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Variation between freshwater and terrestrial fungal communities on decaying bamboo culms

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Abstract

Fungal communities on decaying culms of a bamboo host (*Phyllostachys bambusoides*) from freshwater and adjacent terrestrial habitats were identified. Collections were made at Xiao Bai Long Mountain, Yiliang, Yunnan, China in the winter and summer. In each collection, 100 similar-sized bamboo culms were collected, comprising 50 submerged samples from a stream and 50 terrestrial samples from adjacent riparian vegetation. A total of 82 fungal taxa were recorded from the samples, including 30 ascomycetes and 52 anamorphic fungi. The frequency of occurrence of these fungi were recorded and the Shannon–Weiner indices (H') were applied to evaluate fungal diversity. The results showed that variation of the fungal diversity between the summer and winter collections was insignificant ($0.2 < p < 0.5$). Fungal diversity on submerged bamboo however, was significantly higher than that on terrestrial bamboo ($p < 0.001$). Further findings were that: (1) some commonly recorded freshwater and terrestrial taxa were found in both habitats, but overall there were only 15 overlapping species between the two habitats; (2) the dominant species in each habitat were considerably different, and (3) only a few fungi were dominant, while most species were rare, being recorded only once or twice. Factors responsible for the distribution patterns and variations in composition of the fungal communities are discussed.

Introduction

Dead plant substrates are essential components in terrestrial (Boddy and Watkinson 1995; Delaney et al. 1997) and freshwater ecosystems (Maser and Sedell 1994; Jacobson and Jacobson 1999). Their decomposition in these ecosystems, resulting either from physical or biological factors, is a vital process in the recycling of carbon and other nutrients. Wood-inhabiting fungi have been shown to play an important role in this process because they can produce various wood decay enzymes (Wong et al. 1998; Pointing 2001; Bucher et al. 2005).

Various aspects of the systematics, distribution and biodiversity of wood-inhabiting fungi have been studied in terrestrial ecosystems (e.g. Lodge 1997; Sigler et al. 2000; Edman and Jonsson 2001; Norden and Paltto 2001). Wood-inhabiting fungi in freshwater environments however, have received less attention. Most investigations of freshwater fungi had previously been carried out in temperate regions such as the UK and the USA, but recently

there have been more studies in tropical and subtropical regions (e.g. Tsui et al. 2000; Ho et al. 2001; Tsui and Hyde 2004). Nevertheless, there are large unstudied continents and there is a need for studies on the differences of fungal communities between terrestrial and freshwater habitats.

Bambusicolous fungi have been investigated by several authors. Hyde et al. (2001) provided a checklist of saprobic fungi on *Bambusa* and *Dendrocalamus* spp. The vertical distribution and succession of saprobic fungi occurring on decaying bamboo culms have also been studied (Hyde et al. 2002; Zhou and Hyde 2002). These studies however, focused on terrestrial fungi. There is only one previous study focusing on fungi on submerged bamboo, from the Liput River in the Philippines (Cai et al. 2003). The objectives of the present study were to investigate the fungal communities occurring on bamboo culms (*Phyllostachys bambusoides*) and to examine the variation of fungal communities from different habitats. Factors that might be responsible for the distribution patterns of the different fungal communities are addressed.

Materials and methods

Visits were made to a small stream in Xiao Bai Long Mountain, Yiliang, Kunming, Yunnan, China on 6 January 2003 (winter) and 6 July 2003 (summer). The collection site is located 54 km to the south-east of Kunming City, and the climate in this area is warm temperate without snow in winter (average year temperature 16.3 °C, ranging from 8 to 21 °C). The wet season is from May to October, with 80–85% rainfall for the whole year. The riparian vegetation is dominated by a bamboo species, *Phyllostachys bambusoides*, that grows densely alongside the stream, and with large amounts of dead, decayed culms on the forest floor and submerged in the stream. Samples were randomly collected along a 300 m stretch of the stream. Caution was taken to ensure that the bamboo samples were in a similar state of decay, i.e. with fungal communities expected to be in a late or medium succession stage. During each visit, 50 submerged bamboo culms were collected from the stream and 50 terrestrial bamboo culms were collected from the forest floor. The dimensions of these samples ranged from ca. 1 cm diameter × 30 cm to ca. 5 cm diameter × 30 cm. Samples were placed in snap lock plastic bags and returned to the laboratory. They were then incubated at room temperature in plastic boxes in which moistened tissue paper was added to maintain humidity. Bamboo culms were examined under a dissecting microscope for fungal fruiting bodies after one week, then periodically over the next month. Fungi were identified to species level where possible, while those we could not identify were also differentiated into morphospecies. Materials supporting fungi were then air-dried and deposited in HKU(M).

