Eur. J. Entomol. **107**: 73–79, 2010
http://www.eje.cz/scripts/viewabstract.php?abstract=1511
ISSN 1210-5759 (print), 1802-8829 (online)

Incidence of infection of carabid beetles (Coleoptera: Carabidae) by laboulbenialean fungi in different habitats

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Key words. Coleoptera, Carabidae, ectoparasitic fungi, Ascomycetes, *Laboulbenia*, microhabitat, overwintering sites

Abstract. The prevalence of obligate parasitic fungi may depend partly on the environmental conditions prevailing in the habitats of their hosts. Ectoparasitic fungi of the order Laboulbeniales (Ascomycetes) infect arthropods and form thalli on the host's body surface. Although several studies report the incidence of infection of certain host species by these fungi, quantitative data on laboulbenialean fungus-host arthropod interactions at the host assemblage level are rarely reported. To clarify the effects of host habitats on infection by ectoparasitic fungi, the incidence of infection by fungi of the genus *Laboulbenia* (Laboulbeniales) of overwintering carabid beetles (Coleoptera: Carabidae) in three habitats, a riverside (reeds and vines), a secondary forest and farmland (rice and vegetable fields), were compared in central Japan. Of the 531 adults of 53 carabid species (nine subfamilies) collected in the three habitats, a *Laboulbenia* infection of one, five and one species of the carabid subfamilies Pterostichinae, Harpalinae and Callistinae, respectively, was detected. Three species of fungus were identified: *L. coneglanensis*, *L. pseudomasei* and *L. fasciculate*. The incidence of infection by *Laboulbenia* was higher in the riverside habitat (8.97% of individuals; 14/156) than in the forest (0.93%; 2/214) and farmland (0%; 0/161) habitats. Furthermore, the incidence of infection by *Laboulbenia* in the riverside habitat ranged from 0 to 33.3% and differed significantly in the ten microhabitats (riverbank, edge of track, tall reeds, kudzu vines, slope of a hollow, rotten wood, vine reeds, under stones, the shoulder of a terrace and marshy ground) where the carabid beetles overwintered. These results suggest that host habitats and microhabitats are closely associated with successful infection by laboulbenialean fungi.

INTRODUCTION

Fungi associated with arthropods are known to have various types of relationships with their hosts (e.g., pathogenic, parasitic, phoretic and mutualistic; Roy, 1994; Vega & Blackwell, 2005; Roy & Cottrell, 2008). Ectoparasitic fungi of the order Laboulbeniales are obligate ectoparasites that infect arthropods, mainly insects, and form thalli on the host's body surface (Tavares, 1985; Weir & Hammond, 1997a, b). As laboulbenialean fungi are easy to detect on the integument of host arthropods (Weir & Hammond, 1997a, b) there are several studies of the incidence of infection of certain hosts by these fungi (Welch et al., 2001; Zerm & Adis, 2004; Riddick & Schaefer, 2005; Harwood et al., 2006; Riddick, 2006). Quantitative data on laboulbenialean fungus-host arthropod interactions at the host assemblage level (multiple host species), however, are rarely reported.

