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Dactylospora inopina (Lecanorales), a new biotrophic parasite on *Radula* (Hepaticae) from the Cape Horn Archipelago, Chile

Peter Döbbeler[1] and William R. Buck[2]

[1] Ludwig-Maximilians-Universität München, Systematische Botanik und Mykologie, Menzinger Str. 67, D-80638 München, Germany

[2] Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126, U.S.A.

With 12 figures

Abstract: The lecanoralean fungus *Dactylospora inopina* Döbbeler & W.R.Buck sp. nov. (Dactylosporaceae) is described on the liverwort *Radula* spp. (Radulaceae, Jungermanniales) based on collections from southernmost Chile. The species is characterized by small, warty apothecial ascomata, polysporous asci and subcylindrical, four-celled, brown ascospores. Polyspory has previously been known only in five lichenicolous species having two-celled spores. The combination of polyspory and phragmospory is a new character in the genus. The parasite grows by a mycelium within the host cell walls and does not cause visible damage. *Dactylospora inopina* is one of the relatively few hepaticolous discomycetes known so far. Apart from two *Octosporella* species with perithecia-like apothecia it is the first one on the large genus *Radula*, which is a good host for pyrenocarpous ascomycetes.

Key words: Bryophilous fungi, hepaticolous ascomycetes, intercellular mycelium.

Introduction

Dactylospora Körb., with 89 epithets (http://www.indexfungorum.org/names/Names.asp), is the only genus of the lecanoralean family Dactylosporaceae. It is characterized by dark apothecial ascomata and inoperculate asci with an amyloid external cap of gelatinous material (*Dactylospora*-type, Bellemère & Hafellner 1982). Spore characters vary considerably regarding size, color (colorless to brown), structure of epispore, and especially septation (one to several transverse septa to submuriform spores) and number per ascus (eight or polysporous). The genus has a wide ecological amplitude ranging from saprotrophs to parasites on bark and wood, lichens, fungi and liverworts. Lichenized species and mosses as hosts are unknown. Most species are lichenicolous. They prefer crustose lichens exhibiting a varying degree of host

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specialization. The fungicolous *D. epimyces* (Tobisch) Hafellner occurs on corticioid fungi. Several xylophilous species are restricted to decaying wood (Hafellner 1979, Triebel 1989), including driftwood in marine habitats (Kohlmeyer & Volkmann-Kohlmeyer 1998, Pang et al. 2014). *Dactylospora heimerlii* (Zukal) Döbbeler & Triebel on *Plagiochila asplenioides* (L.) Dumort. *s. lat.* and other leafy liverworts is the best known hepaticolous species. It is widespread but not common in Europe and reported in several remote extra-European regions. There are more than 60 collections on jungermannialean hepatics belonging to several families (Döbbeler & Triebel 1985, Marsh et al. 2010, Döbbeler & Hertel 2013).

In the summer of 2013 the senior author taught a class on bryophilous fungi at the Eagle Hill Institute (http://www.eaglehill.us/) in coastal Maine, U.S.A. The junior author was one of the five students in the class. Subsequently, Buck continued to search for and collect these fungi, many of which are sufficiently small to be invisible in the field. However, Buck's primary research is the bryoflora of the Cape Horn Archipelago in southernmost Chile (Buck et al. 2015). After having taken Döbbeler's class, Buck began collecting those fungi visible to the eye as part of his fieldwork. What initially was thought to be a single species of fungus growing over hepatics, was later proved to be multiple species of fungi, both lichenized and non-lichenized. One of the lichenized fungi was recently described as a new species of *Catinaria* (Lendemer et al. 2016). One of the more common non-lichenized fungal taxa that was encountered seemed to be restricted to growing on the thalli of the hepatic genus *Radula* on the trunks of *Nothofagus*. It forms small, black, lumpy apothecia on what appear to be healthy liverwort leaves and perianths. We take this opportunity to describe it as new.

