



Laboulbeniales parasitic on American small carrion beetles: new species of *Corethromyces*, *Diphymyces*, and *Rodaucea*

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ABSTRACT

Ten new species of Laboulbeniales parasitic on small carrion beetles (Coleoptera, Leiodidae, Cholevinae) from the American continent are described: *Corethromyces bernardii* on *Dissochaetus* spp. from Bolivia, Costa Rica, Ecuador, and the USA; *Diphymyces anthracinus* on *Ptomaphagus brevior* from the USA; *D. blackwelliae* on *Ptomaphagus giaquintoii* from Guatemala; *D. costaricensis* on *Adelopsis* sp. from Costa Rica; *D. dichromus* on *Adelopsis marinae* from Argentina; *D. newtonii* on *Ptomaphagus fumosus* from the USA; *D. obesus* on *Ptomaphagus brevior* from the USA; *Diphymyces perreai* on *Ptomaphagus nevadicus* from the USA; *D. polycarpus* on *Paulipalpina pillahuata* from Peru; and *Rodaucea hermanii* on *Adelopsis* sp. from Costa Rica. The hosts for all 10 species have been retrieved from museum collections (1 was collected in the field as well). The following new combination is proposed: *Rodaucea bruchii*, bringing the number of species in the recently established genus *Rodaucea* to three.

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INTRODUCTION

Eight species of Laboulbeniales (Fungi, Ascomycota) have been reported on American Cholevinae, or small carrion beetles (Coleoptera, Leiodidae). These are *Asaphomyces cholevae* Thaxt. in the USA, *Columnomyces ptomaphagi* R.K. Benj. in the USA, *Corethromyces bruchii* Speg. in Argentina, *Diphymyces arnaudii* W. Rossi & Santam. in Chile, *D. pusillus* W. Rossi & Santam. in Ecuador, *D. silphidarum* (Thaxt.) I. I. Tav. in Chile, *Rhachomyces elsae* W. Rossi & Proaño in Ecuador, and *Rodaucea salgadoi* W. Rossi & Santam. in Ecuador (Thaxter 1918, 1931; Spegazzini 1924; Benjamin 1955; Rossi and Máca 2006; Rossi and Proaño Castro 2009; Rossi and Santamaria 2010, 2012).

In the present paper, 10 new species occurring on Cholevinae are added to this list. The hosts for all 10 species were retrieved from museum collections; only 1 was supplemented by field collections. Seven of the species described here originated from pinned specimens at the American Museum of Natural History (AMNH) in New York City.

MATERIALS AND METHODS

In 2013–2015, D.H. visited the entomology collection at the AMNH and screened parts of the collection for presence of Laboulbeniales. A Nikon SMZ-U

stereomicroscope was used. Of the 24,009 pinned insects that were screened, 6.1% (= 1476 specimens) bore thalli of Laboulbeniales (Haelewaters, unpublished). Focusing on the host group discussed in this paper, 4.5% (= 39) out of 864 Cholevinae specimens were infected with Laboulbeniales.

Thalli were removed from the host's integument using a Minuten Pin (BioQuip no. 1208SA; Rancho Dominguez, California) and embedded in Amann solution (Benjamin 1971) with the help of a drop of Hoyer's medium (30 g Arabic gum, 200 g chloral hydrate, 16 mL glycerol, 50 mL double-distilled water [ddH₂O]) as described in Haelewaters et al. (2015).

The hosts for *D. newtonii* and *D. polycarpus* were preserved in 75% alcohol solution. Some insects bearing *Corethromyces bernardii* were collected in the field by W.R. Permanent slides of these three species were prepared following Rossi and Santamaria (2015). Microscopic slides are deposited at FH (Farlow Herbarium, Harvard University), QCA (Pontificia Universidad Católica del Ecuador), and FI (Natural History Museum, Firenze).

Observations and measurements of fungal specimens were made using an Olympus BX40 light microscope with Olympus XC50 digital camera and MicroSuite Special Edition software 3.1 (Soft Imaging Solutions GmbH, Münster, Germany). Photomicrographs of