The diversity of Laboulbeniales depends on the host arthropod taxa. For example, the insect order Coleoptera includes 80% of the known host arthropod species (Weir & Hammond, 1997b). Furthermore, the coleopteran families, Carabidae and Staphylinidae, include 30% and 27% of coleopteran host species of Laboulbenialean fungi in Europe and 27% and 26% in Asia, respectively (Weir & Hammond, 1997a, b). The diversity of laboulbeniales also depends on the host arthropod guilds and habitats (e.g., predators and forest litter; Weir & Hammond, 1997b). Laboulbenialean fungi are likely to infect hosts that overwinter as adults and have overlapping generations of adults (Weir & Hammond, 1997a, b). In these fungi, the adhesive ascospores are transmitted during direct contact between two host individuals, which often involves sexual encounters (Weir & Hammond, 1997b). Indirect infection (substrate infection) is thought to be extremely unimportant compared to direct infection because spore survival is extremely short and not greatly affected by environmental conditions (De Kesel, 1996a, b; Weir & Hammond, 1997b). However, the successful infection of hosts by laboulbenialean fungi is likely to depend on the conditions in the microhabitats occupied by the hosts (De Kesel, 1996b). Only a few studies explore the difference in the incidence of infection by laboulbenialean fungi among microhabitats (Andersen & Skorping, 1991; De Kesel, 1996b). Andersen & Skorping (1991) examined the incidence of infection in assemblages of the carabid genus *Bembidion* in different microhabitats along a riverbank and showed it is higher in vegetation than in open habitats. De Kesel (1996b) experimentally infected several carabid species living in different microhabitat conditions (i.e., in terms of soil composition) and showed that host microhabitats as well as host taxa are important for the successful establishment of these fungi.

Beetles of the family Carabidae, the most abundant host group for laboulbenialean fungi (Weir & Hammond, 1997a, b), inhabit various types of environment (Lövei & Sunderland, 1996). Therefore, carabid beetles have frequently been used as environmental indicators of urbanization and forest fragmentation (Niemelä et al., 2002; Rainio & Niemelä, 2003). Habitats such as grasslands,

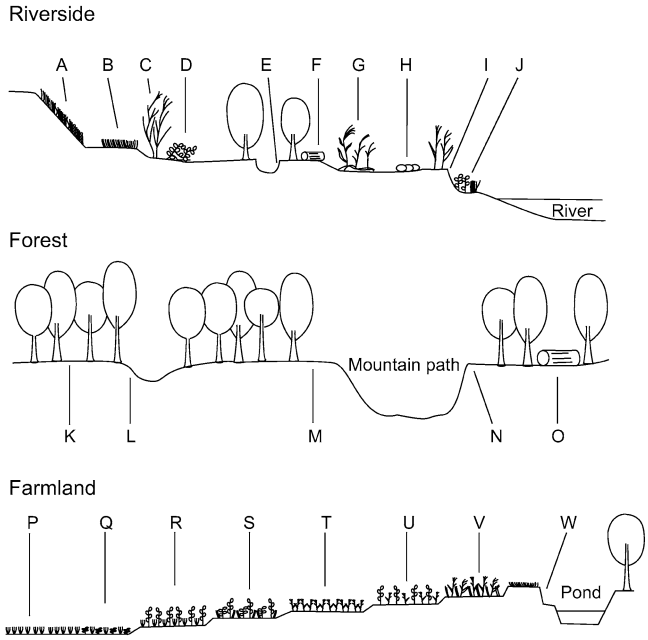

Fig. 1. Cross-sectional outline of the ten, five and eight microhabitats sampled at the riverside, forest and farmland sites, respectively. A – riverbank; B – border of path; C – tall reeds; D – kudzu vine; E – slope of a hollow; F – rotten wood; G – vine reeds; H – stones; I – shoulder of a terrace; J – marshy ground (see Table 1 for details); K – forest floor; L – small hollow in the forest; M – forest edge; N – side of a mountain path; O – rotten wood; P – arable rice field; Q – wet fallow rice field; R – dry fallow rice field; S – fallow vegetable field 1; T – fallow potato field; U – fallow vegetable field 2; V – old fallow field; W – bank of an irrigation pond (see Yamazaki et al., 1999, 2002, 2003 for details).

forests and anthropogenic vegetation constitute the larger spatial features of environments, whereas microhabitats such as marshy ground, rotten wood and the undersides of stones constitute the smaller features of environments. The incidence of infection by laboulbenialean fungi may depend on the habitats and microhabitats in which the host carabids occur. However, the relationship between carabid assemblages and the ectoparasitic fungi has not been explored at spatial scales larger than microhabitats.

