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Dematiaceous hyphomycetes inhabiting decaying blackish needles of *Abies firma* and their distribution in the Kanto district, Japan*

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Dematiaceous mitosporic fungi darkening decaying fir needles on the ground were studied. Fungal communities on decaying, blackish fir needles were investigated in nine sites of the Kanto district, Japan, using a washing method. A total 108 taxa was recorded from 540 sampled needles. Among abundantly occurring dematiaceous fungi, *Anungitea continua*, *A. uniseptata* and *Endophragmiella uniseptata* were recognized as the major colonizers, forming a hyphal network on the surface of decaying fallen needles and darkening them. The effects of climate on the distributions of seven dematiaceous fungi included the major colonizers were analyzed. The abundance (proportion of needles colonized by a fungal species) of *Chaetopsina fulva* showed a significantly positive correlation with annual mean air temperature at each sampling site. No other significant correlations between the selected climatic factors and the distributions of dematiaceous fungi were recognized.

Key Words——*Abies firma*; dematiaceous hyphomycetes; distribution; fungal community; litter fungi.

Information on the fungi involved in the decomposition of fir needles was very scarce in comparison with that of pine needles when Millar (1974) reviewed the fungal decomposition of coniferous material. Since then, information has gradually accumulated through studies of fungal successions associated with the needle decay in Europe (Gourbière, 1979; 1982; Aoki et al., 1992) and in Japan (Aoki et al., 1990), and of geographical distributions on selected fungal species of fir leaf litter in Europe and environs (van Maanen and Gourbière, 1997).

It has been shown in many prior studies on the fungal succession on decaying pine needles (Kendrick and Burges, 1962; Hayes, 1965; Tubaki and Saitô, 1969; Mitchell and Millar, 1978; Ponge, 1991; Tokumasu, 1996) that several species quickly colonize freshly fallen needles from the underlying O horizon and often become dominants in the F_1 layer; a few of these form a hyphal network on the surface of needles to darken the needles (Kendrick and Burges, 1962). Gourbière and Pépin (1983) suggested that among the leaf litter fungi on fir needles in France, *Polyscytalum verrucosum* Sutton and *Endophragmiella* sp. are dematiaceous species with a similar growth habit. In Japan, Aoki et al. (1990) found that *Dactylaria naviculiformis* Matsushima, *Dictyochaeta simplex* (Hughes & Kendrick) Holubova-Jechova (as *Codinaea simplex*), *Chaetopsina fulva* Rambelli and *Gonytrichum macrocladum* (Saccardo) Hughes abundantly occurred on dark discolored fir needles of the F_1 layer. However, they did not refer to fungi darkening the needles, and thus it is still uncertain whether all the abovementioned species inhabiting fir leaf litter in Japan are ecologically equivalent to the hyphal network formers in pine leaf litter or not, since color tone and growth rates of mycelia of these species in culture vary. In addition, the number of studies on the fungi of fir leaf litter is still fewer than that on pine leaf litter, and the information on the fungal decomposition of fir needles is insufficient.

In this study, we attempt to find which dematiaceous fungi involved in the decay of fir needles correspond to the hyphal network formers on decomposing pine needles. For this purpose, the fungal communities on decaying blackish fir needles which almost corresponded to the F_1 layer needles in the mor-type O horizon were studied at nine sites in the Kanto district, Japan. Using the same data, we also try to analyze the effects of climate on the distribution of both the network formers and several additional species.

Materials and Methods

Distribution and ecology of momi fir Momi fir (*Abies*

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Table 1. Brief descriptions of sampling sites.

Site name	Latitude (N)	Longitude (E)	Altitude (m)	Ann. mean tem. (°C)	Precipitation (mm)
Kashima	35°58′	140°38′	30	14.4	1467
Kiyosumi	35°09′	140°08′	230	14.1	1320
Hatoyama	35°58′	139°19′	70	13.4	1352
Takao	35°37′	139°16′	220	13.4	1423
Tsukuba	36°12′	140°06′	330	11.8	1270
Matsuida	36°19′	138°41′	630	10.0	1196
Ooyama	35°26′	139°14′	790	9.9	1727
Hakone	35°11′	139°05′	930	9.3	3683
Yamanaka	35°26′	138°56′	1070	8.2	2309

firma Sieb. & Zucc.) is an indigenous conifer of Japan and distributed in the warmest climatic region among *Abies* species. It inhabits the transitional zone from warm-temperate to cool-temperate climate and is latitudinally distributed from 30°15′N to 39°C30′N (Hayashi, 1960). In most places where the species naturally occurs, it is a member of mixed forests and rarely forms pure stands. Its needles normally fall on the sixth or seventh yr after needle expansion. About 70% of annual needle fall occurs in autumn (Ando et al., 1977), although it continues throughout the year.

