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REGULAR PAPER

On *Diphymyces* (Laboulbeniales, Ascomycota) in Malaysian Borneo

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Background – Laboulbeniales (Fungi, Ascomycota) are microscopic ectoparasites of Arthropoda. Since many Laboulbeniales are known to be host-specific, wet tropical areas with high arthropod diversity are likely to house a high diversity of Laboulbeniales, as well. In this paper, we reveal the presence of the genus *Diphymyces* I.I.Tav. in Malaysian Borneo. After fieldwork in disturbed and pristine tropical rainforest in Borneo, representatives of this genus were discovered that did not match the description of any of the fourteen known species.
Methods – Insects were collected with dry pitfall traps baited with Limburger cheese. Fungal material was studied and described using morphology-based methods.
Key results – A new species, *Diphymyces sabahensis* Haelew. & Pfister, is described and illustrated. Hosts for this species are recently described taxa in *Ptomaphaginus* Portevin, 1914 (Coleoptera, Leiodidae, Cholevinae, Ptomaphagini), representing a new host genus for *Diphymyces*. Other, morphologically distinctive records of *Diphymyces* were found; on one host specimen they co-occur with *D. sabahensis*. These divergent thalli are remarkable in their restricted occurrence on the metatibiae, and thus may represent a morphological variant of *D. sabahensis*. A review of all described species of *Diphymyces*, with hosts and geographical distribution, is also presented in tabulated form.

Key words – Ascomycota, buffer organ, Cholevinae, *Diphymyces*, Laboulbeniales, Malaysia, morphotypes, parasitic fungi, phenotypic plasticity, Ptomaphagini, taxonomy.

INTRODUCTION

Laboulbeniales (Fungi, Ascomycota) are microscopic ectoparasites of arthropods – insects, millipedes, and mites. They do not form a mycelium but rather produce small thalli (Tavares 1985) attached to the host by a haustorium. The main axis of a thallus is formed by the receptacle, which supports all parts of the thallus. The perithecium is the only spore-forming structure in Laboulbeniales because an asexual state is not present. The primary appendage system is a prolongation of the receptacle axis and bears antheridia, which produce spermatia. Diversity in the group is still largely underexplored and many questions of taxonomy and biology of these fungi remain unresolved. Since many Laboulbeniales are known to be host-specific, parasitizing one or a limited number of related host species (Thaxter 1896, Scheloske 1969, Tavares 1985, Majewski 1994, De Kesel 1996), wet tropical areas with high arthropod diversity are likely to be centers of diversity for Laboulbeniales as well. One such area is Borneo. The island of Borneo, together with Peninsular Malaysia, Sumatra, and Java, is part of 'Sundaland', which is recognized as a biodiversity hotspot, an area housing exceptional concentrations of endemic species and often experiencing exceptional habitat loss. In Sundaland only about 7.8% of the pristine vegetation remains (Myers et al. 2000).

No large-scale inventories of Bornean arthropod diversity are available. It is likely that the coleopteran fauna of Borneo amounts to tens of thousands of species (we here adopt 50,000 as a rough estimate). For this reason, we assume that a high number of insect-parasitizing Laboulbeniales can be found. Reviewing all available literature of Laboulbeniales collected from Borneo yielded 93 species for the island (Thaxter 1899, 1908, 1915, 1918a, 1924, 1926, 1931, Sugiyama 1971, Sugiyama & Mochizuka 1979, Sugiyama & Yamamoto 1982a, 1982b, Sugiyama & Nagasawa 1985, Lee & Majewski 1986, Majewski & Sugiyama 1986, Benjamin 1994).

The subject of this paper is the discussion of the genus *Diphymyces* I.I.Tav. in (Malaysian) Borneo. All species of *Diphymyces* share the following characteristics: (1) cells II and VI that lie next to each other and are separated by a vertical septum, (2) apical or subapical outgrowths of the

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perithecium, and (3) four tiers of perithecial wall cells (Tavares 1985). No members of *Diphymyces* have been reported from Asia with the exception of *D. appendiculatus* (Thaxt.) I.I.Tav., the single host specimen of which was collected in Java, Indonesia (Thaxter 1915, 1931).