Here, we report differences in the incidence of infection by laboulbenialean fungi of overwintering carabid beetles (Coleoptera: Carabidae) in three habitats in central Japan: riverside, secondary forest and farmland habitats. Most laboulbenialean host species, such as carabids, overwinter as adults and have overlapping adult generations (Lövei & Sunderland, 1996; Weir & Hammond, 1997a, b; Yamazaki et al., 1999, 2002, 2003, 2004). Overwintering sites of carabid beetles occur within, or near, the habitats they occupy in summer (Yamazaki et al., 1999, 2002, 2003, 2004), which makes overwintering carabid beetles appropriate subjects for investigating the effects of habitats on the incidence of infection by laboulbenialean fungi.

MATERIAL AND METHODS

To quantify the effects of host habitat on infection by ectoparasitic fungi, the incidence of infection of adult carabids by laboulbenialean fungi was determined by systematically sampling three habitats, a riverside (Yamazaki et al., 1999), a secondary forest (Yamazaki et al., 2002) and farmland (Yamazaki et al., 2003). We focused on infection during winter, when many carabid beetles hibernate as adults underground and inside rotten wood, because the incidence of infection by laboulbenialean fungi is known to vary seasonally (Zerm & Adis, 2004). Beetles were collected at a riverside site in the middle reaches of the Kizu River, Kyoto (34°53′N, 135°41′E; ca. 10 m elev.) in Mar 1997, at a secondary forest site on the west-facing slope of Mt. Nukatayama, Osaka (34°40′N, 135°41′E; 370–450 m elev.) in Dec 1998 and Mar 1999 and at a farmland site in a rural area of Son-enji, Osaka (34°48′N, 135°43′E; ca. 100 m elev.) in Dec 1999, Mar 2000, and Mar 2001. The distance between sites (habitats) ranged from 8 to 24 km. The riverside site comprised a mosaic of grassland and willow shrubs (Fig. 1.; Table 1; Yamazaki et al., 1999). The secondary forest was composed of evergreen and deciduous broad-leaved tree species such as

TABLE 1. Microhabitats at the riverside site on the middle reaches of the Kizu River, Kyoto.

Code[1]	Microhabitat[1]	Description[2]
A	Riverbank	The waterside slope of the river bank. This habitat was at the farthest point on the slope above the river. *Lolium multiflorum* grew on fine sand with humus.
B	Edge of track	A track running along the outer edge of the main terrace. *Lolium multiflorum*, *Rosa multiflora*, *Rumex acetosa* and *Lycoris radiata* grew beside the track and the soil consisted of fine sand with humus.
C	Tall reeds	The outer edge of the main terrace was covered mainly by tall reeds (*Phragmites karka*) growing in fine sand with rich humus.
D	Kudzu vines	The outer edge of the main terrace was covered mainly with kudzu (*Pueraria lobata*) growing in fine sand with rich humus.
E	Slope of a hollow	A small hollow under willow trees (*Salix* spp.) in the middle of the main terrace. The soil consisted of coarse sand with willow roots and little humus.
F	Rotten wood	Rotten willow wood on the ground on the main terrace.
G	Vine reeds	Vine reeds (*Phragmites japonica*) growing along the inner edge of the main terrace. The soil consisted of relatively dry coarse sand with little humus.
H	Under stones	Fist- to rugby ball-sized stones on the ground of the main terrace.
I	Shoulder of terrace	A narrow terrace 2–3 m above the river. The soil chiefly consisted of wet hard clay. *Phragmites communis* and *Solidago altissima* grew on this terrace.
J	Marshy ground	Along the edge of the narrow terrace, weeds such as *Polygonum longisetum*, *Rorippa indica* and grasses grew on the marshy ground consisting of clay and fine sand.

[1] Microhabitats and their codes are illustrated in Fig. 1; [2] The definition of the microhabitats follows Yamazaki et al. (1999).

