

MITES AS FUNGAL VECTORS? THE ECTOPARASITIC FUNGI OF MITES AND THEIR ARTHROPOD ASSOCIATES IN QUEENSLAND

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Abstract

We examined log-inhabiting arthropods and their associated mites for ectoparasitic fungi (Ascomycetes: Laboulbeniales) in South-east Queensland and Far North Queensland. Fungus host records were: *Rickia berlesiana* (Baccarini) on most species of Fedrizzidae (Acari: Mesostigmata) and three species of Passalidae (Coleoptera); *Rickia leptaulacis* Thaxter on two species of *Fedrizzia* (Fedrizzidae), one species of *Megisthanus* (Mesostigmata: Megisthanidae), and two species of Passalidae; *Rickia* sp. A on two species of *Paradiplogynium* (Mesostigmata: Diplogyniidae) and the cockroach *Panesthia tryoni* Shaw (Blaberidae); *Rickia* sp. B on two species of *Fedrizzia*; *Rickia* sp. C on one species of *Megisthanus*; *Rickia* sp. D on *Promegistus armstrongi* (Mesostigmata: Promegistidae); and *Dimorphomyces* sp. A on a species of *Micromegistus* (Mesostigmata: Parantennulidae). Our data are the first records of *Dimorphomyces* in Australia, *R. leptaulacis* on mites, and Laboulbeniales on members of the Diplogyniidae, Parantennulidae, and Promegistidae. At a species-level, 15% per cent of mites were infested with Laboulbeniales; the most thalli found on a single mite was 34. Thalli of *R. berlesiana* and *R. leptaulacis* were especially common on old passalid beetles, but were rare on young beetles. Thalli were common on the ventral prothorax, and leg femora and tibiae, but were mostly found on the mesothoracic episternum and anterior elytra of beetles. Given the protected positions that most thalli occur, and that these positions are the preferred sites for mite associates, we hypothesise that mites are important vectors of fungi between beetles.

Introduction

While perusing specimens, an observant biologist may come across foreign seta-like or branched structures attached to their arthropod of interest. These structures are likely to be members of the Laboulbeniales, an unusual group of small fungi that are obligate ectoparasites of arthropods, especially insects. However, the cryptic nature of these fungi means their existence is often overlooked. Furthermore, mycologists and entomologists dedicated to the Laboulbeniales are few and far between (Weir & Beakes 1995), probably discouraging entomologists with a passing interest in the fungi they discover. Entomologists in Australia and New Zealand are further hampered by a lack of knowledge in their geographic area: only 1 per cent of the 2,000 described species of Laboulbeniales are reported from this region (Rossi 1984).

Members of the Laboulbeniales produce fruiting bodies (thalli) of determinate growth, usually bearing antheridia and perithecia on a receptacle. The form of the receptacle, antheridia and perithecia differ markedly between species, and identifications are made on the form of the mature thallus (Thaxter 1926). Mature thalli have ascospores within the perithecium (Weir & Beakes 1995). The thalli attach to their host's integument by a basal cell of the receptacle, where they make contact with host tissue, either through the cuticular pores or by active penetration of the host's integument (De Kesel 1996; Tavares 1985). However, the Laboulbeniales are considered harmless despite their parasitic nature (De Kesel 1996). The entire life cycle is spent on one host, there are no free-living stages, and only sexual reproduction is known (De Kesel 1996; Tavares 1985; Weir & Beakes 1995).

Most species of Laboulbeniales are considered host-specific, and some are even specific to a position on their host, and perhaps their host's sex (Weir & Beakes 1995). However, fungi living on mites (Acari) are rarely, if ever, host-specific, and are often parasitic on the arthropod with which the mite associates (Tavares 1985). To date, 72 species and eight genera of Laboulbeniales are known from mites (Balazuc 1990). *Rickia berlesiana* (Baccarini) is the only mite-associated Laboulbeniales recorded in Australia, and was taken from *Fedrizzia gloriosa* Berlese and *Fedrizzia grossipes* Canestrini (Balazuc 1990; Paoli 1912).

Fedrizzia belongs to the family Fedrizziiidae, whose members (21 described species) are probably all associated with passalid beetles (Womersley 1959). Passalid beetles are host to an incredible diversity of mites (Hunter 1993; Seeman 2000), and also to a multitude of fungi that live on their exoskeleton and in their hindguts (Lichtwardt *et al.* 1999). Therefore, although our study examines a broad array of mites associated with log-inhabiting arthropods, we focus on the plethora of mites and fungi living on passalid beetles.

