomycètes résupinés: V. Essai sur le genre *Strereum* Pers. ex S. F. Gray. Rev. Mycol. **24**: 197–225.

Boidin, J. and Lanquetin, P. 1984. Le genre *Amylostereum* (Basidiomycetes) intercompatibilités partielles entre espèces allopatriques. Bull. Soc. Mycol. France **100**: 211–236.

Breitenbach, J. and Kränzlin, F. 1986. Fungi of Switzerland, vol. 2. Non-gilled fungi. Verlag Mykologia, Lecerne.

Chamuris, G. 1988. The non-stipitate stereoid fungi in the northeastern United States and adjacent Canada. Mycologia Mem. No. 14. Stuttgart.

Eriksson, K. and Ryvarden, L. 1973. The Corticiaceae of North Europe, vol. 2. Fungiflora, Oslo.

Francke-Grosmann, H. 1939. Über das Zusammenlebeb von Holzwespen (Siricinae) mit Pilzen. Z. Angew. Entmol. **25**: 647–680.

Gaut, I. P. C. 1969. Identity of the fungal symbiont of *Sirex noctilio*. Aust. J. Biol. Sci. **22**: 905–914.

Gaut, I. P. C. 1970. Studies of siricids and their fungal symbionts. PhD thesis, Univ. Adelaide, Australia.

Ginns, J. and Lefebvre, M. N. L. 1993. Lignicolous corticioid fungi (Basidiomycota) of North America, Systematics, distribution, and ecology. Mycologia Mem., No. 19. Minnesota.

Hayashi, Y. 1974. Studies on the genus *Peniophora* Cke. and its allied genera in Japan. Bull. Gov. For. Exp. Sta. **260**: 1–98.

Kanamitsu, K. 1978. Woodwasps and their hymenopterous parasitoids in Japanese conifers. Kontyu **46**: 498-508. (In Japanese.)

Kitajima, K. 1938. Forest pathology (Jubyogaku-oyobimokuzaifukyuron), pp. 442–443. Yokendo, Tokyo. (In Japanese.)

Nishiguchi, H., Shibata, E., and Yamanaka, K. 1981. Discoloration of sugi (*Cryptomeria japonica*) wood caused by the attack of the horntails. Trans. 32th Meeting Kansai Br. Jpn. For. Soc., pp. 257–260. (In Japanese.)

Okuda, K. 1985. Discoloration of hinoki (*Chamaecyparis obtusa*) wood caused by the attack of the Japanese horntail (*Urocerus japonicus*). Trans. 96th Meeting Jpn. For. Soc., pp. 487–488. (In Japanese.)

Okuda, M. 1989. Japanese horntail. Ringyo-to-yakuzai **108**: 1–8. (In Japanese.)

Sano, A. 1992. Japanese horntail. Ringyo-to-yakuzai **122**: 1–8. (In Japanese.)

Sano, A., Mihara, Y. and Ito, S. 1995. The fungus isolated from the mycangia of *Urocerus japonicus* and *U. antennatus*. Trans. 43th Meeting Chubu Br. Jpn. For. Soc, pp. 125–126. (In Japanese.)

Stalpers, J. A. 1978. Identification of wood-inhabiting Aphyllophorales in pure culture. Stud. Mycol. (CBS) **16**: 1–248.

Stillwell, M. A. 1966. Woodwasps (Siricidae) in conifers and the associated fungus, *Stereum chailletii*, in Eastern Canada. For. Sci. **12**: 121–128.

Suto, Y. 1994. Wood stain caused by *Amylostereum* sp. in *Cryptomeria japonica* and *Chamaecyparis obtusa*, Influence of life and death of the trees on the stain occurrence and fungal survival. Trans. Kansai Br. Jpn. For. Soc. **3**: 163–164. (In Japanese.)

Takeuchi, K. 1962. Insecta Japonica: Siricidae, pp. 1–12. Hokuryukan, Tokyo. (In Japanese.)

Terashita, T. 1970. A Basidiomycetes symbiotic to a siricid in Japan. J. Jpn. For. Soc. **52**: 313–316. (In Japanese.)