TABLE 2. The number of carabid beetles collected at the three habitats (the number infected with *Laboulbenia*).

Subfamily	Species	Habitat			Total
		Riverside	Forest	Farmland	
Carabinae	*Calosoma maximowiczi* (Morawitz)	0	1	0	1
	Damaster blaptoides Kollar	16	0	0	16
	Ohomopterus yaconinus Bates	4	21	1	26
Scaritinae	*Clivina niponensis* Bates	0	0	1	1
	Dyschirius ordinatus Bates	1	0	0	1
	Scarites terricola pacificus Bates	0	0	3	3
Bembidiinae	*Tachyura laetifica* (Bates)	1	0	0	1
Pterostichinae	*Agonum chalcomus* (Bates)	2	0	8	10
	Colpodes japonicus (Motschulsky)	0	0	1	1
	Lesticus magnus (Motschulsky)	2	0	1	3
	Pterostichus haptoderoides japanensis Tschitscherine	0	0	13	13
	Pterostichus latemarginatus (Straneo)	0	90	0	90
	Pterostichus longinquus Bates	0	0	25	25
	Pterostichus microcephalus (Motschulsky)	6	0	2	8
	Pterostichus planicollis Motschulsky	3(2)	0	0	3(2) [1]
	Pterostichus sulcitarsis Morawitz	1	0	2	3
	Pterostichus yoritomus Bates	0	21	0	21
	Trigonotoma lewisii Bates	0	20	0	20
Zabrinae	*Amara chalcites* DeJean	35	0	13	48
	Amara congrua Morawitz	0	0	18	18
	Amara gigantea Motschulsky	1	0	0	1
	Amara macronota ovalipennis Solsky	2	0	0	2
	Amara simplicidens Morawitz	4	0	0	4
Harpalinae	*Acupalpus inornatus* Bates	0	0	1	1
	Anisodactylus punctatipennis Morawitz	0	0	1	1
	Anisodactylus sadoensis Schauberger	13	0	0	13
	Anisodactylus signatus (Panzer)	4	0	18	22
	Anoplogenius cyanescens (Hope)	0	0	2	2
	Bradycellus grandiceps (Bates)	0	0	6	6
	Bradycellus subditus (Lewis)	2	0	13	15
	Harpalus capito Morawitz	3	0	0	3
	Harpalus chalcentus Bates	0	0	13	13
	Harpalus eous Tschitscherine	8(6)	0	0	8(6) [1]
	Harpalus griseus (Panzer)	3(1)	0	0	3(1) [1]
	Harpalus jureceki (Jedlicka)	2	0	4	6
	Harpalus niigatanus Schauberger	1(1)	0	1	2(1) [1]
	Harpalus platynotus Bates	4	0	0	4
	Harpalus sinicus Hope	3(2)	0	2	5(2) [1]
	Harpalus tinctulus Bates	1	0	0	1
	Harpalus tridens Morawitz	4	0	0	4
	Oxycentrus argutoroides (Bates)	11	6(2)	3	20(2) [2]
	Stenolophus fulvicornis Bates	0	0	1	1
	Stenolophus iridicolor Redtenbacher	0	0	5	5
	Trichotichnus congruus (Motschulsky)	0	1	1	2
	Trichotichnus noctuabundus Habu	0	0	1	1
Licininae	*Diplocheila zeelandica* (Redtenbacher)	0	1	0	1
Callistinae	*Chlaenius inops* Chaudoir	3(2)	0	0	3(2) [3]
	Chlaenius kurosawai Kasahara	7	0	0	7
	Chlaenius naeviger Morawitz	0	26	1	27
	Chlaenius pallipes Gebler	8	0	0	8
	Chlaenius posticalis Motschulsky	1	0	0	1
	Haplochlaenius costiger (Chaudoir)	1	25	0	26
Lebiinae	*Lebidia octoguttata* Morawitz	0	2	0	2
	Total no. individuals (no. infected individuals)	156(14)	214(2)	161(0)	531(16)
	No. species	31	11	28	53
	No. infected species	6	1	0	7

Fungal species: [1]*Laboulbenia coneglanensis*, [2]*L. pseudomasei*, [3]*L. fasciculata* (see Table 3).