Diphymyces penicillifer A.Weir & W.Rossi was found on the rove beetles (Staphylinidae) *Stenomalium helmsi* Cameron, 1945, *Allodrepa decipiens* Steel, 1964, and *Nesomalium pacificum* (Kiesenwetter, 1877) (Weir & Rossi 1997, Hughes et al. 2004). All the other species of *Diphymyces* have been described from hosts in the family Leiodidae, subfamily Cholevinae. The identity of some of the host species remains uncertain (Tavares 1985, Rossi & Santamaría 2010).

A review of all described species of *Diphymyces*, with their hosts and geographical distribution, is presented in table 1.

MATERIAL AND METHODS

The hosts were collected by the second author with dry pitfall traps baited with Limburger cheese (see Schilthuizen et al. 2011, for the trapping method). Traps were placed in disturbed and pristine tropical rainforest before and during the Crocker Range / Kinabalu expedition, which took place from 10 to 25 Sep. 2012 (Anonymous 2012). Traps were left in the field for four to nine days and then retrieved and emptied. Leiodidae were immediately preserved in pure ethanol. In the laboratory, each insect was identified and screened using a Leica dissecting microscope. Body parts with thalli attached were transferred with a size 1 insect pin into a tube containing pure ethanol and sent to the first author for further study of the Laboulbeniales. Screening for infection and removal of thalli was done at 50× magnification with a stereomicroscope. Thalli were transferred with the help of a BioQuip Minuten Pin and embedded in Amann solution (Benjamin 1971). Cover slips were ringed with transparent nail varnish. Morphological analyses and measurements were made using an Olympus BX40 light microscope with Olympus XC50 digital camera and MicroSuite Special Edition software 3.1 (Soft Imaging Solutions GmbH). Photography was done at the Harvard Center for Biological Imaging using a Zeiss AxioImager microscope equipped with differential interference contrast optics and running on ZEN software. Microscope slides are deposited at the Farlow Herbarium, Harvard University (FH) and the National Herbarium Netherlands, Leiden University branch (L).

Host taxonomy follows Schilthuizen & Perreau (2008).

TAXONOMY

Diphymyces sabahensis Haelew. & Pfister, **sp. nov.**
MycoBank No. MB 805572

Diagnosis – Differs from the other *Diphymyces* species by the following characteristics: the outer portions of cells II and III very dark brown; both cells II and VI 3.5–4× longer than broad; the finger-like projection of the perithecium. – Type: Malaysia, Sabah, location Poring Hot Springs, 6°02.894'N 116°41.957'E, alt. 625 m, disturbed primary lowland forest on serpentine soil, 15–20 Sep. 2012, leg. M.Schilthuizen, on male *Ptomaphaginus bryantioides* Schilthuizen & Perreau, 2008 (Coleoptera, Leiodidae, Cholevinae, Ptomaphagini), RMNH.INS.555625, fungal specimens D.Haelew. 124e1 (holotype), 124d1-2 and 124f1-3, and 124e2 (isotypes), all specimens collected from abdominal sternites, both upon midline and just right of midline.

Etymology – Referring to the easternmost state of Malaysia, where the type material originated from.