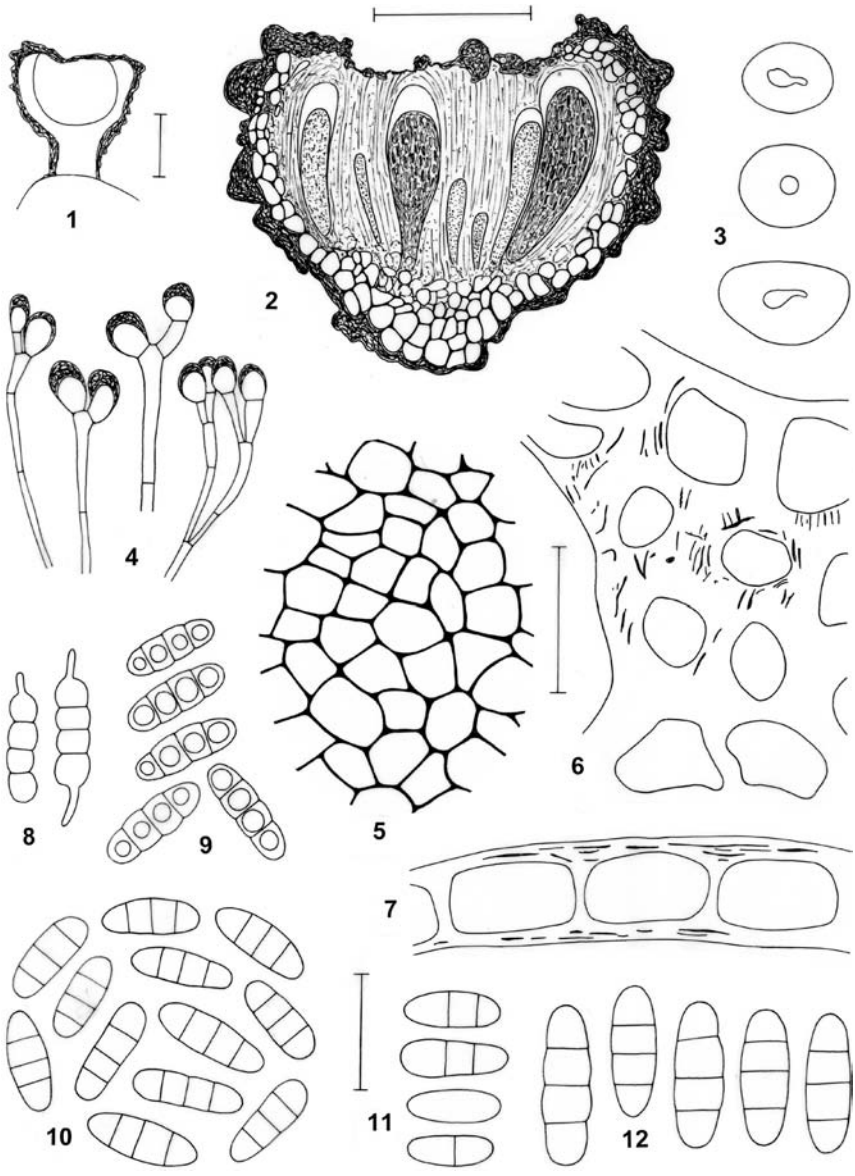
Dactylospora inopina Döbbeler & W.R.Buck **sp. nov.** (Dactylosporaceae, Lecanorales) Figs 1–12

Mycobank no.: 819218

Etymology: *inopinus* (Latin) = unexpected, refers to the combination of polysporous asci and four-celled spores – a combination hitherto not known within the genus.

Latin Diagnosis: Species nova characteribus communibus generi *Dactylospora* bene congruens, sed ascomatibus verruculosis, ascis polysporis et sporis triseptatis, brunneolis, 8–10 × 3 µm magnis distincta. Habitat parasitice ad folia plantarum vivarum hepaticae corticalis *Radula* spp.