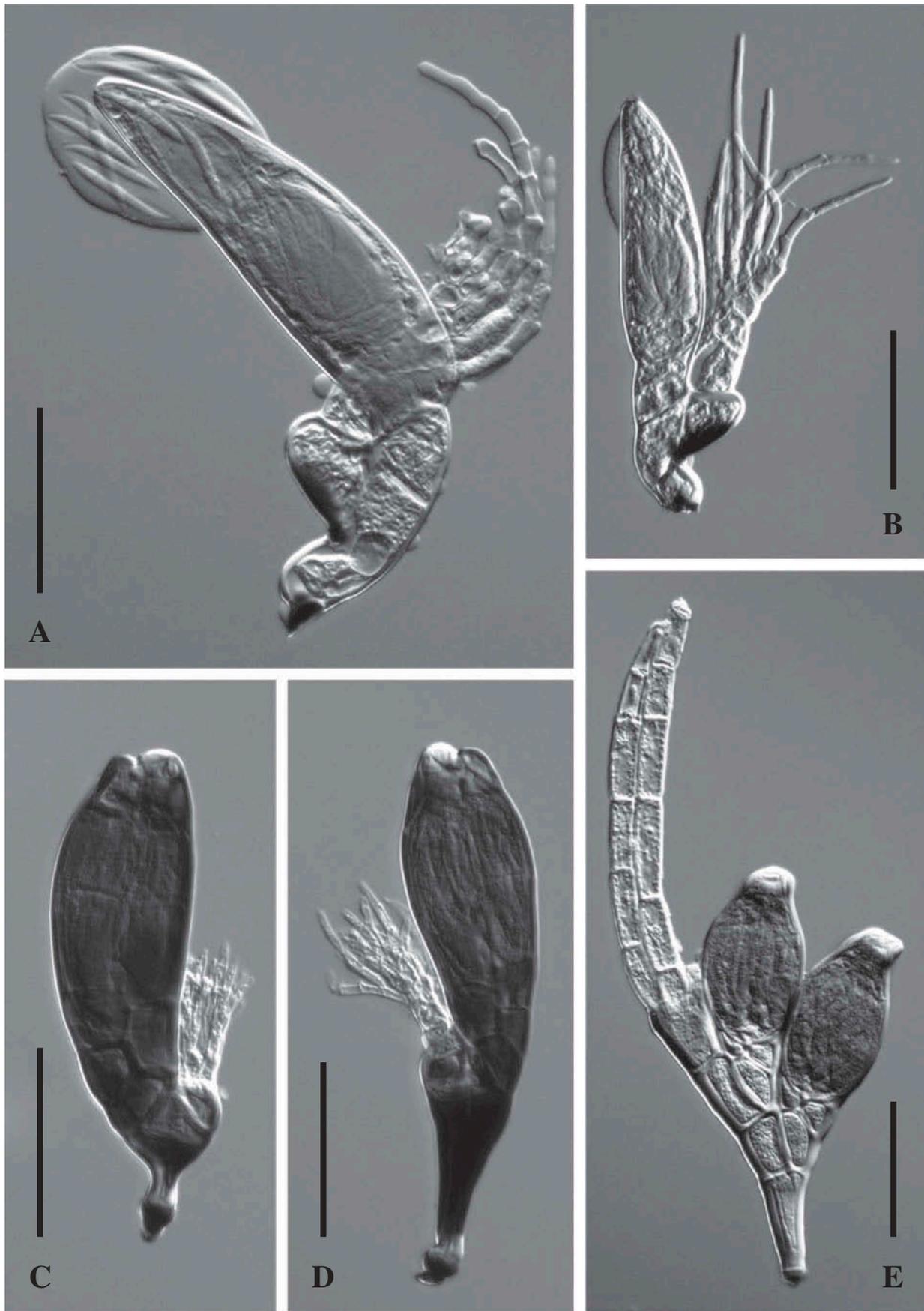


Figure 1. A, B. *Corethromyces bernardii*, sp. nov. (holotype, WR 3918). C, D. *Diphymyces newtonii*, sp. nov. (holotype, WR 3945). C. Thallus from elytron. D. Thallus from leg. E. *Diphymyces polycarpus* (holotype, WR 3939). Bars = 50 μ m.

Plate 1 were made with a Jenoptik ProgRes 10 Plus digital camera (Jena, Germany) on a Leica DMR microscope (Leica Microsystems, Barcelona, Spain) equipped with differential interference contrast optics (DIC). Additional photography was done at the Harvard Center for Biological Imaging using a Zeiss Cell Observer microscope (Thornwood, New York) equipped with DIC, running on ZEN software (Carl Zeiss MicroImaging Inc., Jena, Germany). Images were optimized (with Levels and Brightness/Contrast tools) and cropped in Adobe Photoshop CS 8.0 (San Jose, California).

TAXONOMY

Corethromyces bernardii Haelew. & W. Rossi, sp. nov. FIG. 1A, B

MycoBank MB819149

Typification: ECUADOR. ZAMORA-CHINCHIPE PROVINCE: Estación Científica San Francisco, 3°58' 17.19"S, 79°04'44.06"W, about 1900 m, 10–14 Aug 2014, *M. Bernardi*, *W. Rossi* & *J. Torres*, on female *Dissochaetus intermedius* Salgado 2016, slide WR 3918 (**holotype** in FI).

Etymology: Named after Matteo Bernardi, one of the collectors of the new species.

Description: Outer margin of cell III blackened, contrasting with the rest of the thallus, which is hyaline, except for the pale-yellowish perithecium. Cell I relatively small, about as long as it is broad or slightly longer, irregular in outline, with the posterior margin more convex than the anterior. Cell II much larger than cell I, up to 2 times longer than broad, separated from cells I and VI by distinctly oblique septa. Cell III broadly cordiform, with the posterior margin strongly bulging outwards. Lower cell of the appendage large, pentagonal in outline, slightly longer than broad. Main axis of appendage consisting of up to 10 gradually smaller cells, each giving rise to a branchlet at the upper, inner side; these produce antheridia near their base, which are replaced by short branchlets in older specimens, thus forming a dense tuft, sometimes exceeding the perithecial apex. Cell VI much broader than long, distinctly oblique. Perithecium asymmetrically fusiform, broadest at the lower third, with the anterior margin more convex; the conical tip not distinguished from the venter, ending in an undifferentiated, rounded apex. Length from foot to perithecial apex 140–188 μm . Perithecium: 90–117 \times 26–35 μm . Longest appendages 130 μm . Ascospores about 30 μm in length.

Other specimens examined: Same data as the holotype, slide WR 3916 (FI). ECUADOR. NAPO

PROVINCE: Volcán Sumaco, Refugio Laguna, 2695 m, 29 Dec 2010, *A. Barragán*, on elytra and pronotum of *Dissochaetus grossus* Salgado 2014, slide WR 3595 (FI). BOLIVIA. MANUEL MARÍA CABALLERO PROVINCE: Parque Nacional Amboró, 17°50.124'S, 64°23.454'W, 2070 m, dung-baited pitfall trap, 19–20 Oct 2001, *S. Spektor* & *J. Ledezma*, on left elytron of *Dissochaetus* sp., *D. Haelew.* 591, in coll. AMNH, slide FH 00313611; same data, *D. Haelew.* 592, in coll. AMNH, slide FH 00313612. COSTA RICA. PUNTANERAS PROVINCE: Monteverde, 1500 m, lower montane wet forest, 4–11 Feb 1989, *D.A. Grimaldi*, on left elytron of *Dissochaetus* sp., *D. Haelew.* 424, in coll. AMNH, slide FH 00313608 (FH). USA. FLORIDA: Highlands County, Highlands Hammock State Park, 7–14 Apr 1971, *A. Newton*, on elytra of *Dissochaetus oblitus* (LeConte 1853), *D. Haelew.* 396, in coll. AMNH, slide FH 00313562; TENNESSEE: Blount County, Great Smoky Mountains National Park, Cades Cove valley, 5–27 Aug 1965, *S. & S. Peck*, on elytra of *D. oblitus*, *D. Haelew.* 397, in coll. AMNH, slide FH 00313563; same data, *D. Haelew.* 398, in coll. AMNH, FH 00313564 (**paratypes**).