Description – Colour: upper portion of cell I and outer portions of cells II and III very dark brown; the rest of the fungus irregularly olive brown, with much paler lower portions of the perithecium and cell I. Cell I up to four times longer than broad, slender and elongate, regularly broadening upwards. Cell II about four times longer than broad, rectangular or trapezoidal in optical section. Cell III up to three times longer than broad, rectangular, giving rise distally to a single appendage. Appendage's lower cell similar to, but smaller than cell III; in very young thalli appendage consisting of 3–5 superimposed cells, giving rise to short branchlets. Antheridia terminal on these branchlets. Cell VI obtriangular, shorter than cell II but with the upper portion wider than the same. Perithecium stout, elliptical to distinctly asymmetrical, straight, curved or flexed, the tip not particularly distinguished, bearing anteriorly a darkened finger-like projection

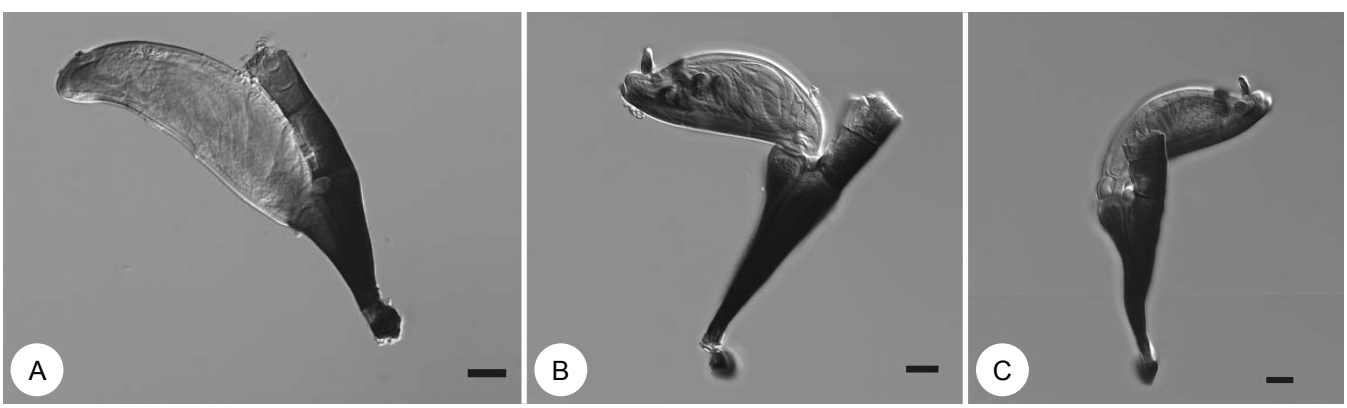

Figure 1 – *Diphymyces sabahensis* sp. nov., showing thalli with straight or bent perithecium: A, thallus D.Haelew. 120b1, collected from last tergite of *Ptomaphaginus* cf. *bryantioides*; B, thallus D.Haelew. 124d1 (isotype), collected from abdominal sternite of *P. bryantioides*; C, thallus D.Haelew. 124e1 (holotype), collected from abdominal sternite of *P. bryantioides*. Scale bars = 10 μm.

Table 1 – Currently described species of *Diphymyces*, with host information and geographical distribution.
Species are ranked chronologically, according to the year of description. Also all further records are listed, in alphabetical order with reference to the host species name (if applicable).