Description: Ascomata apothecial, superficial, initially almost globose to ellipsoidal, later more or less turbinate, without or rarely with a short, thick stalk, 120–250 (–380) µm diam., 140–300 µm high (in water), margin lacking or inconspicuous, disc slightly concave in small ascomata, later plane or even convex, dark to black brown, apart from the lighter ascomatal base, disk of immature ascomata slightly lighter, whole surface (including the disc) from the beginning covered with small warts caused by strongly thickened outer cell walls; ascomata shrinking when drying. – Excipulum seen from the outside of angular, 4–10 µm large cells (*textura angularis*) each with a semiglobose or conical dark outgrowth of the wall measuring to as much as about 10 µm high, these coverings towards the top becoming dense, hiding the cellular excipular structure, towards the base gradually disappearing; excipulum in section (15–)20–30 (–38) µm thick, of few layers of angular cells; hypothecium little developed.



Figs 1–12: *Dactylospora inopina*. 1. Stalked ascoma in median longitudinal section, scale = 100 µm. 2. Ascoma with two mature asci in tangential longitudinal section, scale = 60 µm. 3. Discharged asci seen from above in diluted Lugol's solution, apical opening indicated. 4. Paraphyses with colored apical cells. 5. Cells of lower excipulum seen from the outside. 6. Hyphae within cell walls of stem in transverse section. 7. Hyphae within cell walls of leaf in transverse section. 8. Germinating ascospores. 9. Ascospores in KOH. 10. Ascospores. 11. Atypical ascospores. 12. Unnaturally large ascospores of a 16-spored ascus. Figs 1, 2, 4–8, 10–12 mounted in lactophenol cotton-blue. Figs 3–7 scale = 20 µm. Figs 8–12 scale = 10 µm. Figs 1, 9 Buck 62330 (M). Figs 4, 5, 10–12 holotype, Buck 58904 (NY 02696316). Figs 2, 3, 6–8 Buck 58630 (NY 02696319).

– Paraphyses like the asci imbedded in compact hymenial gel, longer than the asci, apically ramified forming the ca 10 µm thick epihymenium, end cells subglobose, together with their dark caps (like those of the excipular cells) to 6(–8) µm diam., sometimes also the subapical cell dark colored. – Asci unitunicate, narrowly ellipsoidal to claviform, rather thick-walled, polysporous (more than 32 spores), 40–65(–80) × (13–)15–20 µm (in lactophenol-cotton blue, including the apical cap), completely surrounded by gelatinous material; apical gelatinous cap to 6 µm thick, gelatinous cover at the outside not sharply delimited; empty asci seen from above in iodine with an irregular apical aperture. – Ascospores cylindrical to narrowly ellipsoidal, 4-celled, gray to light brown to brown, (7.5–)8–10 × (2.5–)3(–3.5) µm (in lactophenol-cotton blue), not or slightly to strongly constricted at the septa (sometimes resulting in 4 almost globose cells), often one large oil drop per cell visible, epispore smooth, irregularly arranged in the asci and filling the ascus lumen (only cells but not individual spores visible in unsquashed asci), neither cytoplasm nor wall reacting with cotton blue; germinating spores with hyphae arising from the end cells; one ascoma of the type collection included an ascus with only about 16 spores measuring (10–)11–13(–13.5) × 3.5–5 µm. – Hyphae inconspicuous and difficult to trace, colorless, irregularly growing within the walls of leaf and especially stem cells, extremely delicate (often less than 0.5 µm thick), abundant, resulting in eroded cell walls; hyphae over and even within few host cells only at the attachment point of the ascomata, brown or colorless, to 3 µm wide. – No anamorph observed.

Chemical Reactions: Iodine reaction (Lugol, without pretreatment with KOH) complex, hymenium immediately deep black blue; iodine in low concentration: gelatin surrounding the ascus wall light blue, gelatinous ascus cap dark blue; iodine in higher concentration: light blue color changing to an intensive dirty red brown often with olive or lilac tints, apical cap black blue, without inamyloid pore; iodine reaction reversible. – KOH reaction of excipulum lacking.

Hosts: *Radula flavifolia* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *R. magellanica* Schiffn. (once *Frullania* sp. intermingled with *Radula*), growing on the bark of *Nothofagus* trees.