Species-area curves were plotted for each collection to examine the sample size (Begon et al. 1992). In order to compare the dominance of fungi among different collections, the data acquired from each collection are presented as frequency of occurrence, which is the number of samples that a particular species occurred on divided by the number of samples examined. The total number of species, frequency of occurrence of each species and the number of fungi per sample were recorded and calculated. Shannon–Weiner diversity index (H'), which incorporate species richness and species evenness (Begon et al. 1992), was applied to evaluate the diversities of fungal communities. A t-test was performed to compare the Shannon–Weiner indices between different fungal communities (Hutcheson 1970). Dominance-diversity curves were plotted as a reflection of the relative abundance of species in each sampling habitat (Kent and Coker 1992). To compare the similarity of the species composition between different habitats, Sørensen's index of similarity (S') was applied and expressed with values between 0 (no similarity) and 1 (absolute similarity) (Magurran 1988).

Results

A total of 200 bamboo culms (100 from the winter collection and another 100 from the summer collection) were examined for fungi, yielding 30 ascomycetes (representing 37% of all taxa) and 52 anamorphic taxa (63%). The list of taxa from each collection and their frequency of occurrence are given in Table 1. The total frequency of occurrence of each species, species richness, species evenness, number of fungi per sample and Shannon–Weiner diversity index (H') of each

collection were calculated and are also shown in Table 1. Species area curves were plotted to indicate the increasing number of fungi with the examination of samples (Figure 1). The asymptotes were reached at around 24–40 samples (Figure 1). Therefore, the samples size (50 samples for each collection) used in this investigation can provide a reasonable estimate of the fungal community in this particular ecological niche.

Several common genera were identified in this study such as *Annulatascus*, *Dictyochaeta*, *Massarina* and *Spadicoides*, with each genus represented by more than three different species. Overall, the most common taxon was *Astrosphaeriella trochus*, with 18% frequency of occurrence. Other common species were *Spadicoides bambusicola* (16%), *Sporidesmium bonarii* (15.5%), *Annulatascus biatriisporus* (12.5%), *Corynespora cassiicola* (11%) and *Sporidesmiella hyalosperma* (11%) (Table 1). Five of the most common species from each specific collection are also indicated in Table 1. It was found that *S. hyalosperma*, *C. cassiicola*, *A. trochus* are shared by two freshwater collections; while *S. bambusicola*, *A. biatriisporus, S. bonarii* are shared by two terrestrial collections (Table 1). However, with the exception of *S. bonarii*, no common species overlapped between different habitats (Table 1).

Species abundance curves were plotted and shown in Figure 2. In the winter and summer collections, there were only four and three fungi with more than 10 occurrences, respectively, while a high proportion of species occurred only once or twice (Figure 2). By evaluating the Sørensen's indices of similarity between different fungal communities, it was found that the highest similarity (S') was that between the two terrestrial collections in the winter and summer (0.478), followed by that between two freshwater collections in winter and summer (0.338). The lowest similarity is from two unrelated communities of summer/terrestrial and winter/freshwater (0.258).

Higher species richness was found from the submerged samples compared with the terrestrial samples (37 vs. 21 in the winter, 40 vs. 25 in the summer). The number of fungi per sample, and the Shannon–Weiner indices are also higher in freshwater samples (Table 1). The *t*-test indicates