Fungus epithet	Author(s)	Host family	Host subfamily	Host tribe	Host species	Author	Continent	Distribution	Reference
appendiculatus	(Thaxt.) I.I.Tav.	Leiodidae	Coloninae		*Colonellus* [?] (as *Colon* sp.)	Szymczakowski, 1964	Asia	Indonesia	Tavares 1985
bidentatus	(Thaxt.) I.I.Tav.	Leiodidae	Cholevinae	Anemadini	*Paracatops* [?] (as *Choleva* sp.)	Portevin, 1907	Oceania	New Zealand	Tavares 1985
curvatus	(Thaxt.) I.I.Tav.	Leiodidae	Cholevinae	Anemadini	*Paracatops* [?] (as *Choleva* sp.)	Portevin, 1907	Oceania	New Zealand	Tavares 1985
niger	(T. Majewski) I.I.Tav.	Leiodidae	Cholevinae	Ptomaphagini	*Ptomaphagus sericatus*	(Chaudoir, 1845)	Europe	Poland	Tavares 1985
					Ptomaphagus subvillosus	(Goeze, 1762)		Finland, Russia	Tavares 1985
					Ptomaphagus varicornis	(Rosenhauer, 1847)		Poland	Tavares 1985
					Ptomaphagus sericatus	(Chaudoir, 1845)		Spain	Santamaría 1993
silphidarum	(Thaxt.) I.I.Tav.	Leiodidae	Cholevinae	Anemadini	*Eunemadus* [?] (as *Choleva* sp.)	Portevin, 1914	South America	Chile	Tavares 1985
urbasoli	Santam.	Leiodidae	Cholevinae	Leptodirini	*Euryspeonomus (Urbasolus) eloseguii*	(Español, 1948)	Europe	Spain	Santamaría 1993
penicillifer	A.Weir & W.Rossi	Staphylinidae	Omaliinae	Omaliini	*Stenomalium helmsi*	Cameron, 1945	Oceania	New Zealand	Weir & Rossi 1997
					Allodrepa decipiens	Steel, 1964		New Zealand	Hughes et al. 2004
					Nesomalium pacificum	(Kiezenwetter, 1877)		New Zealand	Hughes et al. 2004
depressus	M.B.Hughes, A.Weir & C.Judd	Leiodidae	Cholevinae	Anemadini	*Paracatops campbellicus*	(Brookes, 1951)	Oceania	New Zealand	Hughes et al. 2004
leschenii	M.B.Hughes, A.Weir & C.Judd	Leiodidae	Cholevinae	Anemadini	*Paracatops campbellicus*	(Brookes, 1951)	Oceania	New Zealand	Hughes et al. 2004
spelaei	W.Rossi	Leiodidae	Cholevinae	Leptodirini	*Anthroherpon latipenne* ssp. *latellai*	Giachino & Vailati, 2005	Europe	Albania	Rossi 2006
		Leiodidae	Cholevinae	Leptodirini	*Anthroherpon taxi* ssp. *trezzii*	Giachino & Vailati, 2005			Rossi 2006

Table 1 (continued) – Currently described species of *Diphymyces*, with host information and geographical distribution.

Fungus epithet	Author(s)	Host family	Host subfamily	Host tribe	Host species	Author	Continent	Distribution	Reference
arnaudii	W.Rossi & Santam.	Leiodidae	Cholevinae	Anemadini	*Nemadiopsis (Nemadiopsella) curvipes)*	Salgado, 2002	South America	Chile	Rossi & Santamaría 2010
					Nemadiopsis (Nemadiopsicus) barbarae	Szyczakowski, 1965			Rossi & Santamaría 2010
					Nemadiopsis (N.) fastidiosus	(Fairmaire & German, 1859)			Rossi & Santamaría 2010
					Nemadiopsis (N.) rufimanus	Jeannel, 1962			Rossi & Santamaría 2010
giachinoi	W.Rossi & Santam.	Leiodidae	Cholevinae	Anemadini	*Nargiotes annalaurae*	Giachino & Peck, 2003	Oceania	Australia	Rossi & Santamaría 2010
					Nargiotes gordoni	Giachino & Peck, 2003			Rossi & Santamaría 2010
					Nargiotes montifuscis	Giachino & Peck, 2003			Rossi & Santamaría 2010
pavicevicii	W.Rossi & Santam.	Leiodidae	Cholevinae	Leptodirini	*Pholeuonopsis magdelainei*	Jeannel, 1924	Europe	Serbia	Rossi & Santamaría 2010
pusillus	W.Rossi & Santam.	Leiodidae	Cholevinae	Ptomaphagini	*Adelopsis bioforestae*	Salgado, 2002	South America	Ecuador	Rossi & Santamaría 2010
sabahensis sp. nov.	Haelew. & Pfister	Leiodidae	Cholevinae	Ptomaphagini	*Ptomaphaginus bryantioides*	Schilthuizen & Perreau, 2008	Asia	Malaysian Borneo	present study
					Ptomaphaginus kinabaluensis	Schilthuizen & Perreau, 2008			present study
					Ptomaphaginus similipes	Schilthuizen & Perreau, 2008			present study
metatibial thalli		Leiodidae	Cholevinae	Ptomaphagini	*Ptomaphaginus bryantioides*	Schilthuizen & Perreau, 2008	Asia	Malaysian Borneo	present study
					Ptomaphaginus similipes	Schilthuizen & Perreau, 2008			present study

directed outwards, the blunt apex consisting of four unequal, rounded lips. Fig. 1A–C.

