### Melaspilea demissa (Tuck.) Zahlbr. (lichenized Ascomycota) in eastern North America with a key to North American species of Melaspilea s. lat.

#### Gary B. PERLMUTTER, Shirley C. TUCKER, Eimy RIVAS PLATA, Philippe CLERC and Robert LÜCKING

Abstract: Recently collected specimens of the crustose lichen *Melaspilea demissa* from south-eastern USA have been compared with those of *Melaspilea* spp. previously determined from North America. A review of both the historical and contemporary treatments of this species is provided. A lectotype was selected from the type collection of *M. demissa* in FH and is here proposed as it best matches incomplete citations in the original treatment. We also discuss the nomenclatural and taxonomic status of the name *Opegrapha cymbiformis* var. *deformis* (considered a synonym of *M. gibberulosa*). North American specimens of *M. gibberulosa* were found to be misidentifications, as were specimens attributed to *M. lentiginosula*, *M. mesophlebia* and *M. octomera*. We therefore recommend that these species be removed from the North American lichen checklist. We also present a key to North American *Melaspilea*.

Key words: lichens, Melaspileaceae, morphology, Opegrapha, taxonomy

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#### Introduction

The lichen genus *Melaspilea* Nyl. (Ascomycota) in its traditional sense contains species with arthonioid (round to irregular-shaped) to opegraphoid (ellipsoid to lirellate) ascomata producing 1-septate spores with thin walls and septa, often becoming brown when mature (Ryan & Nimis 2004; Sanderson *et al.* 2009). Species in this genus are either lichenized or lichenicolous, with the

lichen species often barely lichenized and some possibly non-lichenized on bark, a situation comparable to Arthopyrenia s. lat. (Harris 1995). The genus is highly heterogeneous (Ryan & Nimis 2004; Sanderson et al. 2009), including several distinct morphotypes. The type species, M. arthonioides (Fée) Nyl., forms immersed, arthonioid ascomata with exposed discs and reduced excipula (Fink 1935; Redinger 1938; Thomson 2003). A similar morphology is found in other species, such as M. maculosa (Fr.) Müll. Arg. In contrast, many species have sessile, opegraphoid ascomata with well-developed excipula and often-concealed discs. Whereas the latter are easily confused with Opegrapha s. lat. or, more rarely, Graphis, the arthonioid morphotype resembles Arthonia s. lat., Arthothelium and the recently described genus Eremithallus (Lücking et al. 2008; Lumbsch et al. 2011). Another genus similar to the opegraphoid taxa of Melaspilea is Hemigrapha (Müll. Arg.) R. Sant. ex D. Hawksw., a small genus of chiefly lichenicolous species which shares with Melaspilea the opegraphoid ascomata

G. B. Perlmutter: University of North Carolina Herbarium, North Carolina Botanical Garden, CB# 3280, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280, USA. Email: gary.perlmutter@gmail.com.

S. C. Tucker: Cheadle Center for Biodiversity, University of California, Santa Barbara, CA 93106-9610, USA; & Santa Barbara Botanic Garden, 1212 Mission Canyon Rd., Santa Barbara, CA 93105.

E. Rivas Plata: Science & Education, Integrative Research Center, The Field Museum, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, USA.

P. Clerc: Conservatoire et Jardin botaniques de la Ville de Genève, CH-1292 Chambésy, Switzerland.

R. Lücking: Science & Education, Integrative Research Center, The Field Museum, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, USA.

and 1-septate, thin-walled, hyaline to brown spores, but differs in the thin, plate-like excipulum (Hawksworth 1975; Matzer 1996; Diederich & Wedin 2000).

The phylogenetic relationships and exact circumscription of Melaspilea were unclear until recently. The genus has been variously with Arthoniales, connected Caliciales, and Ostropales (Wirth & Hale 1963; Poelt 1969; Eriksson 1982; Ryan & Nimis 2004; Sanderson et al. 2009; Lumbsch & Huhndorf 2010), but also with the Dothideomycetes (Von Arx & Müller 1975). In a recent molecular phylogenetic study, Ertz & Diederich (2015) showed that Melaspilea s. lat. consists of several unrelated lineages, all situated within Dothideomycetes: Melaspilea s. str. was found closely related to or conspecific with Eremithallus in Eremithallales (which, however, differs from the type of Melaspilea arthonioides in the distinctly zeorine, lobulate margins), whereas other species form several genera within Asterinales. Apparently, many more species require molecular study to be accurately placed. Due to their usually small size and nondescript nature, these taxa are often overlooked or misidentified, which can have an impact on the accuracy of site biodiversity assessments.