Study sites Nine natural forests with momi fir trees were selected as study sites in the Kanto district. They are named "Kashima", "Kiyosumi", "Hatoyama", "Takao", "Tsukuba", "Matsuida", "Ooyama", "Hakone", and "Yamanaka" (Table 1 and Fig. 1). These forests were mixed-forests mainly with various trees such as

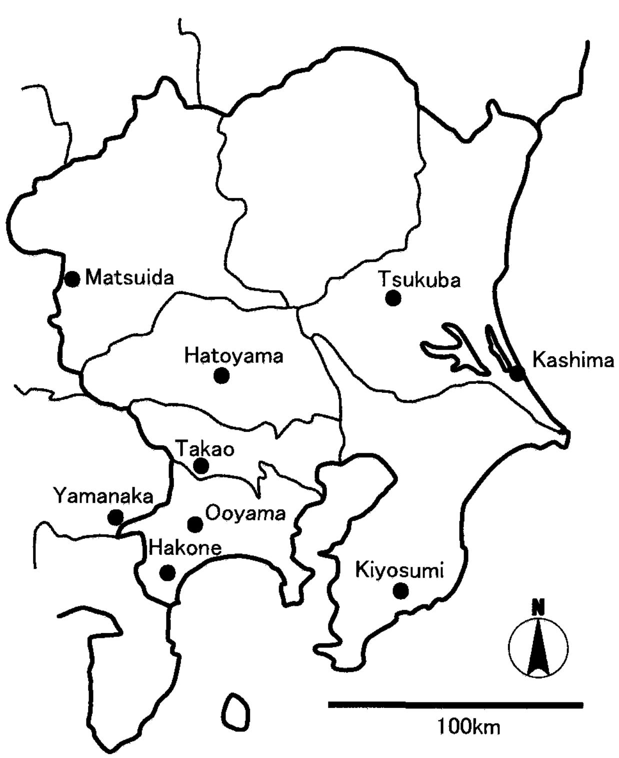

Fig. 1. Distribution of sampling sites in the Kanto district.

Japanese cedars, pines and evergreen or deciduous oaks. The density of fir tree is low in all the stands. In most forests, fir trees grow on the escarpment and form only poor leaf litter.

Collection of fallen needles Fallen needles were sampled three times (spring, summer and autumn) at all sites from April through November in 1998. At the sites where leaf litter accumulated thickly under the canopy of fir trees, a litter block (10 cm × 10 cm square, 2–4 cm thick) was cut from the O horizon, while needles were gathered from wider area at the sites with undeveloped leaf litter. Collected samples were put into clean paper bags and brought back to the laboratory. The wet or dump litter samples were naturally dried as quickly as possible and kept in the laboratory.

Selection of needles Twenty dark brown to black, fragile but not collapsed needles were collected from every litter sample. The decay stage of these needles most nearly corresponded to that of needles in the F_1 layer in the mor-type O horizon.

Observation of fungi To remove attached soil particles, organic fragments, fungal spores and other microorganisms from sampled needles, a washing method (Tokumasu, 1980) was adopted in this study. Twenty needles sorted from a sample were put into a sterile test tube with plastic cap. Ten ml of a washing detergent, sterilized 0.005% (w/v) Aerosol OT solution (di-iso-octyl sodium sulfosuccinate) was poured into the tube with a sterile pipette. The tube was shaken vigorously in a vortical mixer for 90 s and the old detergent was removed with a sterile pipette. The washing procedure with detergent was repeated five times. Then the needles were rinsed with sterile water three times using the same procedure. The rinsed needles were transferred to a sterile filter paper in a 9 cm Petri dish and dried for 24 h to suppress vigorous bacterial growth after plating. Four needles were placed on the surface of 0.2% corn meal agar (Nissui Pharm. Co., Ltd.) in a 9 cm Petri dish. The plates were incubated at room temperature in the laboratory.