Materials and Methods

Adult and immature arthropods were collected from rotting logs in South-east Queensland and Far North Queensland between 1995 and 1999. Sites and collection dates in South-east Queensland were: Bunya Mountains (26°51'S, 151°03'E) on 12–14.ii.1996; Goomburra State Forest (28°02'S, 152°07'E) on 3.i.1997, 18.iii.1997; Jimna State Forest (26°39'S, 150°28'E) on 16 & 17.iii.1996, 24.x.1996, 21.xi.1996, 17–20.ii.1997, 16–18.ii.1998; and Lamington National Park (28°12'S, 153°10'E) on 25.v.1995, 25.ii.1996, 15.xi.1996, 2 & 3.xii.1996, 7.v.1997, 4.viii.1997. In Far North Queensland: Atherton Tablelands (17°15'S, 145°28'E) on 27 & 28.i.1996, 1.ii.1996; Cape Tribulation (16°08'S, 145°26'E) 29 & 30.i.1996; and the Mossman-Mt Lewis Region (16°26'S, 145°16'E) on 31.i.1996. Log-inhabitants were collected by rolling logs over, breaking them apart, picking the arthropods up in forceps, and placing them into vials of 80% ethanol or empty plastic containers. Log-inhabitants collected into containers were returned to the laboratory and killed in 80% ethanol.

All mites on the arthropods were removed, counted, and representatives of each morpho-species were cleared in Nesbitt's solution and slide-mounted in Hoyer's medium or Heinze polyvinyl alcohol medium (Evans 1992; Krantz 1978). These mites were identified to species, if possible, and the number and species of Laboulbeniales recorded. We also used a dissecting microscope ($\times 63$) to search arthropods that harboured mites infested with fungi, recorded the number and position of thalli, removed them with a micro-pin, slide-mounted them in Heinze polyvinyl alcohol medium, and identified them to species where possible. Mites were identified to the family level with Krantz (1978), and to species with the works of Schuster & Summers (1978) (Diarthrophallidae) and Womersley (1937, 1958a, b, 1959) (Megisthanidae, Diplogyniidae, Paramegistidae and Promegistidae, Fedrizziiidae, respectively). Laboulbeniales were identified to species with the descriptions and illustrations of Thaxter (1926). Voucher specimens of mites infested with each species of Laboulbeniales have been lodged with the University of Queensland Insect Collection.

Results

Ectoparasitic fungi of mites

We examined 754 mites representing 50 species and 13 families. Most of the families were from the Mesostigmata (9); the other acarine suborders were Astigmata (2), Oribatida (1) and Prostigmata (1) (Table 1). Thalli of Laboulbeniales were found on two species of Diplogyniidae, nine species of Fedrizziiidae, five species of Megisthanidae, one species of Parantennulidae, and one species of Promegistidae (Table 2). These families all belong to the Antennophorina, a basal group of Mesostigmata (Camin & Gorirossi 1955).

The Laboulbeniales *Dimorphomyces* and *Rickia* infested and developed to maturity on mites (Figs 1, 2 [see back cover for Figure 2]). The former was represented by one species that occurred only on an undescribed species of *Micromegistus* (Parantennulidae) (Fig 1a; Table 2). The latter comprised six species, two of which were identified as *R. berlesiana* and *R. leptaulacis* Thaxter (Thaxter 1926). *Rickia berlesiana* occurred on nearly all species of Fedrizziiidae found in Far North Queensland and South-east Queensland, and *R. leptaulacis* occurred only on two species of *Fedrizzia* and one species of *Megisthanus* in South-east Queensland (Table 2).

Thalli of *R. berlesiana*, *R. leptaulacis*, and three unidentified *Rickia* (sp. A, B, D) generally arose from the body and legs of their host mites, but rarely from body setae (Fig. 2). However, an unidentified, minute *Rickia* (sp. C) occurred only on the ambulacra, tarsus, and tarsal setae of four species of the giant *Megisthanus* (idiosomal length = 2.5–4 mm), sometimes in large numbers. *Rickia* sp. A has an attractive, stout thallus and was found on two undescribed species of *Paradiplogynium* (Fig. 1b, 2b; Table 2).