During the first author's exploration of lichen diversity in parts of the south-eastern United States (North Carolina, South Carolina and Virginia), a small, thin, corticolous, crustose lichen was encountered with a shiny tan thallus and minute, scattered Superficially this microlichen lirellae. resembled Opegrapha Ach. (Opegraphaceae), but the brownish, 2-celled spores, together with the multilayered excipulum, place it in Melaspilea Nyl. (Melaspileaceae). While the determination of these specimens to Melaspilea s. lat. was straightforward, species identification proved to be a challenge due to the lack of a current treatment containing keys and species descriptions for this genus in North America. Recent literature includes regional lichen floras that cover only few species [three species in Wisconsin (Thomson 2003); one in the Sonoran Desert (Ryan & Nimis 2004); and one in the Ozark Highlands (Harris & Ladd 2005)]. The only seemingly comprehensive revision of the genus in North America was in Bruce Fink's posthumous work, *The Lichen Flora of the United States* (1935), which includes a key and descriptions of 12 species. However, the validity of some of the species described therein is uncertain. Therefore, the specimens were reported as *Melaspilea* sp. in the resulting checklists (Perlmutter 2008; Hodkinson *et al.* 2009; Hodkinson 2010; Perlmutter & Beeching 2011).

In an effort to identify the aforementioned material, detailed descriptions were made and compared with loaned specimens from other herbaria, as well as recent and historical species treatments in the literature. Similar analyses were made of six species from SCT's Louisiana collections. The undetermined specimens keyed to both *Melaspilea demissa* and *M. deformis* in Fink (1935). Consequently, European material named *M. deformis* was also examined.

#### **Materials and Methods**

Our material consisted of 17 collections of unidentified Melaspilea from North Carolina, South Carolina and Virginia (NCU), plus six specimens from Louisiana (LSU, SBBG). We also examined Louisiana collections of M. amota Nyl., M. arthonioides (Nyl.) Fée, M. deformis (Schaer.) Nyl., M. maculosa (Fr.) Müll. Arg., and M. tribuloides (Tuck.) Müll. Arg. (all from LSU, SBBG). Material on loan from F, MICH, MSC, WIS, and US, was also studied for many of these same species, along with M. constrictella (Stirton) A. L. Sm., M. cupularis Müll. Arg., M. demissa (Tuck.) Zahlbr., M. octomera Müll. Arg., and M. proximella Nyl. For M. cinerascens (Willey) Fink and M. lentiginosula (Nyl.) A. L. Sm., two additional species listed by Fink (1935), adequate material could not be located. Type material of several species traditionally assigned to Melaspilea, including M. arthonioides, M. demissa, M. deformis and M. maculosa, was loaned from FH, G and UPS and examined for comparison with the south-eastern USA material.

Material was examined under an AO Spencer binocular dissecting microscope (by GBP) or a Wild dissecting microscope (by SCT) with an emphasis on accomatal size, as this was a character used in Fink (1935) for species determination. Spot tests (K, C, KC and P) as well as UV tests were conducted on thalli. Ascomatal sections were prepared in water mounts and examined under light microscopy using a Zeiss Standard 14 compound microscope (by GBP) or a Leitz Wetzlar compound microscope (by SCT). Tissue characters (excipular carbonization, hymenial height and colour, thickness of paraphyses, and ascus abundance) and

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spore characters (colour, number per ascus, width and length measurements) were recorded. K and KI tests were performed on section mounts based on notes in Ryan & Nimis (2004). We paid particular attention to the presence of heaped ascomata, a feature that characterized *M. constrictella* and *M. lentiginosula*, but is absent from other North American species. The ascomata are not only clustered but growing over one another in groups of  $\sim$ 8–12.

Chemistry was tested by RL using thin-layer chromatography (Orange *et al.* 2010) on three specimens of the material in question. Due to the endoperidermal nature of these taxa, we ran comparative TLC on material scraped directly off the bark surface, containing ascomata and endoperidermal thallus, and bark tissue from underneath the uppermost periderm layers. TLC was performed in solvent C.

Descriptions of the ascomatal and spore features of each collection of the unknown *Melaspilea* species were made and compared with those derived from loaned material of known *Melaspilea* species. Comparisons were also made with published species descriptions in the literature. A distribution map of all specimens determined as *M. demissa* was created with the aid of Google maps. In addition, a key to the examined *Melaspilea* s. lat. species in North America was generated.