Fungi growing on or around the needles were observed with an optical microscope after 3 d, 1, 2 and 4 wk after the start of incubation. A few characteristic species were directly identified on the plates, although most fungi were also isolated for later identification. Finally, lists of recorded species were made for individual needles.

Statistics Species abundance (van Maanen et al., 2000) of a given species at each sampling site was calculated as follows:

Species abundance (%)=number of needles on which the species occurred/total number of needles examined at each sampling site (60) × 100.

A correlation between climatic elements and abundance of each fungal species was examined by Pearson' moment correlation coefficient (*r*). Values of *r* were taken as significant if $p \leqq 0.05$.

Climatic elements Annual mean air temperature and annual precipitation were selected as analyzing climatic elements. The annual mean temperatures of individual sites were calculated based on the data of the closest meteorological stations to the sites by using a temperature laps rate of 0.65°C per 100 m. The mean values at the meteorological stations were sub-normal values during 1979–1990 (Japan Meteorological Agency, 1996).

Results

Species richness A total 2690 isolates was obtained from 540 fir needles examined, and 108 taxa were recognized in this study (Tables 2–4). Table 2 shows the number of species recorded from each site at each sampling time. The largest number of species (51) was recorded at Hatoyama; the number varied from 33 to 44 at the other sites. The largest number at one sampling time (33 spp.) was recorded at Hatoyama in autumn.

Among these 108 taxa, three occurred on one-third or more (180 needles or more) of needles examined and ten occurred with intermediate frequency (on 60–180 needles, Table 3). Fifty taxa appeared on fewer than 5 needles (Table 4).

Table 2. Number of species recorded from each site in every season.

Site name	Sampling season			Total
	Spring	Summer	Autumn	
Kashima	23	17	28	41
Kiyosumi	28	22	23	43
Hatoyama	24	26	33	51
Takao	22	24	26	43
Tsukuba	23	27	16	44
Matsuida	19	16	21	33
Ooyama	21	21	14	37
Hakone	17	9	25	35
Yamanaka	18	21	21	38
Mean	22	20	23	41
Total	63	62	73	108

Taxonomic range A large number of mitosporic fungi were recorded in this study, and 68 taxa among them were dematiaceous (Tables 3, 4). In contrast, both mucoralean and ascomycetous fungi were fewer in number. Basidiomycetous fungi forming rhizomorphs were found on some needles, but they were not included in the total number of species.

Species abundance The fungi recorded with the abundance values of more than 10% were listed in Table 3. *Trichoderma* spp. showed the highest abundance as a whole. *Penicillium* spp. also showed high abundance. Three dematiaceous species, *Anungitea continua* Mat-

Table 3. Summed abundances[a] and the number of recorded sites of selected fungi (more than 10.0% summed abundances).

Species name (*: dematiaceous species)	Summed abundance (%)	Number of recorded sites (Max 9)
Trichoderma spp.	65.0	9
Penicillium spp.	47.2	9
**Anungitea continua*	40.6	9
**Anungitea uniseptata*	30.2	8
**Dictyochaeta simplex*	27.2	9
Mucor spp.[b]	25.0	9
Pestalotiopsis spp.[c]	20.0	9
Mortierella isabellina	18.0	9
**Endophragmiella uniseptata*	15.6	7
**Chaetopsina fulva*	15.4	8
Monacrosporium sp. 1	14.1	9
**Cladosporium* spp.[d]	12.8	8
**Dactylaria naviculiformis*	11.3	6

[a] Summed abundance (%)=number of needles on which the species occurred/total number of needles examined in this study (540) × 100.
[b] "*Mucor* spp." is mostly consisted of *Mucor hiemalis* and its varieties.
[c] "*Pestalotiopsis* spp." is consisted of *P. neglecta* and *P. foedans*.
[d] "*Cladosporium* spp." is mostly consisted of *C. cladosporioides*.
The rest is *C. tenuissimum* and *C. oxysporum* with only a few isolations.

Table 4. List of fungi with lower abundances (less than 10.0% summed abundances[a]).