The ascomata develop superficially on leaves or between them (preferentially on the dorsal side) and on stems, occasionally also on perianths. The species is regarded as a biotrophic parasite. Infected shoots remain healthy and do not show signs of damage, or they began to wither when becoming older. Algal cells may be present on the hepatic leaves but obligate relations of *D. inopina* hyphae to them could not be demonstrated. The host tissue at the attachment point is often stained brownish.

Specimens Examined: Chile, Prov. Antártica Chilena, Comuna Cabo de Hornos, Parque Nacional Alberto de Agostini, Isla Grande de Tierra del Fuego, W coast of Caleta Olla, at E end of Brazo Noroeste of Beagle Channel, 54°56'26"S, 69°09'27"W, coastal *Nothofagus antarctica* forest, on *Radula magellanica*, 29 Jan 2012, W.R.Buck 58904 (holotype NY 02696316). Parque Nacional Alberto de Agostini, S shore of Isla Aguirre, SE side of Seno Quo Vadis, 54.5725°S, 71.9945°W, 5 m, *Nothofagus*/*Drimys winteri* coastal woodland, underside of horizontal *Nothofagus betuloides* twig, on *Radula flavifolia*, 29 Jan 2011, B.Shaw 13522A (NY 02696325), 13523A (NY 02696326). Parque Nacional Alberto de Agostini, north-central coast of Isla Hoste, ca. 5 km W of the eastern tip of Isla Gordon along Brazo Sudoeste of Beagle Channel in unnamed sound, 55°00'21"S, 69°12'13"W, *Nothofagus-Drimys-Maytenus* forest grading into Magellanic tundra, on lower trunk of young *Nothofagus*, on

Radula magellanica, 19 Jan 2012, W.R.Buck 58369 (NY 02696318). Parque Nacional Alberto de Agostini, N shore of Isla Hoste, SE end of Península Cloué, E side of Estero Fouque opposite Punta Blanco near river draining small lake, 55°09'48"S, 69°31'01" W, stunted coastal *Nothofagus* forest, on *Radula magellanica*, 21 Jan 2012, W.R.Buck 58630 (NY 02696319), on *Radula magellanica* on base of *Nothofagus betuloides*, W.R.Buck 58633 (NY 02696320). Parque Nacional Alberto de Agostini, Isla Hoste, NW shore of Península Rous at E end of unnamed sound sharing its mouth with that of Estero Webb, 55°17'58"S, 69°33'24"W, narrow *Nothofagus betuloides* forest, on *Radula magellanica* together with *Catinaria radulae* and on *Frullania* sp., 23 Jan 2012, W.R.Buck 58740 (NY 02696321). Parque Nacional Alberto de Agostini, E end of Isla Gordon, S side of Punta Divide on Brazo Sudoeste of Beagle Channel, 54°58'15"S, 69°07'50"W, *Nothofagus* forest, on *Radula flavifolia*, 19 Jan 2005, W.R.Buck 47945 (NY 02696317). Parque Nacional Alberto de Agostini, Isla Gordon, Bahía Romanche, N-facing slope with waterfall 5 km SSW of Brazo Noroeste of Beagle Channel, 54.95402°S, 69.49407°W, 3 m, steep rock outcrops and *Drimys winteri* & *Nothofagus betuloides* stunted trees on N-facing slope in a sheltered cove, trunk of *Nothofagus betuloides*, on *Radula flavifolia*, 29 Jan 2012, B.Shaw 15097A (NY 02696327). Parque Nacional Cabo de Hornos, Isla Wollaston, W shore of Caleta Loberos at S end of Seno Alberto, 55°43'12"S, 67°25'45"W, forest in stream valley dominated by *Nothofagus betuloides*, on *Radula magellanica*, 26 Jan 2005, J.J.Engel 26423A (NY 02696324). Parque Nacional Cabo de Hornos, Islas Hermite, E coast of Isla Hermite, Caleta Saint Martin, 55°51'35"S, 67°34'23"W, wet *Nothofagus antarctica-Drimys* forest, on *Radula magellanica*, 19 Jan 2014, W.R.Buck 62602 (M, NY 02696323). E coast of Isla Hoste, Península Hardy, Bahía Orange, Caleta Duck, 55°32'02"S, 68°05'25"W, coastal *Nothofagus betuloides-Drimys* forest, on *Radula magellanica*, 12 Jan 2014, W.R.Buck 62330 (M, NY 02696322).