Twenty-five (nearly to fully) mature and 22 other thalli at various stages of development were examined.

Commentary: Based on material from both collection studies and field work, we present records of *C. bernardii* in North America (USA), Central America (Costa Rica), and South America (Bolivia, Ecuador). On average, the North American thalli (Florida, Tennessee) have a more slender perithecium in comparison with the Ecuadorian thalli.

Corethromyces bernardii is quite different from any described species, and it is difficult to suggest any relationship within the genus. It differs greatly also from the two other species in the same genus reported thus far on Leiodidae, i.e., *C. henrotii* Balazuc and *C. bicolor* Thaxt. The former of these is parasitic on *Choleva* spp. in Europe and bears a very long appendage, whereas the latter, occurring on Australian Leiodidae, is characterized by a blackened and slender receptacle (Weir and Hughes 2002; Rossi and Mácá 2006).

Diphymyces anthracinus Haelew. & W. Rossi, sp. nov. FIG. 2A

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Typification: USA. MICHIGAN: Clinton County, oak-hickory forest, 14 May 1967, *T. Schuh* & *T. Hlavac*, on tip of left elytron of *Ptomaphagus brevior* Jeannel 1949, *D. Haelew.* 382, in coll. AMNH, slide FH 00313605 (**holotype**).

Etymology: From Greek, referring to the blackish tinge of the thallus.

Description: Thallus smoky gray and much darker on the lower portion; cell I, appendage, and perithecial apex almost hyaline. Cell I short and enlarged in the upper portion. Cell II broadly triangular and isodiametric, separated by a very oblique septum from cell III, which is smaller and paler, longer than broad, subtrapezoidal. Lower cell of the appendage small, slightly longer than broad, giving rise to 4–5 short and erect branchlets. Cell VI relatively large, distinctly broader than long. Perithecium pyriform, broadest just above the middle; gradually tapering to the large tip and ended by the blunt, oblique apex; the lips very unequal, two of them are joint to form a large, rounded protrusion, the other two are free, much smaller, overlapping each other in some thalli. Length from foot to perithecial apex 109–120 μm . Perithecium (including basal cells): 78–83 \times 37–46 μm .

Other specimens examined: Same data as the holotype; on posterior third of right elytron, slide FH 00313557; on tip of right elytron, slide FH 00313558; on right posterior tibia, slide FH 00313559 (**isotypes**).

Six mature and four other thalli at various stages of development were examined.

Commentary: Among the 15 species described thus far in the genus *Diphymyces* (Haelewaters et al. 2014), the one most similar to *D. anthracinus* is *D. niger* (T. Majewski) I. I. Tav., parasitic on *Ptomaphagus* spp. in Europe. However, the latter species is distinctly smaller (max. 80 μm) and stockier, almost elliptical in outline, with a different perithecial tip and more branched appendages (Santamaria 2003).

Diphymyces blackwelliae Haelew. & W. Rossi, sp. nov. FIG. 2D
Mycobank MB819151

Typification: GUATEMALA. ALTA VERAPAZ DEPARTMENT: Senahú, Cueva de Seamay, 24 Aug 1969, S. & J. Peck, on right elytron of *Ptomaphagus giaquinto* Jeannel 1936 (Ptomaphagini), D. Haelew. 298, in coll. AMNH, slide FH 00313605 (**holotype** in FH).

Etymology: Named after Meredith Blackwell, distinguished mycologist and student of the Laboulbeniomycetes.

Description: Thallus pale yellow, except for the foot and the lower part of cell I, which are colored light brown. Cell I subtrapezoidal to slightly broader than long. Cell II quadriangular, about 1.5 times longer than broad. Cell III rectangular, 2 times longer than broad, giving rise to a series of gradually smaller, superimposed cells; each cell of this series separating

from its inner-upper side a short variably ramified branchlet. Cell VI enlarged toward the upper portion, about as long as cell II. Perithecium oblong, bent outwards, with the anterior margin almost straight and the posterior one distinctively convex; the tip not strongly tapered ending in unequal lips, which are pointed posteriorly, subtended on the anterior side by a conspicuous bulge. Length from foot to perithecial apex 96–111 μm . Perithecium (including basal cells): 70–82 \times 22–29 μm .

Other specimens examined: Same data as the holotype, on tip of right elytron, slide FH 00313604 (**isotype** in FH).

Seven mature and two immature thalli were examined.

Commentary: Morphologically, this species is most closely related to *D. silphidarum* (Thaxt.) I.I. Tav. *Diphymyces silphidarum*, however, is straight and has a pointed perithecial apex, never subtended by any outgrowth (Thaxter 1931).

Diphymyces costaricensis Haelew. & W. Rossi, sp. nov. FIG. 3D
Mycobank MB819152

Typification: COSTA RICA. PUNTARENAS PROVINCE: 35 km NE of San Vito near Las Alturas, ca. 7.5 km on trail to Cerro Echandi, Río Bella Vista, litter near stream, 21 Mar 1991, L.H. Herman, on left elytron of *Adelopsis* sp. (Ptomaphagini), D. Haelew. 301, in coll. AMNH, slide FH 00313547 (**holotype**).

Etymology: Named after the country where the host was collected.

Description: Perithecium light brown; base of cell I and cell III and appendage hyaline; the rest of the fungus dark brown. Cell I with the lower portion subcylindrical, distinctly broadening in the upper portion, and separated from cells II and VI by distinctly oblique septa. Cell II about as long as maximum width, with the outer, upper margin rounded and bulging externally. Cell III smaller than the former, broadly pentagonal, bearing in turn two smaller cells, one of which is positioned apically and gives rise to three short branchlets, the other one more internally and giving rise to a bifurcate branchlet. Cell VI irregularly pentagonal, broader than long, separated by oblique septa from the perithecial basal cells. Perithecium irregularly ovoid, less than twice as long as broad, with the anterior margin distinctly more convex than the posterior; the tip short and broad, clearly distinguished only on the anterior side, ending in a blunt apex, consisting of unequal and rounded lips. Length from foot to perithecial apex 103–122 μm . Length from foot to longest appendage 105 μm . Perithecium: 69–73 \times 37–44 μm .