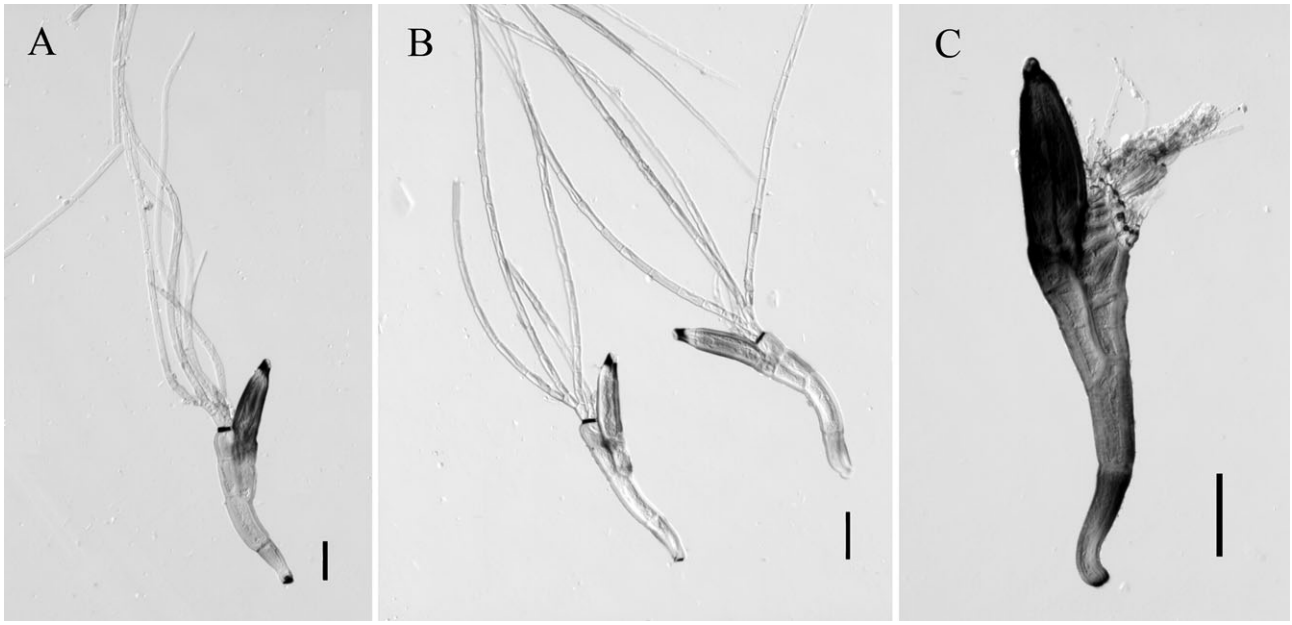

Fig. 2. Mature thalli of *Laboulbenia* species. A – *L. coneglanensis*; B – *L. pseudomasei*; C – *L. fasciculata*. Bars: A = 100 µm; B = 50 µm; C = 100 µm.