Remarks: The main diagnostic features of the new species are small, warty apothecial ascomata (seen by stereomicroscopic magnification), polysporous asci, 4-celled, less than 10 µm long, brown, smooth ascospores, and biotrophic parasitism on corticolous *Radula* spp. Asci with many spores occur in five *Dactylospora* species, namely *D. hafellneriana* Sérus. (Sérusiaux & Wessels 1984), *D. inconspicua* Etayo (Etayo & Sancho 2008), *D. microspora* Etayo (Etayo 1991), *D. pertusariicola* (Willey ex Tuck.) Hafellner (Hafellner 1979), and *D. polyspora* Triebel (Triebel 1989). All differ from *D. inopina* in having smaller, two-celled spores and by ecology, i.e. they occur as parasites on lichens.

Dactylospora inopina is perhaps not strictly host-specific to *Radula*. Several ascomata were observed on an intermingled *Frullania* sp. (Buck 58740, NY 02696321). Due to the sharp color contrast between the light green *Radula* shoots and the dark ascomata the fungus is much easier to detect on that host than on *Frullania*.

Ecology: The new species grows on two south temperate species of *Radula*, *R. flavifolia* and *R. magellanica*. The two host species can be told apart only with a dissecting microscope. *Radula flavifolia* is the larger of the two species, with strongly overlapping leaves with dorsal lobe apices acute to acuminate. *Radula magellanica* is a species of considerably smaller stature with widely-spaced leaves whose dorsal lobe apex is broadly rounded (Engel 1978). Both species seem equally susceptible to infection. In almost every case, the *Radula* was found on the trunk of *Nothofagus* spp., especially *N. betuloides* and *N. antarctica*. *Nothofagus* forests dominate the Cape Horn landscape. The three local species of *Nothofagus* (i.e., those above plus *N. pumilio*) have slightly different habitats, in part differentiated by precipitation levels. In the Cape Horn region, precipitation varies widely with the westernmost areas receiving the most rainfall (ca 4 m/year) while the easternmost areas receive the least (ca 700 mm/yr) (Rozzi et al. 2004). None of the infected material examined came from the wetter, western areas

of the Cape Horn Archipelago. Rather all came from west of longitude 67°25'W and most from west of 69°00'W. This may reflect the habitat preference of the host liverwort rather than requirements for the fungus. Based on geography, it appears as if the region where *Dactylospora inopina* occurs receives between 700 and 1500 mm of precipitation annually (Rozzi et al. 2004).

In a number of the specimens examined (e.g., Buck 58740, NY 02696321) *D. inopina* is associated with a *Radula*-inhabiting lichenized fungus. The two are hard to distinguish, though the lichen has smooth ascomata. Apart from excipulum structure, hymenial features immediately distinguish both species: the lichen has eight two-celled, colorless and thick-walled spores per ascus. The ascus types and their iodine reactions are completely different. Finally, the lichen has a thallus, though inconspicuous and macroscopically invisible. Hyphae surround small groups of green algae. This lichen was recently described as a new species of *Catinaria* (Lendemer et al. 2016), a genus previously included in a broadly interpreted *Lecidea*. It is noteworthy that several *Dactylospora* species were described as *Lecidea*.

The host genus *Radula*, within the unigeneric Radulaceae with about 200 species (Yamada 2003), belongs to the largest genera of liverworts. More than 15 perithecial ascomycetes are known to infect *Radula* spp., almost all on the corticolous *R. complanata* (L.) Dumort. in central Europe and on the epiphyllous *R. flaccida* Lindenb. & Gottsche in Afro-American lowland rain forests. *Dactylospora inopina* is the first discomycete on *Radula* apart from two *Octosporella* species (Pezizales) with perithecium-like apothecia (Döbbeler 1980, Döbbeler & Menjívar 1992) and is one of the relatively few species with apothecial ascomata on liverworts.

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