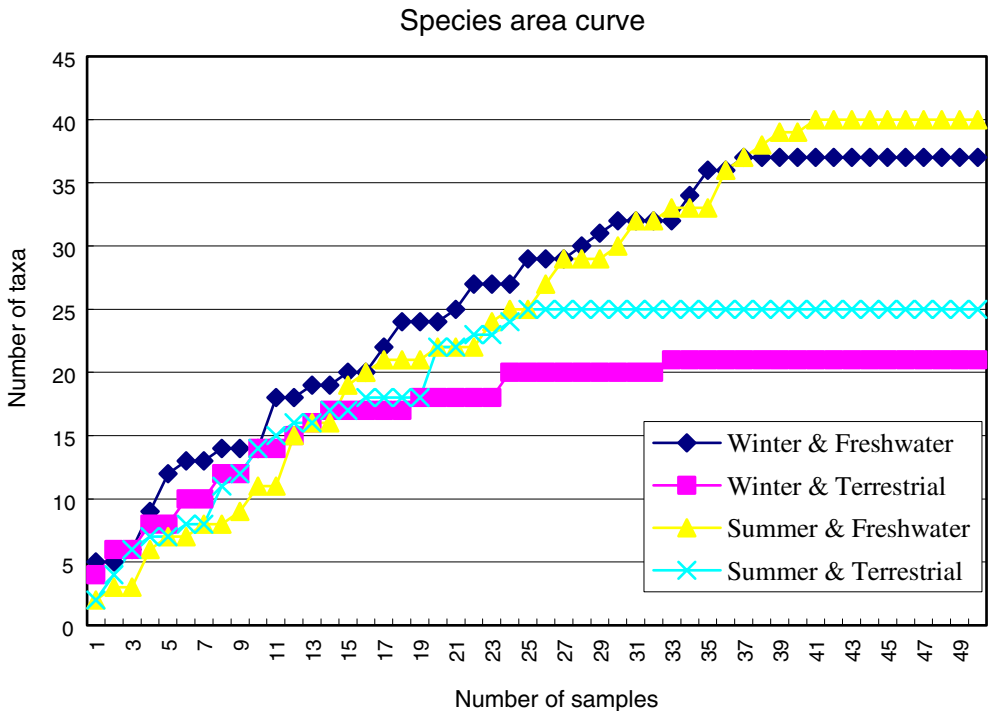

Figure 1. Species-area curve of number of fungi identified against number of samples examined.

Table 1. Frequency of occurrence (FO) of fungi on culms of *Phyllostachys bambusoides*.

Taxa	FO (W and F)	FO (W and T)	FO (S and F)	FO (S and T)	FO (overall 200 samples)
Astrosphaeriella trochus	**26%**	2%	**34%**	10%	**18%**
Spadicoides bambusicola	8%	**42%**		**14%**	**16%**
Sporidesmium bonarii	4%	**14%**	**14%**	**30%**	**15.5%**
Annulatascus biatriisporus	6%	**20%**	6%	**18%**	**12.5%**
Sporidesmiella hyalosperma	**30%**		**14%**		**11%**
Corynespora cassiicola	**32%**		**12%**		**11%**
Delitschia sp.	6%	**20%**	4%	12%	10.5%
Massarina arundinariae				**28%**	7%
Coelomycete sp. 1		6%	4%	**16%**	6.5%
Candelabrum brocchiatum	**20%**		4%		6%
Savoryella lignicola	**16%**		6%		5.5%
Roussoëlla hysterioides	2%	10%	6%	4%	5.5%
Ityorhoptrum verruculosum	14%	4%			4.5%
Nigrospora state of *Khuskia oryzae*		8%	8%		4%
Brachysporiella gayana	4%	2%	8%		3.5%
Cordana uniseptata			8%	6%	3.5%
Erostella minima		**12%**		2%	3.5%
Pseudohalonectria lutea	14%				3.5%
Phaeoisaria clematidis		8%	2%	2%	3%
Aniptodera chesapeakensis	10%				2.5%
Clohesyomyces aquaticus	10%				2.5%
Dictyochaeta fimbriaspora		10%			2.5%
Dictyochaeta sp. 1		2%	2%	6%	2.5%
Halosarpheia sp.	10%				2.5%
Aquaticola ellipsoidea			**8%**		2%
Ceratosporium sp.		4%		4%	2%
Hyphomycete sp. 1	8%				2%
Papulaspora sepedonioides			8%		2%
Spadicoides minuta			8%		2%
Coelomycete sp. 2	2%		4%		1.5%
Coelomycete sp. 3			6%		1.5%
Diplococcium aquaticum	6%				1.5%
Dyrithium sp.		6%			1.5%
Massarina australiensis			6%		1.5%
Massarina desmonci	6%				1.5%
Phaeosphaeria sp. 1	2%		2%	2%	1.5%
Sporoschisma saccardoi	4%		2%		1.5%
Acrogenospora setiformis	2%		2%		1%
Annulatascus fusiformis			4%		1%
Bactrodesmium sp.	4%				1%
Coelomycete sp. 4	2%	2%			1%
Coelomycete sp. 5			4%		1%
Corynespora foveolata	4%				1%
Dictyochaeta sp. 2				4%	1%
Gonytrichum macrocladum	4%				1%
Helicomyces roseus			4%		1%
Massarina eburnea				4%	1%
Nais inornata			4%		1%
Nectria sp.			4%		1%
Payosphaeria minuta			4%		1%
Pseudobotrytis terrestris	2%			2%	1%
Savoryella curvispora			4%		1%
Sphaeromyces sp.	4%				1%
Acremonium kiliense		2%			0.5%
Acrogenospora sphaerocephala			2%		0.5%
Annulatascus aquaticus	2%				0.5%

