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A new lichenicolous lichen from Europe and western North America in the genus *Dimelaena* (Physciaceae)

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ABSTRACT. *Dimelaena lichenicola* is a juvenile parasite on *D. oreina* and *D. thysanota*, developing an independent brown areolate lichenized thallus on gneiss and acid rock. It differs from *D. californica* primarily in producing longer conidia ($6.0\text{--}10.0 \times 1.0$ vs. $5.0\text{--}6.0 \times 1.0$ μm), having a reduced thallus and minute lobes, lacking a well-developed plicate margin and a prothallus, having a different host species (*D. oreina* and *D. thysanota* vs. *D. radiata*), and a different habitat (montane vs. coastal). It is reported from North America (California) and Europe (Italy).

KEYWORDS. Joshua Tree National Park, montane, parasites, taxonomy.



Lichenicolous lichens generally have a two-stage life cycle. They begin as juvenile non-lichenized fungal parasites on lichens, and then develop an independent lichenized thallus (Kocourková et al. 2012). The first stage is usually observed as an infection in which the thallus of the host begins to change colors (**Fig. 1, B & C**). Rarely, for instance in *Buellia badia* (Fr.) A. Massal. or *Placocarpus americana* K. Knudsen, Breuss & Kocourková, the ascomata appear on the host and then later there is an infection. Eventually the new lichenized thallus of the parasite morphs out of the thallus of the host, completely destroying the host, and becomes independent upon the substrate (rock for instance). In a study of the lichenicolous biota of California, including the new species described in this paper, we have identified 22 species of lichenicolous lichens in California in 14 genera, with 5 occurring in *Rhizocarpon* (Knudsen et al. 2013; Kocourková et al. 2012). The most common lichenicolous lichen in California is *Diploschistes muscorum* (Scop.) R. Sant., which is parasitic on *Cladonia* species as well as *Lepraulon americanum* Lendemer & Hodkinson and *Lepraria xerophila* Tønsberg (Kocourková et al. 2012).

Lichenicolous lichens are often confused with lichens that are successional in lichen communities. For example, in the mountains of California the common *Acarospora thamnina* (Tuck.) Herre usually occurs on hard granite boulders among the thalli and areoles of other crustose lichens. Colonization takes place when the substrate and the top layer of granite has begun to decay and become porous in the center of older lichens, so it could easily appear to be parasitic to a casual observer unfamiliar with the region's montane communities. However, neither infections nor morphing have ever been observed for this species.

Dimelaena Norman is known to contain one lichenicolous lichen, *D. californica* (H. Magn.) Sheard. It is a cosmopolitan genus defined by *Beltraminia*-type spores (unthickened spore walls usually with a torus), a conical *Bacida*-type stain, and a radiate-plicate thallus margin with a variety of chemotypes (Mayrhofer et al. 1996; Mayrhofer & Sheard 2004; Obermayer et al. 2004; Sheard 1974; Sheard 1977; Sheard & Mayrhofer 1984). The genus currently comprises at least 7 species, with a possible eighth species described by Aptroot (2008) with 3-septate spores. The type of the genus is *D. oreina* (Ach.) Norman and it occurs in Africa, Asia, Europe, North and South America (Mayrhofer et al.

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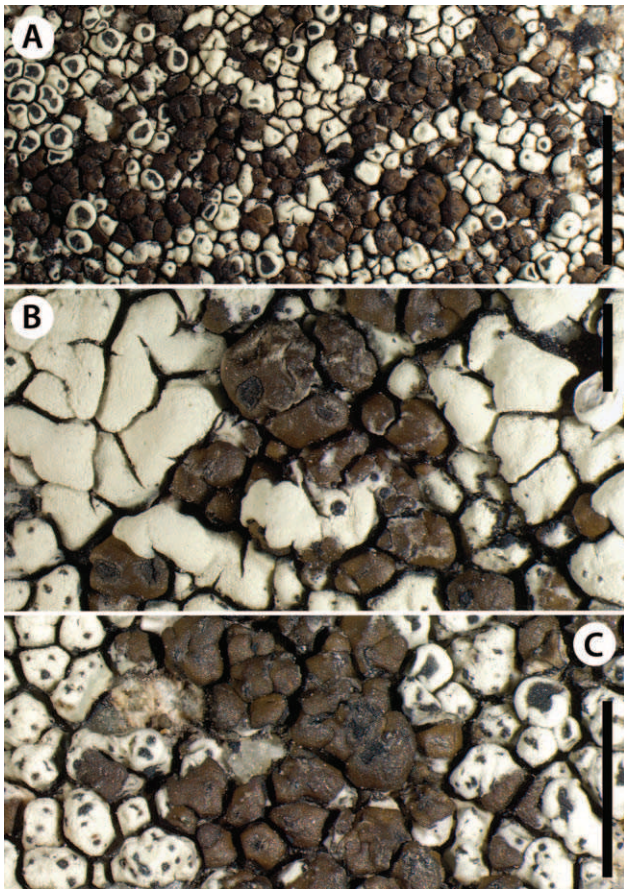