Other specimens examined: Same data as the holotype, on pronotum, slide FH 00313548 (**isotype**).

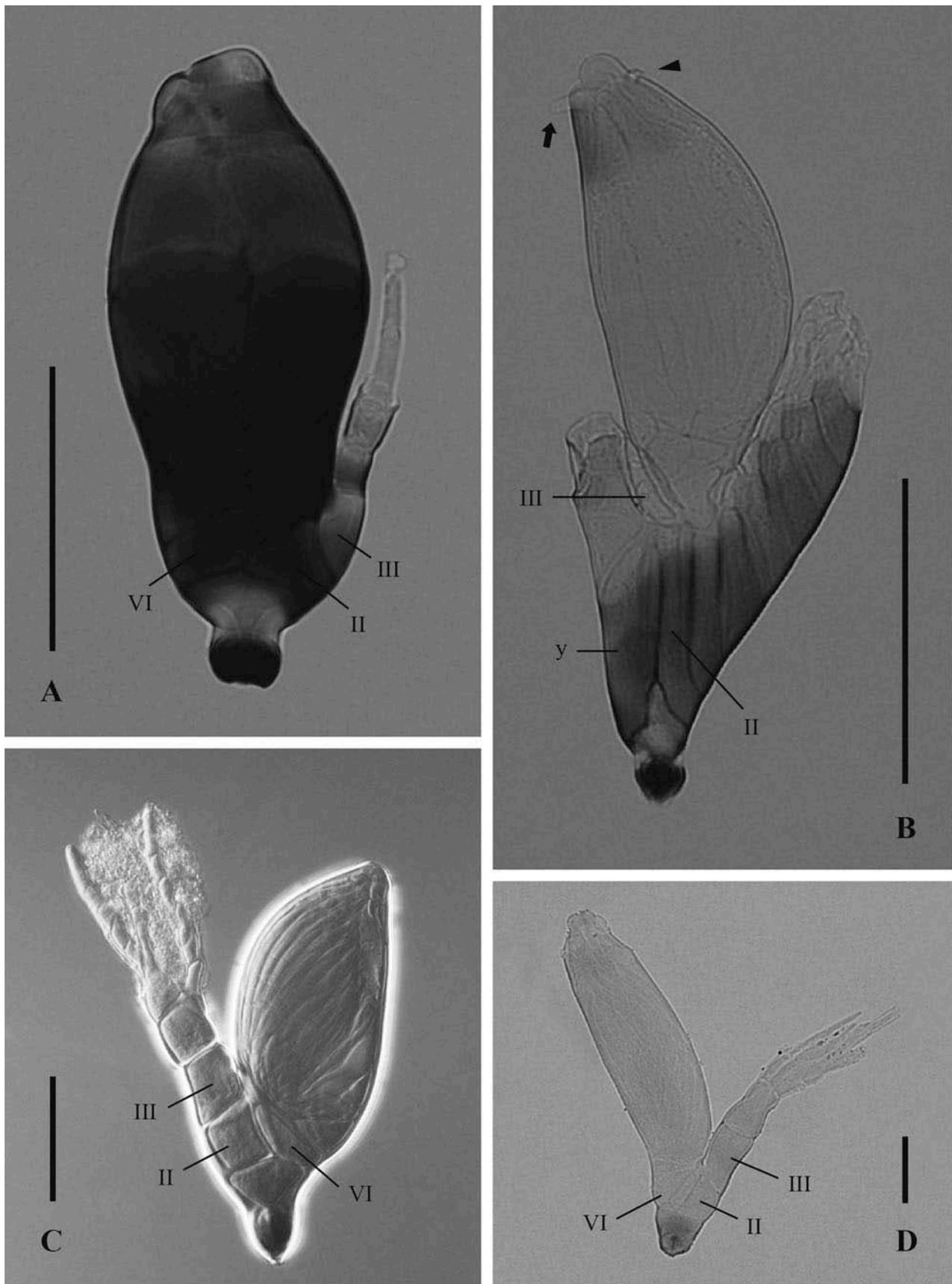


Figure 2. A. *Diphymyces anthracinus*, sp. nov. (holotype, FH 00313555). B. *Rodaucea hermanii*, sp. nov. (holotype, FH 00313569), with indication of cells II, III, and y; as well as the outgrowth of the perithecial apex (arrow), positioned opposite the small but conspicuous papilla (arrowhead). C. *Diphymyces obesus*, sp. nov. (paratype, FH 00313556). D. *Diphymyces blackwelliae*, sp. nov. (isotype, FH 00313604), shown in grayscale to gain contrast. Cells II, III, and VI are labeled in each *Diphymyces* thallus. Bars: A, B = 50 μ m; C, D = 20 μ m.

Two fully mature thalli were examined.

Commentary: *Diphymyces costaricensis* can be easily separated from the other species in the genus by its color pattern and the blunt and rounded perithecial apex. The closest relative appears to be *D. depressus* M.B. Hughes et al., both in general habitus and in the shape of cell III and the appendage. However, in *D. depressus*, the perithecium is inflated at the base and strongly tapered at the apex (Hughes et al. 2004).

Diphymyces pusillus from Ecuador occurs on the same host genus, *Adelopsis* Portevin 1907 (Rossi and Santamaria 2010). This species is much smaller (66–74 µm), its appendage is more reduced, and the perithecial apex has a completely different morphology compared with *D. costaricensis*.

Diphymyces dichromus Haelew. & W. Rossi, sp. nov. FIG. 3A, B

Mycobank MB819153

Typification: ARGENTINA. TUCUMÁN PROVINCE: 4 km SW of San Pedro de Colalao, 16 Oct 1971, L.H. Herman, on left anterior coxa of *Adelopsis marinae* Perreau 2016 (Ptomaphagini), D. Haelew. 431, in coll. AMNH, slide FH 00313571 (**holotype**).

Etymology: From Greek, referring to the two contrasting colors of the thallus.