The description given above is based on fourteen mature, seven submature and 24 immature thalli obtained from a series of eight infested male and female specimens of *Ptomaphaginus* spp., collected at five different localities.

Measurements – Total length from base of foot to perithecial tip 106–154 µm; total length from foot to tip of appendages 110–125 µm; cell II 33–57 × 9–16 µm; cell VI 29–59 × 9–17 µm; perithecium (including basal cells) 63–99 × 22–30 µm; subapical perithecial projection 6–8 µm; cell III 15–29 × 7–14 µm; longest appendages 43 µm; immature ascospores observed (fig. 1B).

Additional specimens examined (paratypes) – **Malaysia**: Sabah, Kiansom, 5°58.444'N 116°12.526'E, alt. 300 m, strongly disturbed lowland forest along stream, 5–7 Sep. 2012, leg. M. Schilthuizen, on male *P. bryantioides*, RMNH.INS.555598, permanent slide D.Haelew. 118a (one specimen collected from penultimate sternite upon midline); on female *P.* cf. *bryantioides*, RMNH.INS.555599, permanent slides D.Haelew. 120a (one specimen collected from right-hand side last tergite) and 120b (three specimens collected from right-hand side last tergite); Sabah, location Poring Hot Springs, 6°02.894'N 116°41.957'E, alt. 625 m, disturbed primary lowland forest on serpentine soil, 15–20 Sep. 2012, leg. M. Schilthuizen, on male *P.* cf. *bryantioides*, RMNH.INS.555626, permanent slide D.Haelew. 119a (four specimens collected from right elytron); Sabah, Sayap substation of Kinabalu Park, no exact coordinates available, alt. 950 m, primary lower montane forest, 11–16 Sep. 2012, leg. M. Schilthuizen, on male *P. similipes* Schilthuizen & Perreau, 2008, RMNH.INS.555614, permanent slide D.Haelew. 122a (one specimen collected from right mesotibia); on male *P. similipes*, RMNH.INS.555613, permanent slides D.Haelew. 123a (four specimens collected from last sternite just right of midline), 123b (three specimens collected from penultimate sternite just right of midline), and 123c (three specimens collected from abdominal sternite just right of midline); Sabah, Sugud, 5°50.361'N 116°07.084'E, alt. 360 m, disturbed lowland dipterocarp forest on ridge, 1–4 Sep. 2012, on female *P.* cf. *similipes*, leg. M. Schilthuizen, RMNH.INS.555594, permanent slides D.Haelew. 125a (seven specimens collected from posterior margin right elytron), 125b (2 specimens collected from right-hand side last tergite), and 125c (nine specimens collected from right-hand side last tergite); Sabah, Gunung Alab, 5°49.766'N 116°20.504'E, alt. 1930 m, cloud forest, 17–22 Sep. 2012, leg. M. Schilthuizen, on male *P. kinabaluensis* Schilthuizen & Perreau, 2008, RMNH.INS.555631, permanent slide D.Haelew. 121a (one specimen collected from penultimate sternite).