Quercus (Fig. 1.; Yamazaki et al., 2002). The farmland site comprised a mosaic of coppice woodland, rice and vegetable fields, irrigation ponds and streams (Fig. 1.; Yamazaki et al., 2003). Based on the European Union Institute for Security Studies (EUNIS) Database (http://eunis.eea.europa.eu/index.jsp), the riverside site was categorized as "Species-rich helophyte beds"; the forest site as "Mixed woodland with [Cupressaceae], [Taxaceae] and evergreen oak"; and the farmland site as "Inundated or inundatable croplands, including rice fields". To examine the effect of microhabitat on the incidence of infection by laboulbenialean fungi, beetles were collected from 23 microhabitats in the three habitats; these included ten riverside microhabitats (Fig. 1; Table 1; riverbank, edge of track, tall reeds, kudzu vines, slope of a hollow, rotten wood, vine reeds, under stones, the shoulder of a terrace and marshy ground), five microhabitats in the secondary forest (Fig. 1; forest floor, small hollow in the forest, forest edge, side of a mountain path and rotten wood), and eight farmland microhabitats (Fig. 1; arable rice field, wet fallow rice field, dry fallow rice field, two types of fallow vegetable fields, fallow potato field, old fallow field, and bank of an irrigation pond). The microhabitats were categorized as in previous studies (Yamazaki et al., 1999, 2002, 2003; Table 1). Three quadrats (1.6 m × 1.6 m) were established on the ground in each microhabitat except for collecting beetles from rotten wood and beneath stones. We then dug out each quadrat to a depth of 0.4 m using a hoe, inspected the soil and collected the beetles. To collect beetles overwintering in rotten wood, soft pieces of wood were selected (e.g., total volume of crushed wood, 0.32 m^3 at the riverside) and any beetles inside the pieces of wood were collected. To collect beetles overwintering under stones at the riverside site, stones with lower surfaces buried to a depth of 10 to 20 mm (n = 43 stones covering 3.17 m^2) were selected, overturned, soil beneath them dug to a depth of 0.4 m and any beetles present collected.

The beetles were pinned and identified using a pictorial encyclopedia of the beetles of Japan (Uéno et al., 1985). The beetles were then examined under a stereomicroscope for the presence of laboulbenialean fungi. Thalli of Laboulbeniales on the surface of the body of a host are easily distinguished from those other fungi by their unique morphology (Tavares, 1985; Benjamin et al., 2004). The mature thalli of laboulbenialean fungi were removed using tweezers, mounted on glass slides in Berlese solution and identified (Benjamin et al., 2004). The species of Laboulbeniales was identified under an optical microscope using taxonomic literature (Sugiyama, 1973; Terada, 1996b, 1998; Rossi & Weir, 1997). Host records of identified species are those cited in the literature (Sugiyama, 1973; Terada, 1996a, b, 1998; Rossi & Weir, 1997; Santamaria, 1998). All specimens of Laboulbeniales collected in this study are deposited in the Forestry and Forest Products Research Institute at Tsukuba, Ibaraki Prefecture, Japan.

A generalized linear model (GLM) with binomial error distribution was used to determine the effects of host habitat on the incidence of infection by laboulbenialean fungi (JMP ver. 6.0; SAS Institute, Cary, NC). Host habitat (riverside, secondary forest or farmland) was the explanatory variable and whether or not (1/0) each beetle was infected by these fungi the response variable. Similarly, a GLM was used to determine the effects of host microhabitat (explanatory variable) on the incidence of infection by laboulbenialean fungi (response variable) at the riverside site. However, as the species composition of host carabids differed among habitats (Yamazaki et al., 2004) this may have caused the differences in the incidence of infection at the three habitats. To avoid the effect that these differences in carabid species composition may have a GLM was used to compare the incidence of infection of the potential hosts (response variable) among habitats (explanatory variable). Potential hosts are those carabid species that are recorded as host species in previous reports. Although the incidence of infection at different times of the year may also vary it was not possible to determine what effect this may have on the incidence of infection in the three habitats because the data set was too small.

RESULTS

A total of 531 adults of 53 carabid species (nine subfamilies) were collected from three habitats (Table 2). The species composition of the carabids differed in the three habitats, with only two species occurring in all three habitats and 13 in two of the habitats (Table 2). An infec-

TABLE 3. Infections by *Laboulbenia* fungi recorded in this study and in the literature.