Description: Fungus distinctly bicolored; the perithecium is russet, strongly contrasting with the remainder of the thallus, which is hyaline. Cell I gradually broadening upwards, about 3× longer than maximum width. Cell II quadrangular, slightly longer than cell I, about twice as long as broad. Cell III also quadrangular, ranging from slightly smaller to slightly larger than cell II. Appendage consisting of three superimposed, broadly pentagonal, and gradually smaller cells, each separating from their upper angles a series of superimposed gradually smaller cells, ending in very short ramified branchlets; the terminal cell of the axis distinctly smaller, bearing a several-celled, erect branch in addition to the lateral branchlets. Cell VI subtriangular, about as long as cell II. Basal cells of the perithecium relatively large, variable in length, from about as long to twice as long as cell VI, thus forming a distinct stalk. Perithecium ovoid, twice as long as maximum width or slightly more, the tip subconical, strongly tapering to the almost rounded, undifferentiated, and paler apex. Length from foot to perithecial apex 168–385 µm. Length from foot to tip of longest appendage 148–295 µm. Perithecium 102–154 × 55–70 µm. Ascospores about 55 µm in length.

Other specimens examined: Same data as the holotype; on left posterior tarsus, slide FH 00313570; on right mouthparts, slide FH 00313572; on left anterior tibia, slide FH 00313573 (**isotypes**).

A total of one immature and eight mature thalli were examined.

Commentary: This new species can be distinguished at first sight from any other in the same genus by the russet perithecium, strikingly contrasting to the rest of the fungus. The structure of the appendage is similar to that of *Diphymyces leschenii* M.B. Hughes et al. from New Zealand (Hughes et al. 2004), but both species are different in almost every other characteristic.

Diphymyces costaricensis and *D. pusillus* occur on the same host genus. They are clearly different from *D. dichromus*: both species are not bicolored and have a much less elongate habitus, among other features (Rossi and Santamaria 2010, this paper). The host of *D. dichromus* was only recently described as a new species (Perreau 2016).

Diphymyces newtonii Haelew. & W. Rossi, sp. nov. FIG. 1C, D

Mycobank MB819156

Typification: USA. TENNESSEE: Sevier County, 8 mi S of Gatlimburg, 3000 ft, Buckeye Trail, Berl. litter, mixed hardwood forest, 7 Oct 1973, A.F. Newton, on *Ptomaphagus fumosus* (Peck) (Ptomaphagini), slide WR 3945 (**holotype** in FI).

Etymology: Named after the distinguished entomologist Alfred F. Newton, Curator Emeritus at the Field Museum of Natural History in Chicago (Illinois) and collector of the host specimen.

Description: Thalli growing on the legs (Fig. 1D): Cell I very dark and opaque for most part of its length; lower portion of cell I, appendages, and perithecial tip hyaline or almost so; the rest of the thallus is chestnut brown. Cell I elongate, with a paler and inflated basal portion, above which it gradually enlarges from below upwards. Cell II irregularly triangular, usually wider than long. Cell III slightly broader than long, distally prominent besides the lower cell of the appendage. The latter is subquadrate or subtrapezoidal, distinctly smaller than cell III, giving rise to a short and erect branch consisting of 3–4 superimposed, elongate, and gradually smaller cells bearing on the inner side short and slender branchlets with divide dichotomously, thus forming a sense tuft never reaching the perithecial apex. Cell VI variable in shape, but not much different in size from cell II. Basal cells of the perithecium relatively large. Perithecium oblong, slightly bent inwards, with the anterior side slightly more convex than the posterior, the tip not strongly tapered ending in very unequal lips, one of which is rounded, much larger and very pale, subtended on the anterior side by an elongate, crest-like outgrowth. Length from foot to perithecial apex 125–135 µm. Length from foot to tip of