Table 1. Continued.

Taxa	FO (W and F)	FO (W and T)	FO (S and F)	FO (S and T)	FO (overall 200 samples)
Chalara sp.	2%				0.5%
Dactylaria sp.			2%		0.5%
Dactylaria triseptata		2%			0.5%
Dendrodochium sp.	2%				0.5%
Dictyosporium schizostachyfolium			2%		0.5%
Dictyosporium zeylanicum				2%	0.5%
Didymosphaeria sp.				2%	0.5%
Eriocercospora balladynae	2%				0.5%
Guignardia sp. 1			2%		0.5%
Guignardia sp. 2				2%	0.5%
Halosarpheia aquadulcis			2%		0.5%
Helicosporium nizamabadense	2%				0.5%
Hypoxylon sp.				2%	0.5%
Monacrosporium sp.	2%				0.5%
Ophioceras guttulatum			2%		0.5%
Phaeosphaeria sp. 2				2%	0.5%
Spadicoides cordanoides			2%		0.5%
Sporoschisma uniseptatum			2%		0.5%
Ascomycete sp. 1		2%			0.5%
Ascomycete sp. 2				2%	0.5%
Coelomycete sp. 6				2%	0.5%
Coelomycete sp. 7				2%	0.5%
Hyphomycete sp. 2	2%				0.5%
Hyphomycete sp. 3	2%				0.5%
Hyphomycete sp. 4		2%			0.5%
Hyphomycete sp. 5			2%		0.5%
Species richness	37	21	40	25	82
Species evenness E	0.88	0.85	0.91	0.85	0.74
Number of fungi per sample	2.78	1.80	2.24	1.80	2.16
Shannon–Weiner indices (H')	3.18	2.60	3.37	2.74	3.30

W: winter; S: summer; F: freshwater; T: terrestrial; FO of the five of the most common species occurring in each collection are in bold.

that the fungal diversity between freshwater and terrestrial samples is significant ($p < 0.001$), while that between winter and summer samples is insignificant ($0.2 < p < 0.5$).

Discussion

Species composition and species abundance

The composition of fungal communities on substrates is thought to be affected by a number of factors (Strong 1992; Lodge and Cantrell 1995). Wood-Eggenschwiler and Bärlocher (1985) have suggested that temperature and geographical factors were crucial in determining the Ingoldian fungal community in streams. There are considerable differences in the fungal communities recorded in the present study (temperate region) and that from submerged bamboo in tropical Philippines (Cai et al. 2003). Only two taxa were recorded at both sites. This may illustrate the effects of temperature plus biogeography on the fungal communities. The effect of temperature on the growth of fungi has been examined experimentally by Yuen et al. (1998). They found tropical fungi grow faster than temperate fungi at 25 °C. This indicates that temperate fungi are unlikely to be able to compete with tropical fungi in tropics. Competitive interactions are also likely to be important in determining fungal communities (Shearer and Zare 1988; Wicklow 1992; Dix and Webster 1995). Yuen et al. (1999a, b) and Fryar et al. (2001) showed that fungi are competitive and inhibit other fungi, probably affecting community structure.