Species name (*: dematiaceous species)
5.0–8.7% summed abundances
* *Chloridium virescens* var. *chlamydosporum*
Fusarium spp.
* *Idriella lunata*
Mortierella spp.[b]
* *Polyscytalum* sp. 1
* *Scolecobasidium constrictum*
* *Selenosporella curvispora*
1.1–4.8% summed abundances
Absidia glauca
* *Alacnophora* sp.
* *Alternaria alternata*
* *Ardhachandra cristaspora*
* *Aureobasidium pullulans*
* *Beltrania rhombica*
* *Camposporium* sp.
* *Chaetendophragmia triangularia*
* *Chalara longipes*
Clonostachys compactiuscula
Clonostachys rosea
* *Dactylaria clavata*
* *Dactylaria* sp. 2
* *Endophragmiella boewei*
Fusidium sp.
* *Gonytrichum macrocladum*
Mariannaea elegans
* *Mirandina corticola*
Monacrosporium sp. 2
Monocillium tenue
Mortierella alpina
Mortierella elongata
Mortierella globulifera
Mortierella minutissima
Mortierella nana
Mortierella ramanniana var. *ramanniana*
Mortierella verticillata
* *Psudodictyosporium wauense*
* *Ramichloridium obovoideum*
* *Rhinocladiella* sp. 1
* *Scolecobasidium humicola*
* *Septonema* sp.
* *Thysanophora penicillioides*
Verticillium lecanii
Verticillium sp. 2
Verticillium sp. 4
* 9804KM01[c]
* 9811KM01
0.2–0.7% summed abundances
Acremonium sp.
* *Acrodontium crateriforme*
* *Arthrinium phaeospermum*
Arthrobotrys sp.
Aspergillus sp.
* *Beltraniella* sp.
* *Camposporium japonicum*
Chaetomium sp.
Colletotorichum gloeosporioides
Cunninghamella sp.
* *Curvularia lunata*
Cylindrocarpon sp.
* *Dactylaria* sp. 1
* *Dactylaria* sp. 3
* *Dactylaria* sp. 4
* *Dactylaria* sp. 5
* *Dactylaria* sp. 6
* *Dictyosporium elegans*
* *Endophragmiella oblonga*
* *Epicoccum nigrum*
* *Gliomastix* sp.
* *Hormiactella* sp.
Hyalodendron sp.
* *Idriella* sp.
Monochaetia sp.
Mortierella alliacea
Mortierella vinacea
* *Murogenella* sp.
Phoma sp.
* *Polyscytalum* sp. 2
* *Polyscytalum* sp. 3
* *Rhinocladiella* sp. 2
* *Scolecobasidium variabile*
* *Selenosporella* sp.
Sphaerulina sp.
* *Sporidesmiella hyalosperma* var. *hyalosperma*
Verticillium sp. 1
Verticillium sp. 3
* 9804MTM03
* 9804MTM06
* 9804OM07
* 9805HM04
* 9808MTM06
* 9808YM03
* 9811HM03
* 9811HM11
* 9811HM12
* 9811KM02
* 9811KSM02
* 9811YM01

a) Summed abundance (%) = number of needles on which the species occurred/total number of needles examined in this study (540) × 100.

b) "*Mortierella* spp." means all *Mortierella* species observed in the samples of spring except for *M. alpina*.

c) The representative culture number of an unidentified recognizable taxa.

Table 5. Abundances (%) of selected dematiaceous fungi[a] at each site.

Species name	Summed abundance	Kashima	Kiyosumi	Hatoyama	Takao	Tsukuba	Matsuida	Ooyama	Hakone	Yamanaka
Anungitea continua	40.6	35.0	61.7	55.0	40.0	43.3	31.7	38.3	50.0	10.0
Anungitea uniseptata	30.2	63.3	15.0	68.3	13.3	43.3	23.3	0.0	15.0	30.0
Dictyochaeta simplex	27.2	31.7	11.7	48.3	53.3	18.3	5.0	36.7	28.3	11.7
Endophragmiella uniseptata	15.6	8.3	0.0	0.0	28.3	15.0	6.7	25.0	26.7	30.0
Chaetopsina fulva	15.4	35.0	10.0	21.7	38.3	18.3	0.0	3.3	1.7	10.0
Cladosporium spp.	12.8	26.7	5.0	18.3	33.3	5.0	15.0	0.0	6.7	5.0
Dactylaria naviculiformis	11.3	0.0	18.3	25.0	13.3	38.3	3.3	0.0	3.3	0.0