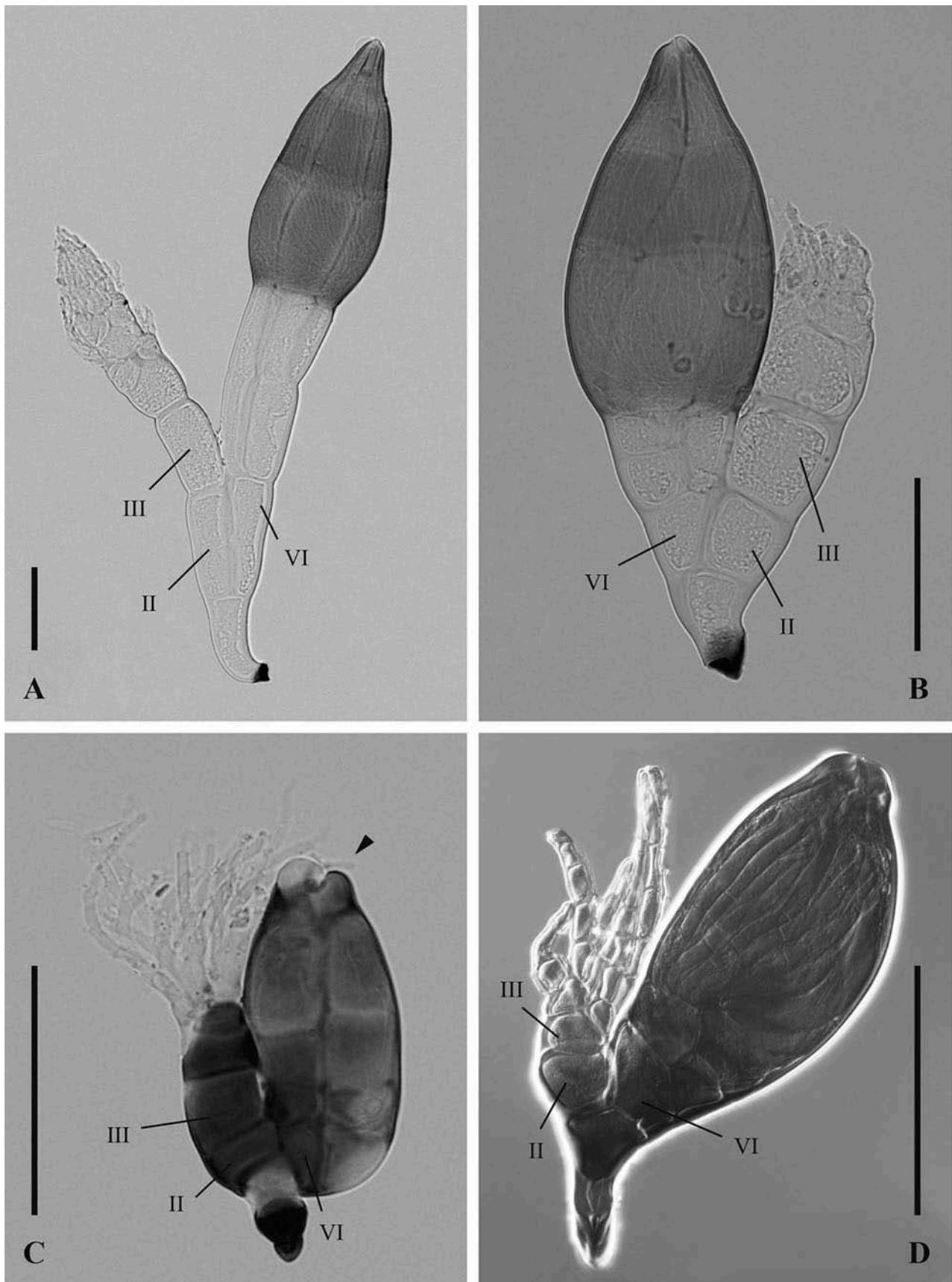


Figure 3. A, B. *Diphymyces dichromus*, sp. nov. A. Thallus from left anterior coxa (holotype, FH 00313571). B. Thallus from left anterior tibia (isotype, FH 00313573). C. *Diphymyces perreaui*, sp. nov. (holotype, FH 00313610); the anteriorly directed outgrowth at the perithecial tip is indicated (arrowhead). D. *Diphymyces costaricensis*, sp. nov. (holotype, FH 00313547). Cells II, III, and VI are labeled in each thallus. Bars = 50 μ m.

longest appendage 140 μm . Perithecium 35–40 \times 65–75 μm .

Thalli growing on the elytra (Fig. 1C): Cell I somewhat different; paler and shorter, subcylindrical in the basal portion and rather abruptly broadened in the upper portion. Length from foot to perithecial apex 145–160 μm .

Other specimens examined: Same data as the holotype, nos. WR 3946, 3947, 3948, 3949 (**paratypes** in FI).

A total of 19 mature and 14 immature thalli were examined.

Commentary: This is not the first polymorphic species of *Diphymyces* to be described. *Diphymyces spelaei* on *Anthroherpon* spp. (Leptodirini) has four morphotypes for thalli growing on the mesosternum; head, pronotum, and elytra; meso- and metafemora; and mesotarsi (Rossi 2006).

Diphymyces newtonii seems to be most closely related to *D. costaricensis*. The latter has a different color, stockier perithecium, different perithecial apex, and longer branches of the appendage. The receptacle of *D. anthracinus* is similar to that of *D. newtonii* thalli growing on the elytra. In *D. anthracinus*, however, cell III is longer than broad and the perithecium is strongly pyriform.

Diphymyces obesus Haelew. & W. Rossi, sp. nov. FIG. 2C

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Typification: USA. MICHIGAN: Shiawassee County, oak-hickory forest, 15 May 1967, T. Schuh & T. Hlavac, on pronotum and left elytron of *Ptomaphagus brevior* Jeannel 1949 (Ptomaphagini), D. Haelew. 383, in coll. AMNH, slide FH 00313560 (**holotype**).

Etymology: From Latin (fat, stout), referring to the shape of the perithecium.

Description: Thallus amber-yellow in color, except for the outer margins of cells I and II, of the appendage axis, and of the perithecium, which are tinged with light brown. Cell I obtriangular and isodiametric. Cells II irregularly trapezoidal in section, slightly longer than broad. Cell III similar to cell II, but up to 2 times longer than it is broad. Lower cell of appendage subpentagonal, slightly smaller than cell III, bearing apically three smaller cells, each giving rise to short, bifurcate branchlets, thus forming a dense tuft hardly exceeding the perithecial apex. Cell VI subtrapezoidal, distinctly shorter than broad. Perithecium asymmetrical, with the anterior margin almost straight and the posterior distinctly convex, broadest just above the middle, and then tapering to the undifferentiated, blunt apex. Length from foot to perithecial apex 63–78 μm .

Perithecium 40–50 \times 16–27 μm . Longest appendage 54 μm .

Other specimens examined: USA. MICHIGAN: Clinton County, oak-hickory forest, 6–14 May 1967, T. Schuh & T. Hlavac, on *Ptomaphagus brevior*, D. Haelew. 381, in coll. AMNH; on left elytron, slide FH 00313552; on pronotum, slide FH 00313553; MICHIGAN: Clinton County, oak-hickory forest, 14 May 1967, T. Schuh & T. Hlavac, on *P. brevior*, D. Haelew. 382, in coll. AMNH; on left elytron, slide FH 00313554; on pronotum and left elytron, slide FH 00313556; on right elytron, slide FH 00313557; CONNECTICUT: Windham County, Hampton, deciduous forest, 24–28 May 1971, J. Schuh, on left elytron of *P. brevior*, D. Haelew. 386, in coll. AMNH, slide FH 00313561 (PARATYPES).

Forty-two thalli were examined, of which 32 mature.

Commentary: This new species is closely allied to *D. bidentatus* (Thaxt.) I.I. Tav., *D. curvatus* (Thaxt.) I.I. Tav., and *D. silphidarum* (Thaxt.) I.I. Tav. However, these three species can be separated from *D. obesus* based on the following characteristics: the perithecium of *D. curvatus* is strongly curved outwardly, the perithecial apex of *D. bidentatus* is subtended by two projections, and both the habitus and perithecium of *D. silphidarum* are much more slender and elongate.

We observed thalli of *D. obesus* growing together with those of *D. anthracinus* on a single host specimen (D. Haelew. 382). *Diphymyces obesus* was found at the base of the elytra and on the pronotum, whereas *D. anthracinus* occurred on the distal portion of the elytra.