The percentage of mites infested with thalli varied considerably within species (15–88%, Table 2). Generally, 1–3 thalli occurred on each mite, but some specimens were leprous. The most thalli found on one specimen was 34 (*Rickia* sp. C), but more impressive were infestations of the large species *R. leptaulacis*. One specimen of *Fedrizzia* sp. A had 19 thalli of *R. berlesiana* and *R. leptaulacis*, the latter species attaining a length of 420 μm on a mite 1020 μm long.

Figure 1. (a) An undescribed species of *Dimorphomyces* from an undescribed species of *Micromegistus* (Mesostigmata: Parantennulidae) taken from the carabid beetle *Trichosternus subvirens*. (b) An undescribed species of *Rickia* sp. A from an undescribed species of *Paradiplogynium* (Mesostigmata: Diplogyniidae) taken from the blaberid cockroach *Panesthia tryoni*. Scale bar represents 20 μ m.

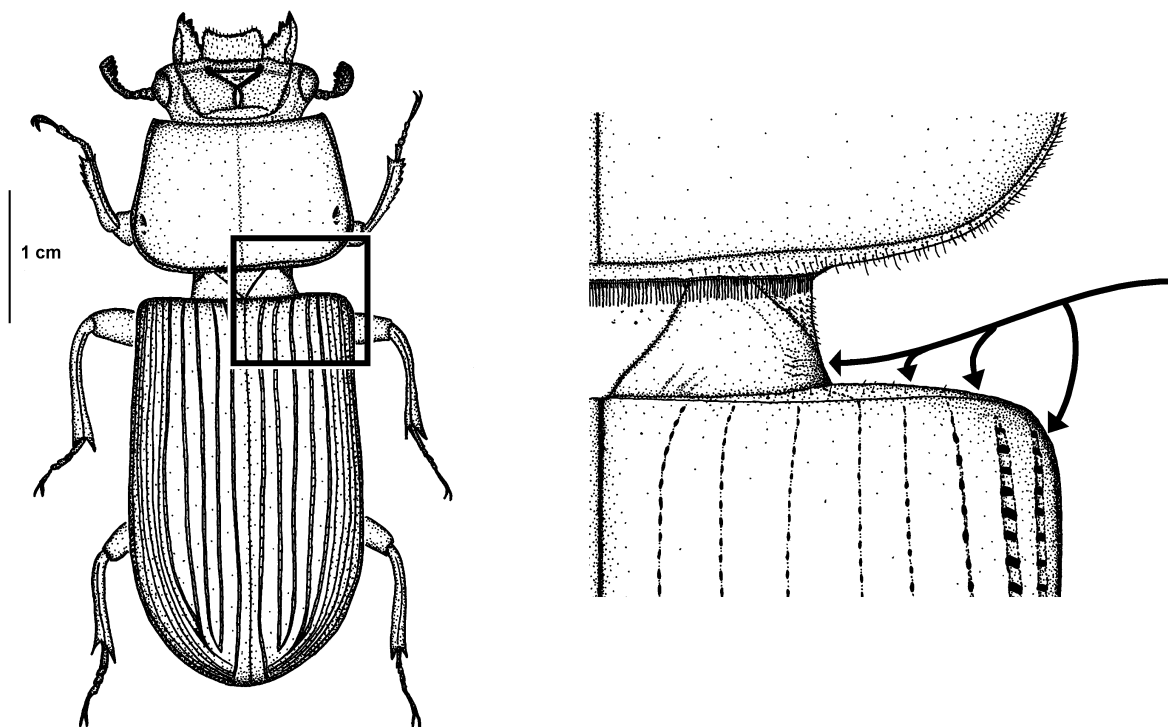


Figure 3. A passalid beetle (*Pharochilus*) and detail of the boxed region. Arrows point to the mesothoracic episternum and anterior elytra where fungi and mites occur most frequently.

Table 1. Laboulbeniales on mites associated with arthropods. A = Astigmata; M = Mesostigmata; O = Oribatida; P = Prostigmata; n = number of mite specimens examined.