Remarks – The thalli of *Diphymyces sabahensis* are variably bent and curved. We have observed different morphologies: thalli bearing a straight or bent perithecium, bending either toward the posterior or anterior side. It is ambiguous whether these morphologies represent position-related morphotypes as in *D. spelaei* W.Rossi (Rossi 2006); in *Rodaucea salgadoi* W.Rossi & Santam., another species parasitic on Cholevinae, different morphotypes were found connected to different parts of the host body (Rossi & Santamaría 2012). We have collected the different morphologies from the same positions on two male host specimens (RMNH.INS.555613 and RMNH.INS.555625: thalli with both straight and bent perithecia growing on abdominal sternites of *Ptomaphaginus bryantioides* and *P. similipes*, respectively). On female hosts we have not observed thalli with bent perithecia (RMNH.INS.555599: three thalli with straight perithecium growing on right-hand side of last tergite of *P.* cf. *bryantioides*). More collections are needed for further elucidation.

Diphymyces sabahensis can be separated easily from all other known species in the genus by the organization of cells II and VI (both 3.5–4× longer than broad) and the finger-like projection of the perithecium. In comparison, the perithecium of *D. spelaei* also bears a finger-like projection, but its thallus has a more massive cell I with cell II just slightly longer than its maximum width; cell VI is much shorter and cuneate. In addition, thalli of *D. spelaei* are greyish brown with darker perithecial tips and outer portions of cell III (Rossi 2006); in *D. sabahensis* cells II and III are very dark brown, cell II at both lower and outer portions whereas cell III dark mainly at its outer portion. Like *D. sabahensis*, *D. appendiculatus* possesses a slender projection, but this is located on the apex as a prolongation of the perithecium (Thaxter 1915, 1931); in *D. sabahensis* the subapically positioned projection is always directed outwards.

The new species superficially resembles *Mimeomyces bicolor* (Thaxt.) I.I.Tav. as to the lower part of the receptacle and the stalk cell of the perithecium (VI). The first part of Thaxter's (1931) description for *M. bicolor* (as *Corethromyces bicolor*) – "foot broader than the base of the long slender receptacle, which is slightly translucent just above it, but otherwise quite opaque" – is entirely applicable to *D. sabahensis*. The latter differs in the receptacle not being bilobed, the perithecium with the venter not opaque, and the distal half of the same, or more, perfectly hyaline.

Thalli of *Diphymyces sabahensis* bear broken appendages, except for the peculiar short branches observed in a few immature thalli. These branchlets bear structures resembling terminal antheridia, which are similar to the ones found in other species in the genus. Unfortunately spermatia have not been detected.

All available mature parasites were found without complete appendages. Thaxter (1918b, 1931), likewise, found that a majority of the individuals of *Diphymyces bidentatus* (Thaxt.) I.I.Tav. (as *Corethromyces bidentatus*) were broken or abnormal and he noted that this was the case, "although a considerable number of specimens of this form [had] been examined." The behavior of the host (*Paracatops* sp., as *Choleva* sp.) was proposed as the key factor in this observation (Thaxter 1931). The thalli could be easily damaged by the typical lifestyle of cholevine hosts. Almost all Cholevinae live underground (Sokolowski 1942). They make extensive use of narrow natural crevices in the soil, which is why, in temperate climates, they are primarily found in mammalian burrows and nests. Movement of hosts through such channels and tunnels might cause thalli to be broken or damaged. Future study of the behavior of these beetles in the tropics deserves attention.

The new species has in common with *D. bidentatus* the variably bent thalli but its much longer cells II and VI and typical coloration easily separate it from the latter species.

Diphymyces sabahensis parasitizes up to three species of *Ptomaphaginus* Portevin, 1918, a new host genus for *Diphymyces*. The other species of *Diphymyces* described so far on members of the leiodid tribe Ptomaphagini (subfamily Cholevinae; Newton 1998) are *D. niger* (T.Majewski)