Diphymyces perreaui Haelew. & W. Rossi, sp. nov. FIG. 3C

Mycobank MB819157

Typification: USA. CALIFORNIA: Siskiyou County, 11 mi S of Macdoel, burrow of *Citellus beldingi*, 8 May 1972, J. Schuh, on tip of left elytron of female *Ptomaphagus nevadicus* Horn, 1880, D. Haelew. 425, in coll. AMNH, slide FH 00313610 (**holotype** in FH).

Etymology: Referring to the French entomologist Michel Perreau (Paris Diderot University), who is a specialist of the Cholevinae and identifier of many of our infected specimens.

Description: Thallus light brown, except for cell I, the appendage branchlets, and the perithecial apex, which are hyaline or almost so. Cell I short, forming like a protrusion out of the rest of the compact thallus, separated by oblique septa from cells II and VI. Cell II rectangular, flattened. Cell III isodiametric or broader than long, followed by two strongly narrowing cells, which give rise to a tuft of ramified branchlets from

their outer-upper side. Cell VI narrow and strongly oblique. Perithecium ovoid, positioned upright, at least twice as high as maximum width, the tip well defined, ending in rounded lips, subtended by a conspicuous, hemispherical outgrowth anteriorly. Length from foot to perithecial apex 75–83 μm . Length from foot to longest appendage 107 μm . Perithecium 56–66 \times 29–36 μm .

Other specimens examined: Same data as the holotype, on right elytron, slide FH 00313609 (**isotype** in FH).

Five mature and nine other thalli at various stages of development were examined.

Commentary: This species is very different from any other in the genus, because of the positioning of cell I, which protrudes as a stalk from the rest of the thallus, and cell VII, which has expanded anteriorly, thus giving the perithecium its upright position.

Diphymyces perreaui seems to be related to *D. depressus*. *Diphymyces depressus* is devoid of outgrowths below the perithecial tip and differs also in the appendage structure, which has branchlets borne on both inner and outer sides of the seriate cells (Hughes et al. 2004, fig 2E).

Diphymyces perreaui may be closest to one of the other species occurring on *Ptomaphagus* spp., *D. niger*, which has been reported only from Europe. Both species have a stout habitus and an ovoid perithecium with an outgrowth at the tip. But the basal part of the thallus is very different in both species. *Diphymyces perreaui* has its cell I protruding out of the compact thallus, with cell II being broader than high and cell VI strongly oblique. In *D. niger*, no protrusion is formed, cell II is higher than broad, and cell VI is not obliquely positioned (Santamaria 2003). In addition, cell VII is strongly developed in *D. perreaui*, whereas in *D. niger* this cell remains small and it is rather cell m that becomes larger.

Diphymyces polycarpus Haelew. & W. Rossi, sp. nov. FIG. 1E

MycoBank MB819158

Typification: PERU. CUSCO REGION: Pillahuata, leaf litter, 25 Sep 1982, L.E. Watrous & G. Mazurec, between the metacoxae of *Paulipalpina pillahuata* Salgado 1996 (Ptomaphagini), slide WR 3939 (**holotype** in FI).

Two mature thalli were examined.

Etymology: Referring to the presence of more than one perithecium.

Description: Fungus distinctly bicolored; the perithecia are russet, strongly contrasting with the remainder of the thallus, which is hyaline. Cell I elongate, regularly tapering downwards. Cell II slightly shorter and

broader than the previous. Cell III as broad as cell II but distinctly longer. Appendage incomplete in both the examined thalli: apparently cell III bears apically two cells, the inner of which is much smaller, the outer giving rise to two long, subequal, simple branches consisting of hyaline and not strongly elongate cells. Both perithecial stalk cells lens-like, about 3 times as long as broad. Perithecia regularly ovoid, with a quite stocky tip ending in the flattened and slightly asymmetrical apex, with the outermost lip more prominent. Length from foot to the tip of upper perithecium 155 μm . From foot to the tip of longest appendage 315 μm . Perithecium 36–43 \times 65–73 μm .

Commentary: Of the two thalli examined, one bears two perithecia and the other bears three, one of which is very immature.

The only species of *Diphymyces* bearing multiple perithecia described thus far is *D. leschenii* M.B. Hughes et al. from New Zealand, which is parasitic on *Paracatops campbellicus* (Brookes 1951). The latter fungus is very different from *D. polycarpus* being stockier, with more branched appendages, slenderer perithecia, and more tapered perithecial apex (Hughes et al. 2004).

Rodaucea hermanii Haelew. & W. Rossi, sp. nov. FIG. 2B

MycoBank MB819159

Typification: COSTA RICA. PUNTANERAS PROVINCE: 35 km NE of San Vito near Las Alturas, ca. 7.5 km on trail to Cerro Echandi, Río Bella Vista, litter near stream, 21 Mar 1991, L.H. Herman, on elytra of *Adelopsis* sp. (Ptomaphagini), D. Haelew. 415, in coll. AMNH, slide FH 00313569 (**holotype**).

Etymology: Named after Lee H. Herman, Curator Emeritus at the American Museum of Natural History (Invertebrate Zoology) and collector of this and many other host specimens for Laboulbeniales.

Description: Cell I light brown, somewhat contrasting to the other cells of the receptacle, which are darker, but gradually paler towards the distal end; perithecium and its basal cells yellow-brownish, with a darker pre-apical area on the anterior side; cell VI, appendages, and perithecial tip almost hyaline. Cell I very small, irregularly rhomboid, its upper portion deeply protruding between cell II and cell y. Cell II slender and erect, superimposed by cell III, which is small and about 2.5 \times longer than broad. Primary appendage relatively short, branched above its lower cell. Secondary receptacle upwardly curved, consisting of a series of 6–7 shorter but slightly broader and almost vertical cells, the distal ones of which bear apically secondary appendages, smaller than the primary appendage; the first cell of this series sometimes gives rise a perithecium. Cell y

similar to cell II but gradually enlarging from below upwards, separated from cell VI by a very oblique septum. Cell VI irregularly quadrangular, slightly longer than maximum width. Perithecium, including basal cells, shaped like a lemon segment, with the posterior margin strongly convex, and the anterior almost straight to slightly convex; the apex consisting of a dome-shaped termination, superimposed by a large, rounded papilla, and subtended by a slender and elongate outgrowth pointing outwards. Length from foot to perithecial apex 126–138 μm . Length from foot to tip of longest appendage 87 μm . Perithecium including basal cells 72–85 \times 25–29 μm .