Mite family	Mite species	Thalli (\pm) (n)	Mite's 'host' family
Anoetidae (A)	unidentified (2 species)	- (n = 51)	Carabidae, Passalidae
Canestriniidae (A)	unidentified (2 species)	- (n = 38)	Carabidae, Passalidae
Diarthrophallidae (M)	<i>Eurysternodes tragardhi</i>	- (n = 4)	Passalidae
	<i>Lombardiniella lombardini</i>	- (n = 30)	Passalidae
Diplogyniidae (M)	<i>Cryptometasternum derricki</i>	- (n = 26)	Passalidae
	<i>C. queenslandense</i>	- (n = 8)	Sphaerotheriidae
	<i>Paradiplogynium</i> sp. A	+ (n = 20)	Blaberidae
	<i>Paradiplogynium</i> sp. B	+ (n = 8)	Blaberidae
Discozerconidae (M)	<i>Discozercon</i> sp. A	- (n = 12)	Scolopendridae
Fedrizziidae (M)	<i>Fedrizzia bornemisszai</i>	+ (n = 6)	Passalidae
	<i>F. grossipes</i>	+ (n = 48)	Passalidae
	<i>F. oudemansi</i>	- (n = 11)	Passalidae
	<i>Fedrizzia</i> sp. A	+ (n = 50)	Passalidae
	<i>Neofedrizzia brooksi</i>	+ (n = 14)	Passalidae
	<i>N. camini</i>	+ (n = 65)	Passalidae
	<i>N. canestrinii</i>	+ (n = 14)	Passalidae
	<i>N. tragardhi</i>	+ (n = 11)	Passalidae
	<i>N. vidua</i>	+ (n = 23)	Passalidae
	<i>Neofedrizzia</i> sp. A	+ (n = 72)	Passalidae
Laelapidae (M)	<i>Coleolaelaps</i> sp.	- (n = 8)	Scarabaeidae
	<i>Hypoaspis</i> sp.	- (n = 12)	various
	<i>Iphiolaelaps myriapodum</i>	- (n = 27)	Julidae
	<i>Scissurolaelaps</i> sp.	- (n = 20)	Blaberidae
Megisthanidae (M)	<i>Megisthanus</i> spp. (9 species)	+ (n = 66)	Passalidae
Mesoplophoridae (O)	unidentified (1 species)	- (n = 8)	Passalidae
Parantennulidae (M)	<i>Micromegistus</i> sp. A	+ (n = 24)	Carabidae
	<i>Micromegistus</i> sp. B	- (n = 14)	Carabidae
Promegistidae (M)	<i>Promegistus armstrongi</i>	+ (n = 9)	Carabidae
Tarsocheylidae (P)	unidentified (1 species)	- (n = 10)	Passalidae
Uropodidae (M)	unidentified (11 species)	- (n = 45)	various

Ectoparasitic fungi of mites' host arthropods

We found thalli of *R. berlesiana* on *Mastochilus australasicus* (Percheron) (Passalidae) in Far North Queensland, and *R. berlesiana* and *R. leptaulacis* on *M. quaestionis* (Kuwert) and *Pharochilus dilatatus* (Dalman) in South-east Queensland. Three specimens of *Rickia* sp. A were also removed from beneath the prothorax of the host of *Paradiplogynium*, the burrowing cockroach *Panesthia tryoni* Shaw.

Young, adult passalid beetles are a tan colour and become black as they age. We searched 4 young and 31 old *M. quaestionis* and 14 young and 20 old *P. dilatatus* for thalli of *Rickia*; only one thallus was found on a young *P. dilatatus*, but 98 per cent of old passalid beetles supported fungus populations. These beetles were collected from Lamington National Park in February and December 1996, and the Bunya Mountains in February 1996 (Table 3). *Mastochilus* always supported many more thalli than the smaller *Pharochilus* (Table 3); the most *Rickia* on a single beetle was 139 on a *M. quaestionis*.

The greatest populations of *Rickia* occurred on the anterior elytra and mesothoracic episternum of *Pharochilus* and *Mastochilus* (Table 3; Fig. 3). However, thalli were also found commonly on the mentum, ventral prothorax, and leg femora and tibiae; less common positions were the antennae, ventral head, ventral metathorax, tarsi, and posterior rim of the elytra, represented collectively by the 'others' classification in Table 3. Almost all *Rickia* were attached to the integument (99.8% of 2184 thalli), and rarely to body setae. Throughout this study, and other collections of passalid beetles (Seeman 2000), mites of the Diplogyniidae, Fedrizziidae, and Megisthanidae were always clustered about the mesothoracic episternum and anterior elytra. The Fedrizziidae and Megisthanidae were almost always present on old beetles, and tended to be more abundant on *Mastochilus* than *Pharochilus* (Table 3).