Figure 1. *Dimelaena lichenicola* (Kocourková 8180, paratype). A–C. Habit, brown thallus of lichenicolous lichen *D. lichenicola* on *Dimelaena oreina* with apothecia. Bars A = 4 mm. B = 1 mm. C = 2 mm.

1996; Mayrhofer & Sheard 2004; Obermayer et al. 2004; Sheard & Ahti 1995).

In southern California, at latitudes 32–35° north, *Dimelaena oreina* is predominately a montane species on hard granite above 1500 m, often dominating large vertical rock faces, usually occurring with *Pleopsidium flavum* (Bellardi) Körb. In the southwestern Mojave Desert in Joshua Tree National Park, *D. oreina* occurs from 1277 m on basalt columns on Malapai Hill to 1636 m on granite on Queen Mountain in 6 isolated populations as a Pleistocene relic of wetter, colder climates (Knudsen et al. 2013). Populations tested with thin-layer chromatography from Joshua Tree National Park are the western North American chemotype (chemotype V) and produce usnic acid, stictic acid complex and menegazziaic acid, with a trace of norstictic acid (Michalová 2012; Obermayer et al. 2004; Sheard 1974).

As with many ancient and wide-spread lichen species, *Dimelaena oreina* has many parasites. Non-lichenized parasites that are host-specific to *D. oreina* include *Arthonia hawksworthii* Halıcı (Halıcı 2008), *Endococcus oreinae* Hafellner (Hafellner et al. 2002),

Lichenostigma dimelaenae Calat. & Hafellner (Calatayud et al. 2004), and *Polycoccum evae* Calat. & V.J. Rico (Calatayud & Rico 1995). The type host of *Endococcus oreinae* is *D. oreina*, but it was also reported recently on *D. thysanota* (Tuck.) Hale & W.L. Culb. in California (Kocourková et al. 2012). Some species of *Acarospora* have been reported as parasites on *Dimelaena* but several taxa may not be lichenicolous lichens, including *A. anatolica* H. Magn. (Magnusson 1929), *A. invadens* H. Magn. (Magnusson 1944) and *A. microcarpa* (Nyl.) Wedd. (Nimis 1993). Other species may be only facultatively lichenicolous, such as *A. succedens* H. Magn., which occasionally is parasitic on other lichens, including *D. oreina* (Knudsen 2011). *Acarospora nashii* K. Knudsen is a lichenicolous lichen that occurs on *D. oreina* and *Pleopsidium flavum* in North America (Knudsen 2011). Four other lichenicolous lichens have been reported on *D. oreina* in North America: *Buellia badia* (Fr.) A. Massal. (Bungartz & Nash 2004), which has wide variety of hosts, *B. imshaugii* Hafellner (Hafellner 1979), *Rhizocarpon dimelaenae* Timdal (Feurerer & Timdal 2004) and *R. renneri* Poelt (Feurerer & Timdal 2004; Poelt 1990), all of which occur in California (Hutten et al. in press; Knudsen et al. 2013; Kocourková et al. 2012).

The brown *Dimelaena californica* is a lichenicolous lichen (Mayrhofer & Sheard 2004; Sheard 1974). It is a juvenile parasite primarily on the common *D. radiata* (Tuck.) Müll. Arg. and is endemic to the coast of California and Mexico, and only frequent on the north Channel Islands (Knudsen & Kocourková 2012). It forms a brown lichenized thallus, eventually with well-developed plicate lobes and a distinct prothallus. In this paper we describe from California and Italy a new lichenicolous lichen, *Dimelaena lichenicola*, which is a juvenile parasite on *D. oreina* and *D. thysanota*, and eventually forms an independent brown thallus. It differs from *D. californica* primarily in having longer conidia, reduced thallus and minute lobes, lacking a well-developed plicate margin and prothallus, as well as in its host species (*D. oreina* and *D. thysanota* vs. *D. radiata*), and habitat (montane vs. coastal).