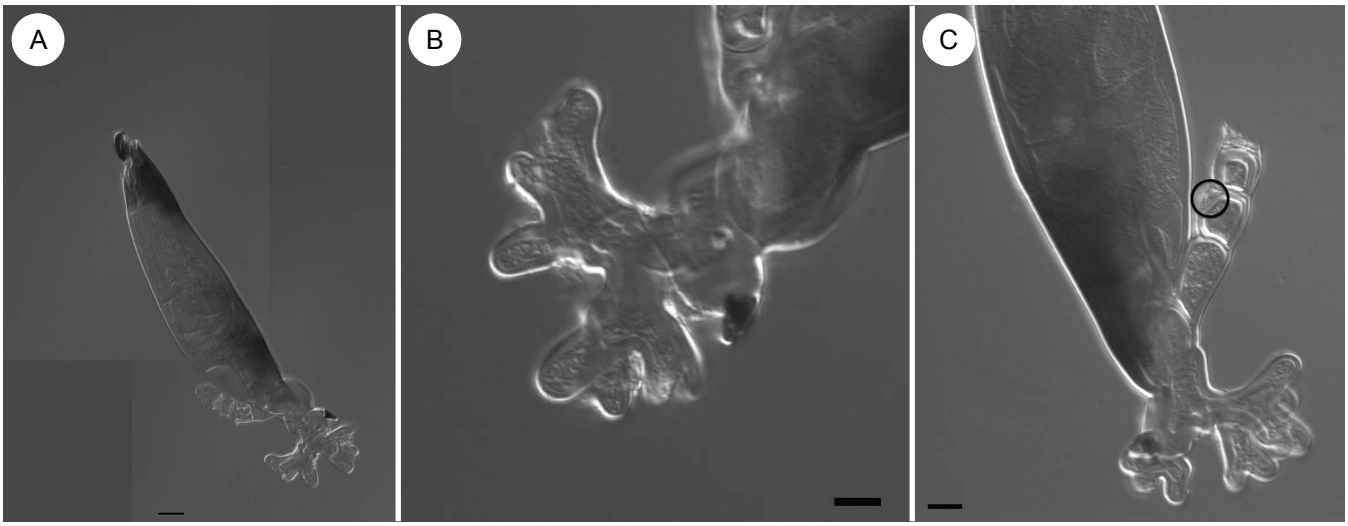

Figure 2 – Metatibial thalli, characterized by the buffer organ, a lateral outgrowth at cell I: A, thallus D.Haelew. 124c1; B, same thallus, detail of continuous buffer organ; C, thallus D.Haelew. 124b4, detail of appendage, showing the antheridium (encircled). Both thalli collected from left metatibia of *P. bryantioides*. Scale bars: A = 10 µm; B, C = 5 µm.

I.I.Tav. from Europe and *D. pusillus* W.Rossi & Santam. from Ecuador. Both species, however, together with *D. depressus* M.B.Hughes, A.Weir & C.Judd, are clearly unlike the new species, since they have a compact, stout appearance with the cell VI broader than long (Majewski 1973, 1994, Santamaría 2003, Hughes et al. 2004, Rossi & Santamaría 2010). Furthermore, *D. depressus* lacks any apical or subapical perithecial "teeth" or projections.

Thalli restricted to the metatibiae

In our study we removed from the metatibiae of two host insects specimens that could represent a position-related growth form of *D. sabahensis* (fig. 2A, B & C). The decision not to formally describe these metatibial thalli as a new species is based on the knowledge that the Laboulbeniales exemplify a highly diverse group for which, for technical reasons, only limited molecular data are available (see Discussion). We report the presence of the metatibial thalli in Malaysian Borneo to draw attention to it in the hope that more thalli will be discovered.

Description – Colour: the upper and lower portions of perithecium, including its basal cells, dark brown, and the median portion of the perithecium, the receptacle, and appendage hyaline or almost so. Cell I irregular, producing laterally a large coral-like buffer outgrowth, the lumen of which is continuous with that one of cell I. Cell II variable in shape, often thick-walled, separated from cell III by an oblique septum. Cell III trapezoidal in optical section, about twice (1.1–2.3) as long as broad, giving rise distally to the appendage. In the available specimens the latter is always incomplete: what remains is a series of 2–4 squarish superimposed cells. Antheridia small, distolaterally borne from appendage cells. Cell VI relatively small, from 1.2 to 2.6 times longer than broad. Perithecium elongated, asymmetrical with the anterior margin distinctly convex and the posterior margin almost straight, the tip not abruptly distinguished except for its darker color, tapering to the apex consisting of two large lips, the anterior of which is distinctly longer, carrying a darkened ovoid projection; a small tooth is present on the anterior side of the perithecial apex.