Table 2. Laboulbeniales on mites: species of fungus infecting each species of mite, percentage of mites with thalli, and number of thalli per mite (mean \pm standard error, means based on infested mites only). Sites: 1 = Bunya Mountains; 2 = Goomburra State Forest; 3 = Jimna State Forest; 4 = Lamington National Park; 5 = Atherton Tablelands; 6 = Cape Tribulation; 7 = Mossman-Mt Lewis region.

Mite family	Mite species and sites	Fungus species	%	Thalli per mite	
Diplogyniidae	<i>Paradiplogynium</i> sp. A (3,4)	<i>Rickia</i> sp. A	60	3.8 \pm 0.9	
Fedrizziidae	<i>P.</i> sp. B (3, 4)	<i>Rickia</i> sp. A	88	2.9 \pm 0.7	
	<i>Fedrizzia bornemisszai</i> (2, 3, 4)	<i>Rickia berlesiana</i>	50	4.0 \pm 4.0	
	<i>F. grossipes</i> (1, 2, 3, 4)	<i>Rickia berlesiana</i>	33	2.6 \pm 0.8	
		<i>Rickia leptaulacis</i>			
		<i>Rickia</i> sp. B			
	<i>Fedrizzia</i> sp. A (1, 2, 3, 4)	<i>Rickia berlesiana</i>	26	2.6 \pm 1.3	
		<i>Rickia leptaulacis</i>			
	<i>Neofedrizzia brooksi</i> (5)	<i>Rickia berlesiana</i>	50	1.7 \pm 0.5	
		<i>N. camini</i> (2, 3, 4)	<i>Rickia berlesiana</i>	31	1.8 \pm 0.2
		<i>N. canestrinii</i> (5, 6, 7)	<i>Rickia berlesiana</i>	15	1.5 \pm 1.0
<i>N. tragardhi</i> (3, 4)		<i>Rickia berlesiana</i>	18	2.0 \pm 1.4	
<i>N. vidua</i> (1, 2, 3, 4)		<i>Rickia berlesiana</i>	65	2.9 \pm 0.7	
<i>Neofedrizzia</i> sp. A (1)		<i>Rickia berlesiana</i>	67	4.0 \pm 0.6	
		<i>Rickia berlesiana</i>			
Megisthanidae	<i>Megisthanus</i> spp. (5 species, all sites)	<i>Rickia leptaulacis</i> (sites 1,3, 4 only)	26	5.8 \pm 2.1	
		<i>Rickia</i> sp. C			
Parantennulidae	<i>Micromegistus</i> sp. A (1, 3, 4)	<i>Dimorphomyces</i> sp. A	38	5.3 \pm 1.4	
Promegistidae	<i>Promegistus armstrongi</i> (1, 3, 4)	<i>Rickia</i> sp. D	44	1.0 \pm 1.0	

Discussion

New records are entirely expected when one examines organisms that are poorly understood. Our study reports the first known members of *Dimorphomyces* in Australia. Previously, *Dimorphomyces* was known to occur in numerous locations around the world, and has been taken from beetles and mites (Balazuc 1990). Our findings of thalli on the Diplogyniidae, Parantennulidae, and Promegistidae represent the first records of these families as hosts for the Laboulbeniales. Additionally, all records of *Rickia* in Australia, except for *R. berlesiana* on *F. grossipes*, are new (Table 2). An incredible diversity of Laboulbeniales are undoubtedly undiscovered, as this survey merely examined those parasitic on Acari that associate with log-inhabiting arthropods in Queensland.

Fungus species exhibited some specificity towards the mite species they infested (Table 2). This specificity does not arise from these species being the only available mites on the host because members of the Fedrizziidae and Megisthanidae share their passalid associates with numerous other mite groups (Hunter 1993; Seeman 2000), and *Paradiplogynium* shares *P. tryoni* with a *Scissuroaelaps* sp. (Table 1). The Laboulbeniales displayed an affinity for the Antennophorina in this study (Table 1) and, considering that the Antennophorina are such a small group of Mesostigmata (about 2.5% of described species), past records demonstrate an unusually high number of Laboulbeniales-Antennophorina associations (23 of 72 records in Balazuc 1990). Why this is so is unknown, but we speculate that their basal position in the Mesostigmata may suggest a long association of antennophorine mites with their arthropod hosts and their associated fungi. Furthermore, we hypothesise that mite-associated Laboulbeniales will tend to occur on the most basal mite group associated with their host arthropod.