MATERIALS AND METHODS

Specimens of *Dimelaena* from GZU, UCR, and the herbarium of Kocourková & Knudsen were prepared with hand sections and studied using standard light microscopy. Measurements were made in water, amyloid reactions tested with Lugol's Solution (IKI), with or without pretreatment with 10% KOH (K), and the structures were studied in K. Ascospore and asci measurements were made with an accuracy of 0.5 μm and given in the form “(minimum–) mean

(–maximum)'' and followed by the number of measurements (n). Macro- and microphotographs were taken with a digital camera Olympus DP72 on Olympus SZX 7 Stereomicroscope and Olympus BX 51 fitted with a Nomarski differential interference contrast. Thin layer chromatography was carried out using solvent systems following the standardized methods of Culberson & Kristinsson (1970).

TAXONOMY

Dimelaena lichenicola K. Knudsen, Sheard, Kocourk. & H. Mayrhofer, *sp. nov.* **Fig. 1 & 2**

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Similar to *Dimelaena californica* but differing in longer conidia and the lack of a prothallus and well-developed plicate lobes.

TYPE: U.S.A. CALIFORNIA. San Bernardino Co., Joshua Tree National Park, upper Covington Flats, small un-named canyon, 34°00'51" N, 116°18'06" W, 1431 m, pinyon pine and juniper woodland, on *Dimelaena oreina* and *D. thysanota* and on gneiss, Nov. 25, 2012, K. Knudsen 15179 & J. Kocourková (holotype: UCR; isotypes: GZU, NY, SASK, PRM).

Description. Thallus (**Fig. 1A–C**) indeterminate, lacking obvious plicate lobes or a prothallus, areolate, areoles brown, plane at first becoming convex, to ca. 1.2 mm wide, surface smooth and often shining at first, becoming rugulose and matt at maturity, sometimes with minute marginal lobes to ca. 0.15 mm wide, often solitary, eventually forming small contiguous patches on or among the host to ca. 1 or 2 cm wide, scattered across the thalli of *Dimelaena oreina* and *D. thysanota*. Infection beginning as brown discolorations of the host, parasite eventually morphing out of the thallus of the host. Cortex 20–40 µm thick, paraplectenchymatous to subparaplectenchymatous, with narrow brown upper layer and thick hyaline lower layer, with thin hyaline epinecral layer. Algal layer continuous, 50–70 µm thick, algal cells mostly 10–14 µm in diam. Medulla interspersed with abundant crystals, hyaline hyphae thin-walled, mostly 4.0–5.0 µm in diam., anticlinal, continuous with endosubstratal hyphae. Apothecia 1 per areole (**Fig. 1B–C**), lecanorine, disc black, epruinose, mostly 0.1–0.3 mm in diam. Exciple prosoplectenchymatous, narrow, expanding up to 60 µm at surface of disc, forming a parathecial ring the same color as the thallus. Hymenium ca. 80 µm high, hyaline, conglutinate, paraphyses 2.0–3.0 µm wide at mid-level, capitate, apical cells to ca. 4.5 µm wide in diffuse dark pigment forming a red-brown epihymenium (**Fig. 2C**), ca. 10 µm tall. Asci cylindrical to clavate, ca. 70 × 30 µm. Ascospores 8 per asci

(**Fig. 2D–F**), *Beltraminia*-type, dark, 1-septate, (12.0 × 7.0–) 13.0 × 7.5 (–14.5 × 9.5) µm (n = 20), the lumina no longer evident at maturity, with a darkly pigmented torus, walls not ornamented, rarely waisted and elongated when over-mature, sometimes halonate. Subhymenium indistinct. Hypothecium dark red-brown (**Fig. 2A**), to 130 µm deep. Pycnidia frequent, 1–4 per areole, immersed, pyriform, ostiole black and conspicuous. Conidia bacilliform, hyaline, simple, 6.0–10.0 × 1.0 µm, rarely longer. Secondary metabolites concentrated in medulla are norstictic acid (major), stictic acid (minor), but lacking menegazziaic acid which occurs in the host (type collection). Spot test: medulla, K+ red with crystals.

Other specimens examined. ITALY. SOUTH TYROL. Vintschgau, dry slope near Eyra, ca. 800 m, on *Dimelaena oreina*, Sept. 4. 1991, J. Poelt & W. Obermayer s.n. (GZU). U.S.A. CALIFORNIA. San Bernardino Co., Joshua Tree National Park, upper Covington Flats, 1431 m, on *D. oreina* and *D. thysanota* and on gneiss, Nov. 25, 2012, J. Kocourková 8180 & K. Knudsen (hb. Kocourková & Knudsen); north side of Queen Mountain, 1627 m, pinyon pine and oak woodland, on *D. oreina* and granite, Mar. 18, 2013, K. Knudsen 15711 & M. Harding (H, FH, JOS, UCR).