Fungal communities comprising a small proportion of dominant species and a large proportion of rare species have been reported from decaying substrates in various habitats (e.g. Lodge

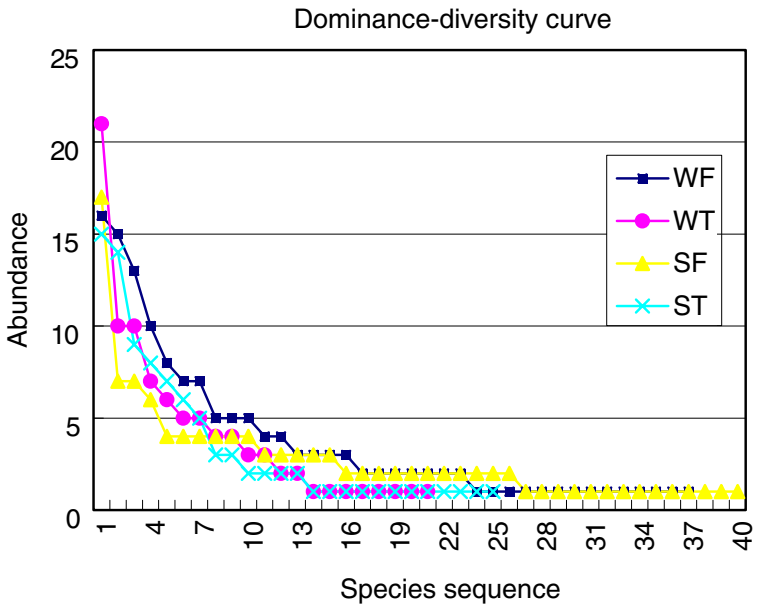

Figure 2. The dominance–diversity curve for summer and winter collections (Abbreviations: S: summer, W: winter, F: freshwater, T: terrestrial).

and Cantrell 1995; Tsui et al. 2000). The dominant species are thought to play an important role in the decomposition of substrates. In the present study, the most common species, *A. trochus*, forms numerous, gregarious, large and carbonaceous ascomata on the bamboo surfaces. Old ascomata leave a flat, shallow sunken area on the host surface, indicating that it may have an important role in decomposing bamboo samples. *A. trochus* is shown to be more effective than many rare fungi in a preliminary investigation of lignin degradation (Cai per. observ.). *Astrosphaeriella striatispora*, another species from a same genus, has been shown experimentally to have significant ability to solubilize lignin, in amounts comparable with some white-rot basidiomycetes (Bucher et al. 2004). The rare fungi however, may also have ecological significance, since the decomposition of the woody debris might be a synergistic process caused by various taxa (Yuen et al. 1999b).

Bamboo decomposing fungi, are they host preferent?

In the present study, most fungi recorded from *P. bambusoides* have previously been reported from a non-bamboo host. For instance, among the 49 species identified to species level, at least 42 have previously been reported from a non-bamboo host, although *A. trochus*, *Cordana uniseptata*, *S. bambusicola* and *Spadicoides minuta* are presently only known from bamboo. Our results suggest a low level of host-specificity in bambusicolous fungi. Similar findings have been reported by Cai et al. (2003) from submerged bamboo in Philippines. Following a review of leaf decomposing fungi, Lodge (1997) has suggested the host preference is often quantitative rather than qualitative, i.e. communities on different hosts have greater differences in relative abundances rather than in species composition. Lodge's suggestion seems applicable for lignicolous fungi. Luo et al. (2004) compared fungi on three monocotyledonous hosts and reported a high similarity in species composition (similarity indices 0.491–0.610), but species abundance in communities was quite different. There seems to be little evidence to support host-specificity of saprobic fungi on bamboo. Hyde et al. (2001) reported a small proportion of overlapping species between two bamboo hosts *Bambusa* and *Dendrocalamus*, and although this would appear to be significant, it should be noted that most bambusicolous fungi

recorded had previously been recorded from other hosts. We can therefore hypothesize that most saprobic bambusicolous fungi are generalists, but the host plays an important role in determining species composition, and the structure of fungal community, especially the relative frequencies of individual species. Nevertheless, our understanding of host preference/specificity is still incomplete. Polishook et al. (1996) hypothesized that most of the host preference of saprobic fungi may be related to physical and chemical characteristics of host rather than host-specificity in a taxonomic sense. Paulus et al. (unpubl. data) also suggested that plant secondary metabolites, leaf minerals and physical characteristics may affect the distribution of saprobic fungi on leaves. For freshwater hyphomycetes, although different substrates in streams may selectively inhibit or stimulate colonization by different fungal species (Bärlocher 1992), most fungi are believed to be capable of colonizing a wide range of hosts (Thomas et al. 1989; Suberkropp 1992; Fabre 1996).