Host		Numbers of individuals collected (number infected)		
Subfamily	Species	*L. coneglanensis*	*L. pseudomasei*	*L. fasciculate*
Pterostichinae	*Pterostichus planicollis* Motschulsky	3(2) [NR]	–	–
Harpalinae	*Harpalus eous* Tschitscherine	8(6) [* T98]	–	–
Harpalinae	*Harpalus griseus* (Panzer)	3(1) [* T98]	–	–
Harpalinae	*Harpalus niigatanus* Schauberger	2(1) [* T98]	–	–
Harpalinae	*Harpalus sinicus* Hope	5(2) [* T98]	–	–
Harpalinae	*Oxycentrus argutoroides* (Bates)	–	20(2) [NR]	–
Callistinae	*Chlaenius inops* Chaudoir	–	–	3(2) [* T96a]
Omophroninae	*Omophron aequalis* Morawitz	–	–	0(0) [* T96b]
Patrobinae	*Patrobus flavipes* Motschulsky	–	–	0(0) [* SU73]
Pterostichinae	*Pterostichus anthracinum* Illiger	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus cristatus* Dufour	–	0(0) [* SA98]	–
Pterostichinae	*Pterostichus gracilis* (Dejean)	–	0(0) [* SA98]	–
Pterostichinae	*Pterostichus luctuosus* (Dejean)	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus micans* Heer	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus minor* (Gyllenhal)	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus nigrita* (Fabricius)	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus oenotrium* (Ravizza)	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus orientalis* Motsch.	–	0(0) [* RW98]	–
Pterostichinae	*Pterostichus rhaeticum* (Heer)	–	0(0) [* RW98]	–
Harpalinae	*Anisodactylus punctatipennis* Morawitz	1(0) [* T98]	–	–
Harpalinae	*Anisodactylus sadoensis* Schauberger	13(0) [* T98]	–	–
Harpalinae	*Harpalus capito* Morawitz	3(0) [* T98]	–	–
Harpalinae	*Harpalus discrepans* Morawitz	0(0) [* T98]	–	–
Harpalinae	*Harpalus jureceki* (Jedlicka)	6(0) [* T98]	–	–
Harpalinae	*Harpalus platynotus* Bates	4(0) [* T98]	–	–
Harpalinae	*Harpalus psedoophonoides* Schauberger	0(0) [* T98]	–	–
Harpalinae	*Harpalus roninus* Bates	0(0) [* T98]	–	–
Harpalinae	*Harpalus simplicidens* Schauberger	0(0) [* T98]	–	–
Harpalinae	*Harpalus tinctulus* Bates	1(0) [* T98]	–	–
Harpalinae	*Harpalus tridens* Morawitz	4(0) [* T98]	–	–
Harpalinae	*Harpalus vicarious* Harold	0(0) [* T98]	–	–
Callistinae	*Chlaenius prostenus* Bates	–	–	0(0) [* T96a]
Callistinae	*Chlaenius vestitus* (Paykull)	–	–	0(0) [* T96a]

*Host records reported in previous studies; citation references, SU73 (Sugiyama, 1973), T96a (Terada, 1996a), T96b (Terada, 1996b), T98 (Terada, 1998), RW98 (Rossi & Weir, 1998), SA98 (Santamaria, 1998); [NR], new host record; – Not recorded.

tion by laboulbenialean fungi of one, five and one species of the carabid subfamilies Pterostichinae, Harpalinae and Callistinae, respectively, were detected (Table 2). Three species of the genus *Laboulbenia* (Laboulbeniales) were identified: *L. coneglanensis* Spegazzini (Fig. 2A), *L. pseudomasei* Thaxt (Fig. 2B) and *L. fasciculata* Peyritsch (Fig. 2C). The thalli of *L. coneglanensis* (Fig. 2A) were present on the surface of the elytra of five species: *Harpalus eous* Tschitscherine, *H. griseus* (Panzer), *H. niigatanus* Schauberger, *H. sinicus* Hope and *Pterostichus planicollis* Motschulsky (Table 3). The thalli of *L. pseudomasei* (Fig. 2B) were present on the surface of the elytra and legs of *Oxycentrus argutoroides* (Bates) (Table 3) and those of *L. fasciculata* (Fig. 2C) on the surface of the elytra and prothorax of *Chlaenius inops* Chaudoir (Table 3). Although most of these host records are not new, two are first records (Table 3). Fourteen species were infected with either *L. coneglanensis*, *L. pseudomasei* or *L. fasciculata* (Table 3).