Additional specimens examined: Same data as the holotype, on left elytron, slide FH 00313568 (**isotype**).

A total of nine thalli, five of which mature, were examined.

Comments: The recently described genus *Rodaucea* W. Rossi & Santam. included a single species: *R. salgadoi* W. Rossi & Santam. on *Eucatops (Eucatops) curtus* Salgado 2004 from Ecuador (Rossi and Santamaria 2012). However, S. Santamaria (pers. comm.) suggested that also *Corethromyces bruchii*, described on *Eucatops formicetorum* (Bruch 1918) [as *Acanthoscatops* sp.] from Argentina (Spegazzini 1924), belongs in the genus *Rodaucea*. Thaxter (1931) had already raised doubt about the taxonomic position of this species, stating that that “its position is somewhat uncertain.” Later, Tavares (1985), too, expressed the opinion that it was not a *Corethromyces*, suggesting that it may belong in *Asaphomyces*. Although Spegazzini’s original material seems to be no more available (J. Chayle, pers. comm.), there is no doubt that this species belongs to *Rodaucea* and therefore the following new combination is established: *Corethromyces bruchii* Speg., Physis 7:236 (1924) = *Rodaucea bruchii* (Speg.) Santam., comb. nov.

Rodaucea bruchii is easily distinguished from the new species by the almost filiform outgrowths around the perithecial ostiole (“antennae” in Spegazzini 1924). *Rodaucea salgadoi* is a larger species (167–198 μm), with slenderer and more numerous receptacle cells, a slenderer and less asymmetrical perithecium, and differently shaped perithecial outgrowths (Rossi and Santamaria 2012).

DISCUSSION

The study of insect collections can yield a lot of unexpected findings, such as the presence of thalli of Laboulbeniales biotrophic fungi on the insect integument. Roy et al. (2015) refer to large systematic museum

collections as treasure troves because they comprise a large “forgotten” diversity of Laboulbeniales, often unknown to entomologists. In his monograph, Thaxter (1896, 1908, 1924, 1926, 1931) cited many insects that he retrieved from museum collections, especially the Harvard Museum of Comparative Zoology (MCZ). Weir (1998) examined 80 000 Coleoptera from Sulawesi, Indonesia at the Natural History Museum (London). Screening this voucher collection revealed 500 infected insects (0.6%), and Weir and Hammond (1997) used this data set to infer an estimate for the number of species of Laboulbeniales exploiting Coleoptera (between 10,000 and 50,000). More recently, Haelewaters et al. (2015) found interesting records of Laboulbeniales after screening a subset of the Boston Harbor Islands insect collection, which is housed at the MCZ. Forty-seven of 1431 insects (3.3%) were found infected with Laboulbeniales. Santamaria et al. (2016) described nine new species of *Rickia* from millipedes (Myriapoda, Diplopoda) preserved at the Natural History Museum of Denmark. With this focused paper, the number of *Rickia* species associated with millipedes went from 5 to 14.

Collections-based research can also aid in understanding changing population dynamics of Laboulbeniales. For example, based on the study of pinned insect collections in Canada and the USA, Haelewaters et al. (2017) were able to theorize a lag time between establishment of *Harmonia axyridis* (Pallas, 1773) ladybird beetles in the wild and acquisition of *Hesperomyces virescens* Thaxt. by this host.

With this paper, we add 10 species to the 8 already known species of Laboulbeniales on American Cholevinae. Of the previously described species, only *Asaphomyces cholevae* has been recorded after description. This demonstrates that we are far from having a complete picture of the group. Thus far known from Cholevinae are species in the genera *Asaphomyces* Thaxt., *Columnomyces* R.K. Benj., *Corethromyces* Thaxt., *Diphymyces* I.I. Tav., *Rhachomyces* Thaxt., and *Rodaucea*. The genera *Asaphomyces*, *Rhachomyces*, and *Rodaucea* are placed in the tribe Teratomyceetae, whereas *Columnomyces*, *Corethromyces*, and *Diphymyces* are part of the Laboulbenieae tribe. Based on the available information, it is clear that the genus *Diphymyces* is highly diversified on cholevine hosts. Of the currently 23 described species in this genus (Haelewaters et al. 2014, this paper), 21 are associated with Cholevinae. Only *D. appendiculatus* (Thaxt.) I.I. Tav. (on Coloninae, Leiodidae) and *D. penicillifer* A. Weir & W. Rossi (on Omaliinae, Staphylinidae) occur on different host groups.

Since 2013, the first author has screened a total of 45 785 insects at different insect collections in North America (AMNH; MCZ; Collection d'insectes du Québec, Canada), Central America (Smithsonian Tropical Research Institute, Panama), Europe (Brabant Museum of Nature, the Netherlands), and Asia (University Kebangsaan Malaysia, Peninsular Malaysia). A total of 1937 specimens bore thalli of Laboulbeniales (4.2%). This large-scale museum study has already led to multiple new records and species descriptions (e.g., Haelewaters 2013; Haelewaters and Yaakop 2014; Haelewaters et al. 2015), while many of the infected host insects still await detailed study.

Researchers are increasingly incorporating museum collections in the study of current and historical biodiversity, taxonomy, systematics, pathogens, vectors of diseases, invasive species, biotic responses to climate change, land management, pollination, and environmental contaminants (Suarez and Tsutsui 2004; Smith and Blagoderov 2012). In the USA alone, over 110 million insect specimens are deposited in the largest entomological collections (Suarez and Tsutsui 2004). Considering that 19 species of Laboulbeniales have been described after carefully screening two groups of potential hosts (millipedes, Santamaria et al. 2016; small carrion beetles, this paper), a multitude of undiscovered Laboulbeniales await study on those preserved insects. After all, Laboulbeniales persist on dead insect hosts and thus are easily observed.

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