Etymology. The name refers to its lichenicolous habit.

Distribution and substrate. North America (California), Europe (Italy) on *Dimelaena oreina* and *D. thysanota* and independently on gneiss and acid rock.

Differentiation. The only other lichenicolous lichen in the genus is *Dimelaena californica* (**Fig. 3**). Besides differing in a thallus with a well-developed plicate margin and a distinct black prothallus, *D. californica* also has shorter conidia than *D. lichenicola* (5.0–6.0 × 1.0 vs. 6.0–10.0 × 1.0 µm). They do not differ significantly in ascospore size, although *D. lichenicola* has some broader ascospores. Both species occur in California, but *D. lichenicola* is a montane species occurring on *D. oreina* and *D. thysanota*, while *D. californica* is coastal occurring on *D. radiata* and occasionally on other crustose lichens. Generally, the thallus of *D. californica* forms large continuous thalli eventually completely replacing the host on the rock and forming a well-developed plicate margin when it becomes independent. In our specimens and field observations, *D. lichenicola* forms only small patches up to ca. 2 cm among the thallus of the host and does not completely replace the host on the rock substrate. Its small thallus size possibly explains why it was not previously described. In the two California sites, small patches of the non-parasitic brown *Acarospora obnubila* H. Magn., as well as the equally brown *D.*