[a] Dematiaceous fungi with more than 10.0% summed abundance.

sushima, *Anungitea uniseptata* Matsushima and *D. simplex* occurred on more than one-fourth of total needles as well as *Mucor* spp. Most of fungi listed in Table 4 appeared in all sites, but five dematiaceous species, *A. uniseptata, Endophragmiella uniseptata* (Ellis) Hughes, *C. fulva, Cladosporium* spp. (mostly *C. cladosporioides* (Fresen.) de Vries) and *D. naviculiformis* were not recorded from one or more sites.

Selection of specific dematiaceous species Table 5 shows the dematiaceous fungi which appeared with more than 10% summed abundance. These fungi were widely distributed and recorded with abundance value of 30% or more in at least one site. *Anungitea continua* and *D. simplex* appeared in all sites. The former species was particularly abundant and colonized one-third of sampled needles at most sites. *Anungitea uniseptata* was another abundant fungus at most sites although it was not recorded at Ooyama.

Table 6 listed dematiaceous fungi which were recorded with 50% or more abundance on at least one sampling time and at one site. Five such dematiaceous species were recorded from Kashima and Hatoyama sites, while only one species was recorded from Kiyosumi, Hakone and Yamanaka sites. Thus, the number of dominant species at each sampling site varied. *Anungitea continua* is listed at eight sites and appears to be a prevailing dematiaceous fungus in this region. In contrast, *Selenosporella curvispora* MacGarvie, *Ramichloridium obovoideum* (Matsushima) de Hoog, *Polyscytalum* sp. and *Chloridium virescens* var. *chlamydosporum* (Beyma) Gams & Holubova-Jechova appeared with 50% or more abundance at only one site (Table 6). However, their values of summed abundances were less than 10%.

Effects of climatic elements on the distribution pattern of dematiaceous fungi The correlations between the species abundances and annual mean temperatures at sampling sites are shown in Table 7. The abundance of *C. fulva* showed a significant positive correlation with increasing temperature, while *E. uniseptata* showed a trend towards decreasing abundance at higher temperatures ($p=0.062$). There were no other significant cor-

Table 6. List of dematiaceous fungi which occur with 50% or more abundance in at least one sampling time.

Kashima	*Anungitea continua* *Anungitea uniseptata* *Chaetopsina fulva* *Cladosporium* spp. *Dictyochaeta simplex*
Kiyosumi	*Anungitea continua*
Hatoyama	*Anungitea continua* *Anungitea uniseptata* *Dictyochaeta simplex* *Ramichloridium obovoideum* *Selenosporella curvispora*
Takao	*Anungitea continua* *Chaetopsina fulva* *Dictyochaeta simplex* *Endophragmiella uniseptata*
Tsukuba	*Anungitea continua* *Anungitea uniseptata* *Dactylaria naviculiformis*
Matsuida	*Anungitea continua* *Polyscytalum* sp.
Ooyama	*Anungitea continua* *Dictyochaeta simplex* *Chloridium virescens* var. *chlamydosporum*
Hakone	*Anungitea continua*
Yamanaka	*Anungitea uniseptata*

Table 7. Correlations between annual mean temperature and abundances of selected dematiaceous fungi[a].

Species name	Correlation (r)	p value
Anungitea continua	0.5731	0.107
Anungitea uniseptata	0.4571	0.216
Dictyochaeta simplex	0.3825	0.310
Chaetopsina fulva	**0.7143**	**0.031**[b]
Endophragmiella uniseptata	−0.6420	0.062
Cladosporium spp.	0.5749	0.105
Dactylaria naviculiformis	0.4126	0.270

[a] Dematiaceous fungi with more than 10.0% summed abundance.
[b] Significance: $p \leqq 0.05$.

relations.

Discussion

In this study, we found that several dematiaceous fungi occurred abundantly and widely distributed on fallen fir needles in the Kanto district. They are *A. continua, A. uniseptata, D. simplex, E. uniseptata, C. fulva, C. cladosporioides* and *D. naviculiformis*. Except for a ubiquitous saprophyte, *C. cladosporioides*, they may invade into dead needles from the O horizon after needle fall.