Table 3. Number and growth positions of *Rickia berlesiana* and *R. leptaulacis* per beetle, and total number of Fedrizzidae + Megisthanidae per beetle, on black (old) *Pharochilus dilatatus* and *Mastochilus quaestionis* collected from Lamington National Park in February and December 1996, and Bunya Mountains National Park in February 1996. Results are presented as means \pm standard errors; n = number of beetles; r = range.

Position on beetle	LNP Feb 1996		LNP Dec 1996		Bunya Mts Feb 1996	
	<i>Pharochilus</i>	<i>Mastochilus</i>	<i>Pharochilus</i>	<i>Mastochilus</i>	<i>Pharochilus</i>	<i>Mastochilus</i>
Anterior elytra/episternum	8 \pm 1.8	19 \pm 4.8	7.2 \pm 2.1	43 \pm 13	5.0 \pm 1.6	53 \pm 7.3
Mentum	0	0	2.0 \pm 1.1	0.6 \pm 0.7	0.2 \pm 0.2	1.0 \pm 0.4
Ventral prothorax	0	1.2 \pm 0.9	1.0 \pm 1.1	5.8 \pm 1.1	0	5.5 \pm 1.5
Femora	0.6 \pm 0.3	0.4 \pm 0.3	1.0 \pm 0.5	12 \pm 6.9	0	5.6 \pm 1.5
Tibia	0.6 \pm 0.7	0.4 \pm 0.4	0.6 \pm 0.5	3.0 \pm 1.5	0	4.1 \pm 0.9
Others	0	0.2 \pm 0.2	0.1 \pm 0.1	1.4 \pm 0.8	0	2.9 \pm 1.1
Total	9.4 \pm 1.5 (r = 7–13)	21 \pm 5.9 (r = 9–30)	12 \pm 3.1 (r = 2–26)	66 \pm 16 (r = 36–111)	5.3 \pm 1.6 (r = 0–9)	72 \pm 9.1 (r = 12–139)
Total Fedrizzidae + Megisthanidae	10.8 \pm 4.8 (n = 5; r = 1–25)	16 \pm 6.9 (n = 5; r = 1–29)	9.7 \pm 2.5 (n = 9; r = 1–23)	19.4 \pm 4.6 (r = 9–29; n = 5)	11.8 \pm 3.9 (r = 2–26; n = 6)	39.5 \pm 5.9 (n = 21; r = 0–106)

Our searching of the mites' hosts revealed the thalli of *Rickia* sp. A, and the large, common species *R. berlesiana* and *R. leptaulacis*. The other species may be arthropod parasites also, but their small size makes them difficult to find. However, we cannot discount the possibility that some Laboulbeniales have become mite specialists.

Most Laboulbeniales are host-specific, or infest a small group of related species. Examples of plurivory (infestation of unrelated hosts) are less common (e.g. *Laboulbenia ecitonis* Blum on the army ant and two of its coleopteran and acarine associates), but are exemplified by those fungi that are parasitic on mites and their associates. Indeed, the majority of mites that harbour fungal parasites are arthropod associates (Balazuc 1990). Plurivory in the Laboulbeniales has been attributed to the similar body chemistry of its cohabiting hosts (specifically *L. ecitonis* in Benjamin 1971), incidental infection, or adaptation to exploit other host species (Scheloske 1969).

The larger populations of thalli on *Mastochilus* compared with *Pharochilus* cannot, at this stage, be attributed to the tendency for *Mastochilus* to support larger populations of mites than *Pharochilus*. Members of *Mastochilus* are much larger than *Pharochilus* (50–55 mm and 30–35 mm long, respectively) and may therefore be host to greater populations of mites and fungi because of their size and possibly their greater longevity.

The association of Laboulbeniales with mites is unlikely to be incidental. Mites are viable and probably important hosts of fungi, for just as the mites are phoretic on beetles (transfer between logs), the fungi are probably reliant on mites for efficient transport between beetles. Our observations of fungi on mites, and the highest densities of thalli in places where mites aggregate (Table 3; Fig. 3), are indicative of this relationship. Additionally, passalid beetles live in tunnels, thus the secluded region of the mesothoracic episternum and anterior, vertical surface of the elytra (Fig. 3) rarely, or never, contacts the substrate or conspecific beetles. The possible role of mites as vectors in the beetle-mite-fungus relationship can be compared to that of more traditional vectors, such as the mosquito in the human-mosquito (*Anopheles*)-*Plasmodium* relationship. However, the beetle-mite-fungus relationship has a curious twist on our usual understanding of vectors: these Laboulbeniales probably do not require mites to complete their life cycle, and likewise they are probably capable of completing their life-cycle on mites alone. Further work on the beetle-mite-fungus relationship will examine how important mites are as facultative vectors of Laboulbeniales.