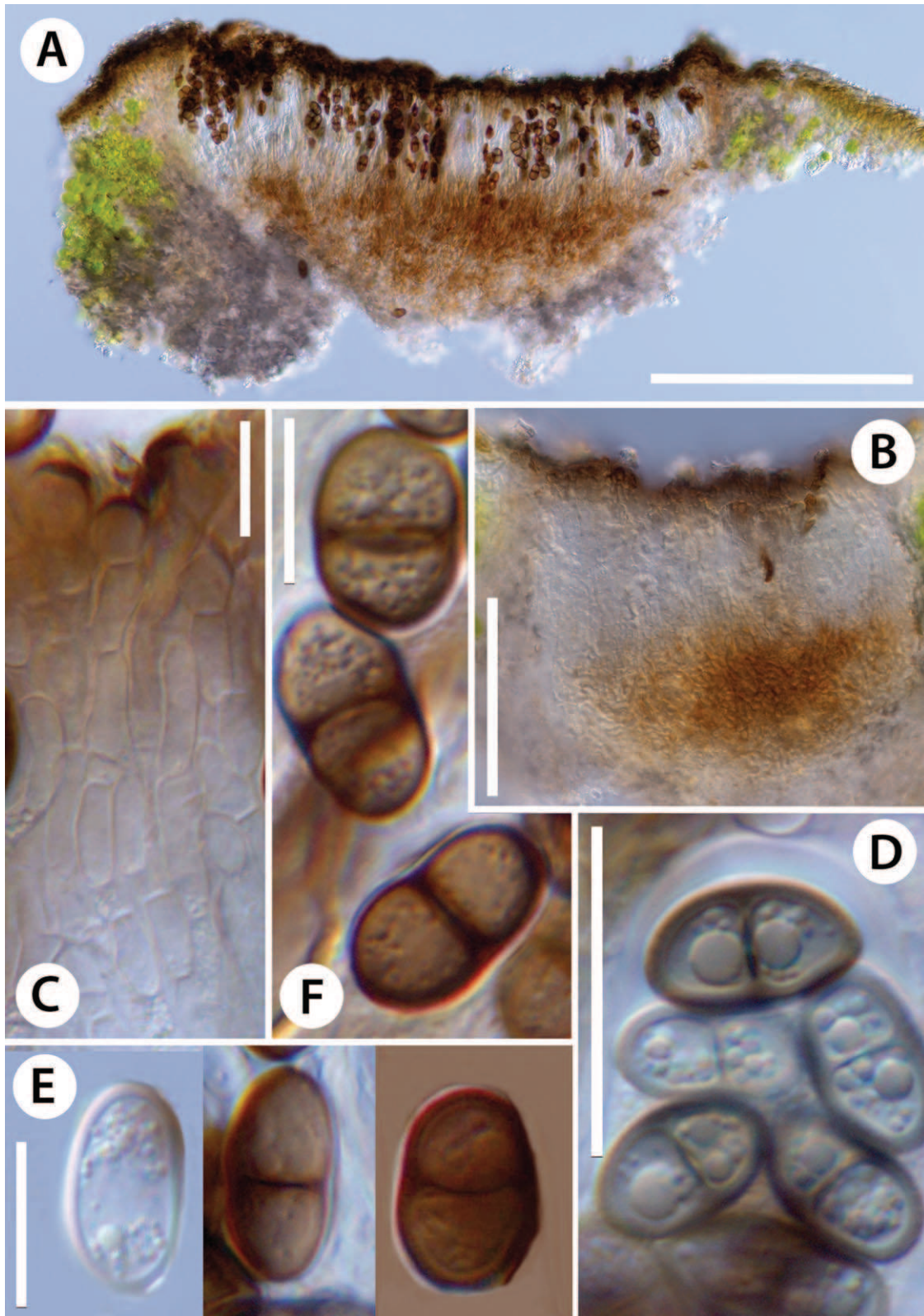


Figure 2. *Dimelaena lichenicola* (Knudsen 15179, holotype). A. Vertical section of apothecium with brown hypothecium. B. Primordium of apothecium. C. Capitulate paraphyses. D. Ascus with semi-mature ascospores. E–F. Young and mature ascospores, sometimes halonate. Bars A, B = 100 μm . C, E, F = 10 μm . D = 20 μm .



Figure 3. *Dimelaena californica* (Knudsen 8955.2, UCR), parasitic on *D. radiata* (white to gray thallus) and *Mobergia angelica* (lighter brown thallus). Bar = 1 mm.

thysanota, were more abundant and intermixed with *D. lichenicola* throughout the thallus of *D. oreina*. Most areoles of *D. lichenicola* were sterile and numerous patches contained only 1 to 5 areoles and were often widely-spaced across the surface area of the host. The small size of the thalli may also explain why J. Poelt collected it in Italy, no doubt looking for one of his specialties, lichenicolous *Rhizocarpon* (Poelt 1990).

DISCUSSION

Dimelaena lichenicola is possibly rare, but the occurrence in California and Italy, its generally small, often sterile, thallus, as well as the wide occurrence of its type host *D. oreina*, suggests that it may be under-collected. In field work in other mountain ranges in California we have not collected *D. lichenicola* as yet.

The genus *Dimelaena* is in part defined by taxa with radiate-plicate lobes. *Dimelaena californica* has a well-developed plicate margin in mature specimens, though it is often lacking in herbarium specimens because they were collected when *D. californica* was in the early stages of development when it is growing in center of the host thallus. At this stage lobes and prothallus usually cannot be observed, though the thallus may be relatively well-developed (Fig. 3). *Dimelaena lichenicola* lacks a determinate margin or lobes. Rare minute lobes (ca. 0.15 mm wide) can sometimes be observed and may possibly be vestigial.

The holotype of *D. lichenicola* and the paratype from Italy look morphologically identical. The ascospores of the specimen from Italy were slightly smaller than the average of the holotype (12.5 × 7.0 vs. 13 × 7.5 μm). The hymenium was more heavily conglutinate in the specimens from California than in the hymenium

of the specimen from Italy. This is possibly due to the arid conditions of the Mojave Desert.

KEY TO GENUS DIMELAENA IN NORTH AMERICA

- 1. Thallus greenish yellow (usnic acid) *D. oreina*
- 1. Thallus white to brown (usnic acid absent) 2
- 2. Hypothecium brown to dark brown 3
- 2. Hypothecium hyaline to ochraceous 5
- 3. Thallus white or gray, to coppery pale brown, not lichenicolous.....
- *D. radiata*
- 3. Thallus brown, lichenicolous 4
- 4. Mainly on *D. radiata*, coastal Mexico and California *D. californica*
- 4. On *D. oreina* & *D. thysanota* *D. lichenicola* K. Knudsen, Sheard, Kocourk. & H. Mayrhofer
- 5. Thallus ochraceous to pale brown, coastal California & Mexico
- *D. weberi*
- 5. Thallus dark brown 6
- 6. Medulla with sphaerophorin, C- (lacking gyrophoric acid), hypothecium hyaline, montane, southwest
- *D. thysanota*
- 6. Medullar lacking sphaerophorin, C+ (gyrophoric acid), hypothecium hyaline to ochraceous, southeastern US
- *D. tenuis* (Beeching 2007)

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