Among them, *A. continua, A. uniseptata* and *E. uniseptata* are dominant surface colonizers of the F_1-type needles of fir in the district, and probably the major dark hyphal network formers to darken fallen needles judging from their wide distribution and stout dark mycelia in culture. On decaying pine needles, the dematiaceous species with this habit, *Sympodiella acicola* Kendrick and *Troposporella monospora* (Kendrick) Ellis (=*Helicoma monospora* Kendrick), were first discovered by Kendrick and Burges (1962). We consider that the three fungal species reported on fir here and the two species on pine are ecologically equivalent. *Dictyochaeta simplex, C. fulva* and *D. naviculiformis* are also dematiaceous species but their mycelia are light colored on decaying fir needles and also on the agar surface. Therefore, their contribution to darkening of needles may be slight.

Unfortunately, the records of the above-mentioned major network formers from decaying fir needles are few. For instance, two *Anungitea* species were described by Matsushima (1975) based on the isolates from decaying pine needles in Japan and *A. continua* was rediscovered on the F_1 layer needles of *Pinus densiflora* Sieb. & Zucc. at Sugadaira in Japan (Tokumasu, 1978). However, there have been no other records on *A. uniseptata* in Japan. Aoki et al. (1990) found an *Anungitea* species on decaying fir needles in Mt. Tsukuba, the Kanto district. Judging from the results of our study, the species might be *A. continua* or *A. uniseptata*.

In Europe and North America, several studies of litter fungi in the O horizon of fir forests have been carried out (Hayes, 1965; Brandsberg, 1969; Gourbière, 1979, 1982; Puppi et al. 1991; Aoki et al., 1992; van Maanen and Gourbière, 1997), but there are no records of *Anungitea* spp. except for Aoki et al. (1992), who reported that *Anungitea* sp. occurred abundantly on decaying fir needles at a site in Germany. In Europe, *A. continua* was recorded from pine needles rather than fir needles. Kirk (1983) reported that *A. continua* appeared to be restricted to pine needles in British Isles. Moreover, Tokumasu et al. (1994) also found *A. continua* with *Anungitea fragilis* Sutton on washed pine needles in Germany. However, the results of our study strongly suggest that *A. continua* and *A. uniseptata* have a stronger preference for fallen needles of *Abies firma* than for those of pines in Japan.

In the present study, *E. uniseptata* was recorded more abundantly from rather high altitudinal sites among the study sites and appears to prefer to cooler climate. Contrary to the species, *C. fulva* tended to occur in relatively warm sites. Tokumasu (1996) noted that this species quickly invaded into fallen pine needles in summer at Sugadaira where a cold temperate climate dominates. Milder climatic conditions at several sampling sites in the Kanto district may be largely contributed to the success of colonization of this species to fallen fir needles. Interestingly, both fungi have not been detected on decaying fir needles in Europe. It seems to reflect the macroclimatic differences between both regions in the composition of the isotopic fungal species.

Gourbière and Pépin (1983) observed that *P. verrucosum* and *Endophragmiella* sp. occurred abundantly in the F_1 layer of silver fir forests in France. Aoki et al. (1992) also observed *P. verrucosum* and *Endophragmiella boewei* (Crane) Hughes on fallen fir needles in Germany, and Puppi et al. (1991) also founded *Polyscytalum* spp. and *Endophragmia* sp. in a woodland in southern Italy. Aoki et al. (1990) also reported *E. boewei* in Mt. Tsukuba of the Kanto district, Japan. In the present study, *Polyscytalum* sp. and *E. boewei* were also recorded but infrequently.

In Europe, *Thysanophora penicillioides* (Roumèguere) Kendrick invades freshly fallen needles vigorously and persists there until the needles darken (Gourbière, 1979, 1982; Puppi et al., 1991; Aoki et al., 1992; Sieber-canavesi and Sieber, 1993; van Maanen and Gourbière, 1997). In this study, however, the species rarely appeared and its abundance was only 1.1%. According to Aoki et al. (1990), *T. penicillioides* occurred on the L and the F_1 layer needles in winter in Mt. Tsukuba, Japan. Unfortunately, we did not examine any sample collected in winter. Therefore, the distribution of this fungus on fallen fir needles in Japan remains uncertain.

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