The association of fungi and mites appears more sinister than the mite-beetle relationship. Mites of the Fedrizziiidae and Megisthanidae have never been observed gaining sustenance from the beetle, and are active predators and scavengers in the laboratory (O. S., pers. obs.). In contrast, the Laboulbeniales are obligate parasites. The Laboulbeniales are probably harmless to their host (De Kesel 1996; Weir & Beakes 1995), but one must doubt their harmless nature when parasitising a tiny mite.

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References

- Balazuc, J. (1990). Les Laboulbeniales (Ascomycètes) parasites d'acariens description d'une espèce nouvelle. *Acarologia* **31**, 103–112.
- Benjamin, R.K. (1971). Introduction and supplement to Roland Thaxter's contribution towards a monograph of the Laboulbeniaceae. *Bibliotheca Mycologica* **30**, 1–155.
- Camin, J.H. & Gorirossi, F.E. (1955). A revision of the suborder Mesostigmata (Acarina), based on new interpretations of comparative morphological data. *Chicago Academy of Sciences Special Publication* **11**, 1–70.
- De Kesel, A. (1996). Host specificity and habitat preference of *Laboulbenia slackensis*. *Mycologia* **88**, 565–573.
- Evans, G.O. (1992). *Principles of Acarology*. (CAB International, Wallingford).
- Hunter, P.E. (1993). Mites associated with New World passalid beetles (Coleoptera: Passalidae). *Acta Zoologica Mexicana Nueva Serie* **58**, 1–37.
- Krantz, G.W. (1978). *A Manual of Acarology*. (Oregon State University Press, Corvallis).
- Lichtwardt, R.W., White, M.M., Cafaro, M.J. & Misra, J.K. (1999). Fungi associated with passalid beetles and their mites. *Mycologia* **91**, 694–702.
- Paoli, G. (1912). Nuovi Laboulbeniomiceti parassiti di Acari. *Malpighia* **24**, 329–340.
- Rossi, W. (1984). New Laboulbeniales from Australia and New Zealand. *Kew Bulletin* **39**, 753–758.
- Scheloske, H.W. (1969). Beiträge zur Biologie, Ökologie und Systematik der Laboulbeniales (Ascomycetes) unter besonderer Berücksichtigung des Parasit-Wirt-Verhältnisses. *Parasitologische Schriftenreihe* **19**, 1–176.
- Schuster, R.O. & Summers, F.M. (1978). Mites of the family Diarthrophallidae (Acari: Mesostigmata). *International Journal of Acarology* **4**, 279–385.
- Seeman, O.D. (2000). Myriad Mesostigmata associated with log-inhabiting arthropods, in R.B. Halliday, D.E. Walter, H.C. Proctor, R.A. Norton & M.J. Colloff (eds). *Proceedings of the Tenth International Congress of Acarology*. (CSIRO Publishing, Melbourne).
- Tavares, I.I. (1985). Laboulbeniales (Fungi, Ascomycetes). *Mycologia Memoir* **9**, 1–627.
- Thaxter, R. (1926). Contribution towards a monograph of the Laboulbeniaceae. Part III. *Memoirs of the American Academy of Arts and Sciences* **15**, 427–580.
- Weir, A. & Beakes, G. (1995). An introduction to the Laboulbeniales: a fascinating group of entomogenous fungi. *Mycologist* **9**, 6–10.
- Womersley, H. (1937). Australian Acari of the genus *Megisthanus* Thorell. *Transactions of the Royal Society of South Australia* **61**, 175–180.
- Womersley, H. (1958a). On some Acarina from Australia and New Guinea paraphagic upon millipedes and cockroaches, and on beetles of the family Passalidae. *Transactions of the Royal Society of South Australia* **81**, 13–29.
- Womersley, H. (1958b). Some new or little known Mesostigmata (Acarina) from Australia, New Zealand and Malaya. *Transactions of the Royal Society of South Australia* **81**, 115–130.
- Womersley, H. (1959). Some Acarina from Australia and New Guinea paraphagic upon millipedes and cockroaches and on beetles of the family Passalidae. *Transactions of the Royal Society of South Australia* **82**, 11–54.