The description given above is based on twelve mature thalli obtained from two specimens (one male, one female) of *Ptomaphaginus* spp., collected from two localities.

Measurements – Total length from base of foot to perithecial tip 101–151 µm; total length from foot to tip of appendages 54–70 µm; cell I 11–15 µm, cell II 7–17 × 5–15 µm; cell VI 10–17 × 5–13 µm; perithecium (including basal cells) 86–119 × 22–31 µm; apical perithecial projection 10–13 × 4–6 µm; cell III 7–17 × 5–8 µm; longest appendages seen 26 µm; ascospores 16–20 µm.

Specimens examined – **Malaysia**: Sabah, location Poring Hot Springs, 6°02.894'N 116°41.957'E, alt. 625 m, disturbed primary lowland forest on serpentine soil, 15–20 Sep. 2012, leg. M. Schilthuizen, on male *Ptomaphaginus bryantioides*, RMNH.INS.555625, fungal specimens D.Haelew. 124a (two specimens), 124b (four specimens), and 124c (three specimens), all specimens collected from left metatibia; Sabah, Sayap substation of Kinabalu Park, no exact coordinates available, alt. 950 m, primary lower montane forest, 11–16 Sep. 2012, leg. M. Schilthuizen, on female *Ptomaphaginus* cf. *similipes*, RMNH.INS.555617, permanent slides D.Haelew. 127a (two specimens) and 127b (two specimens), all specimens collected from right metatibia.

Remarks – A remarkable characteristic in the metatibial thalli, previously unreported for any other species in the genus, is the lateral outgrowth of cell I. All thalli but one carry this buffer organ as first described by Thaxter (1912) as perhaps an anchoring structure.

Other genera with buffer organs are *Hydrophilomyces* Thaxt., *Osoriomyces* Terada, *Rhizopodomyces* Thaxt., *Scelophoromyces* Thaxt., and *Zodiomyces* Thaxt. (Santamaría 2004). *Thaumasiomyces* Thaxt. bears outgrowths laterally at cell I, which form rhizoidal 'secondary attachments' with the host (Thaxter 1931). Thaxter (1912, 1931) suggested these unicellular or multicellular structures maintain the thallus position during the activities of the host but evidence for

this assumption is lacking. Also *Ceratomyces rhizophorus* Thaxt., the only species in that genus, possesses unicellular outgrowths, developing from one or more cells of the receptacle and the basal cell of the appendage, and abruptly curving down toward the host's integument (Thaxter 1931).

DISCUSSION

Thalli of *D. sabahensis* were collected from different positions, mostly upon the midline or at the right-hand side of eight host specimens, both male and female, belonging to *Ptomaphaginus* (cf.) *bryantioides*, *P. kinabaluensis*, and *P.* (cf.) *similipes*. Metatibial thalli were collected from the left and right metatibia of *P. bryantioides* and *P.* cf. *similipes*, indicating a possible position-relatedness. Upon one male *P. bryantioides* host specimen (RMNH.INS.555625), both examples were found: thalli of *D. sabahensis* were taken from the sternites, upon the midline as well as just right of the midline; metatibial thalli with typical buffer organ were removed from the left-hand side. When morphologically different thalli are found on a single host, the question can be raised whether these are different position-specific species (Thaxter 1896, Benjamin & Shanor 1952) or morphotypes ("growth forms") of the same biological species, with a moderate to strong degree of phenotypic plasticity (*sensu* Scheloske 1976). To determine whether the metatibial thalli represent a position-related growth form of *D. sabahensis*, or a new species, additional collections are needed as well as DNA sequences.

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