Why do submerged samples support a higher fungal diversity?

Our results show that submerged bamboo culms support a significantly higher fungal diversity than their terrestrial counterparts. Similar results have also been reported from the woody samples by Fryar et al. (2004), in which the submerged wood supports a higher fungal diversity than the terrestrial wood. Nevertheless, there have been very limited data to support the expansion of this conclusion to other hosts or ecological sites, since other factors such as water chemistry, temperature and riparian vegetation may also impact fungal diversity in streams. In freshwater ecosystems, submerged wood has been shown to play a more prominent role in organic matter uptake and transfer, as compared to terrestrial wood in terrestrial ecosystems (Tank and Winterbourn 1996). Since it has been widely assumed that saprobic heterotrophic fungi are nutrient limited (Dix and Webster 1995; Lodge and Cantrell 1995; Tank and Winterbourn 1996; Koide and Kabir 2001; Hyde et al. 2005), it may be a necessity for fungi in freshwater to be capable of colonizing submerged wood. This may be considered as a reason for the higher diversity of fungi on submerged culms in the present study. In addition, freshwater fungi have various mechanisms to aid spore dispersal and attachment in ecosystems, which have been shown to be very important for fungal colonization and establishment in freshwater (Hyde and Goh 2003). Sridhar and Bärlocher (2000), when considering aquatic fungal communities, pointed out that submerged substrates in aquatic environments are suitable to allow fungal colonization and ultimately establishment of a fungal community. Although the submergence under water may decrease the oxygen concentration around the samples, which might be a negative impact to the fungal diversity, the fact that the fast flowing water in the collection site may largely compensate for the shortage of the oxygen.

Habitat preference

In the present study, species composition on *Phyllostachys bambusoides*, shows variation between different habitats. In the summer collection, 30 species were unique to the freshwater samples and 15 species were unique to the terrestrial samples, with only 10 overlapping species. Freshwater fungi have evolved from terrestrial fungi and many of them have evolved specialized adaptation mechanisms (Shearer 1993; Wong et al. 1998; Hyde and Goh 2003; Belliveau and Bärlocher 2005; Vijaykrishna 2005). In this study, some fungi collected from the submerged bamboo culms are typical freshwater fungi (e.g. *Aquaticola ellipsoidea*, *Aniptodera chesapeakensis*, *Annulatascus aquaticus*, *Annulatascus fusiformis*, *Savoryella curvispora*, *Savoryella lignicola*, *Diplococcium aquaticum*, *Halosarpheia aquadulcis* and *Nais inornata*). They have specialized adaptation mechanisms for life in freshwater, such as a massive apical ascal ring (to actively eject ascospores), ascospore sheaths (aid spore attachment), or ascospore appendages (aid spore attachment and floatation in water) (Hyde and Goh 2003). On the other hand, typical terrestrial fungi such as *Hypoxylon* sp., *Guignardia* sp., *Massarina eburnea*, *Didymosphaeria* sp. and *Ceratosporium* sp. are recorded from the terrestrial bamboo culms in this study. Wong and Hyde (2002) investigated the distribution of fungi on intertidal grasses *Phragmites australis* and sedge *Schoenoplectus litoralis* in Hong

Kong, and also found that typical freshwater taxa, such as *A. chesapeakensis* and *H. aquadulcis* occurred on the submerged parts, while terrestrial taxa such as *Cladosporium cladosporioides*, *Dictyochaeta phragmitis* and *Tetraploa aristata* occurred on the aerial parts. The fact that submerged and terrestrial bamboo are dominated by different fungal communities indicates that habitat may play an important role in determining species composition by selectively stimulating or inhibiting growth of specific fungi. The different fungal communities may result from different mechanisms of species initial colonization, species ability in host exploitation and competition of available resources. Although typical freshwater fungi have been recorded frequently from freshwater, they may not be habitat exclusive. Annulatascaceous species have previously been assumed to be unique to freshwater environment (Wong et al. 1998), but they have been successively recorded from terrestrial habitats (e.g. Dalisay 1998; Fröhlich and Hyde 2000; Hyde et al. 2001). In this study, *A. biatriisporus* was recorded from both freshwater and terrestrial samples. *Jahnula* is probably the only genus which is presently only known from freshwater.

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