The incidence of infection by *Laboulbenia* differed among habitats (GLM, $df = 2$, $\chi^2 = 26.7$, $P < 0.0001$); it was higher at the riverside site (8.97% of individuals; 14/156) than at the forest (0.93%; 2/214) and farmland sites (0%; 0/161; Table 2). The difference in the incidence of infection of the 14 potential hosts by three *Laboulbenia* species in the different habitats was marginally significant (GLM, $df = 2$, $\chi^2 = 5.9$, $P = 0.05$); riverside, 23.7% (14/59), forest, 33.3% (2/6) and farmland, 0% (0/11).

At the riverside site, the incidence of infection by *Laboulbenia* ranged from 0 to 33.3% in the different microhabitats in which the carabid beetles overwintered (Table 4) and differed significantly among microhabitats (Table 4; GLM, $df = 9$, $\chi^2 = 20.6$, $P = 0.0147$).

DISCUSSION

This report provides quantitative data on the incidence of infection by three species of laboulbenialean fungi of 53 species of carabid (Table 2). This study is the first to indicate a difference in the incidence of infection by these fungi at two different scales: habitat and microhabitat (Tables 2, 4). As the incidence of infection by fungi is generally higher in humid environments, carabid beetles, which inhabit the wettest environment (riverside), should

TABLE 4. The percentage incidence of infection of carabid beetles by *Laboulbenia* in the different microhabitats.

Code*	Microhabitat*	Total number of individuals collected	Number of infected individuals (%)
A	Riverbank	5	0 (0)
B	Edge of track	18	6 (33.3)
C	Tall reeds	4	1 (25.0)
D	Kudzu vines	9	0 (0)
E	Slope of a hollow	11	1 (9.1)
F	Rotten wood	24	0 (0)
G	Vine reeds	28	2 (7.1)
H	Under stones	32	1 (3.1)
I	Shoulder of a terrace	18	3 (16.7)
J	Marshy ground	7	0 (0)
	Total	156	14 (9.0)

*Microhabitats and their codes are described in Table 1 and illustrated in Fig. 1.

be subject to high incidences of infection by laboulbenialean fungi. The absence of infection by these fungi at the farmland site may be related to the drier conditions prevailing there. However, this difference in the incidence of infection may result from the difference in species composition of host carabids in the different habitats because laboulbenialean fungi are known to infect a particular host genus or species. For example, although *L. coneglanensis* is recorded from many *Harpalus* species (Table 3; Terada, 1998) no individuals of this genus were infected with this fungus at the farmland site (Table 3).

Factors other than host species are important determinants of the different incidences of infection in the different habitats. Andersen & Skorping (1991) demonstrated experimentally that the differences in the incidence of infection by *Laboulbenia* fungi of assemblages of *Bembidion* beetles are associated with both microhabitat and host taxon. De Kesel (1996b) also suggests that the microhabitat of the host directly affects the growth and development of *Laboulbenia* thalli on the bodies of its hosts. Similarly, both the habitat and microhabitat may be important in determining the successful establishment of these fungi on the bodies of their hosts.

ACKNOWLEDGEMENTS. We thank K. Kawamura for help with the collecting of the carabid beetles, Y. Yamaura for statistical advice, B.S. Holland for helpful advice, and two anonymous reviewers for providing valuable comments on earlier drafts of this manuscript.

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Received July 10, 2009; revised and accepted October 1, 2009