#### **Results and Discussion**

A total of 31 specimens of the undetermined south-eastern species was examined (17 from NCU, five from LSU, and nine from MICH). All match Fink's description of the genus Melaspilea, which agrees with later treatments (Thomson 2003; Ryan & Nimis, 2004; Sanderson et al. 2009). More specifically, the undetermined specimens all share the following characteristics: a pale tan matt or shiny, thin to endoperidermal thallus, in some specimens bearing dark contact lines; minute lirellae with closed to open, blackish brown discs; brownish hymenial tissues that react KI+ pale bluish; and abundant, clavate, 8-spored asci bearing 2celled, hyaline to brownish spores. In Fink (1935), the unknown species keyed to either M. demissa or M. deformis. The Fink key relied strongly on ascomatal size and shape; however, we learned that these characters are somewhat variable.

#### Comparisons with other North American *Melaspilea*

Several species we examined have ascomata that are arthonioid (round to irregular). Melaspilea proximella [now referred to the reinstated genus Melaspileella (Ertz & Diederich 2015)] has minute discs [0.1-0.2(-0.3) mm]diam.], and occurs in the British Isles (Sanderson et al. 2009) but is quite rare in USA collections [five of M. proximella were recorded from 64 institutions as posted on CNALH; US specimens examined by GBP were from Vermont and New Hampshire (one each)]. Four other North American species examined with arthonioid ascomata are M. amota, M. arthonioides, M. constrictella and M. maculosa. Melaspilea arthonioides and M. maculosa are relatively common species with large ascomata:  $0.8-1.5 \,\mathrm{mm}$  diam. in M. arthonioides and 1.0-1.5 mm diam. in M. maculosa. The type specimen of M. maculosa, loaned from UPS, was examined by ERP and found to contain ascomata that were heavily carbonized with indistinguishable internal tissues. The spores of determined M. maculosa specimens are comparable  $(18-24 \times 8-11 \,\mu\text{m})$  to those of the undetermined material. Melaspilea maculosa appears to be a Gulf Coast species, frequent in southern Louisiana (Müller 1895; Fink 1935; Tucker 2010), particularly on bark of Fraxinus; M. arthonioides appears to be more widespread (Fink 1935; Thomson 2003; Harris & Ladd 2005). According to published concepts, M. amota has smaller ascomata (0.2-0.8 mm diam.) than M. arthonioides and M. maculosa; however, the type material of *M. arthonioides* in G has very small ascomata, up to  $0.5 \,\mathrm{mm}$  diam., and hence the taxonomy and correct nomenclature of these species needs to be further studied. We were unable to locate satisfactory material of M. constrictella; several collections were examined, although some were fragments and others appeared to be other species. Fink (1935) described the ascomata of M. constrictella as elongate, but Redinger (1938) described them as round, elliptical or 2-3-lobed.

We also examined species that had opegraphoid (ovoid to lirellate) ascomata. According to Fink (1935), *M. demissa* grows on bark and has the smallest lirellae  $(0\cdot 2-0\cdot 4 \times 0\cdot 1-0\cdot 2 \text{ mm})$  while *M. cinerascens* has larger lirellae  $(0\cdot 4-0\cdot 8 \times 0\cdot 10-0\cdot 25 \text{ mm})$ and grows on old wood. However, no satisfactory material of M. cinerascens could be found, as the only collection we examined, from Louisiana (Langlois s. n., MICH 113010), keyed to M. constrictella. The descriptions for M. cinerascens and M. constrictella in Fink (1935) are nearly identical, except that the ascomata in M. constrictella are sometimes clustered in heaps. Melaspilea tribuloides [now referred to the genus Melanographa (Ertz & Diederich 2015)] is distinct among the lirellate Melaspilea in being lichenicolous and commonly found on the brilliant red crustose thalli of Pyrenula cruenta, as well as other Pyrenula species and Trypethelium. Two very rare species, M. cupularis and M. epigena, are also lichenicolous (on Pyrenula spp. and Reimnitzia santensis, respectively).

We are disregarding *Melaspilea octomera* Müll. Arg., mentioned by Fink (1935); it was described as having 5–7-septate spores and examination of the type material revealed it belonging to *Opegrapha astraea*; also, several examined specimens named *M. octomera* were determined by SCT and GBP as *O. astraea* Tuck. Similarly, *M. mesophlebia* Müll. Arg. (Esslinger 2011) should be transferred to *Opegrapha* or related taxa. Further discussion regarding *O. astraea* will be presented in a forthcoming report.

A key to the above species represent ing *Melaspilea* s. lat. is presented below. Detailed descriptions and further discussion of these *Melaspilea* taxa will be presented in forthcoming reports.

## Nomenclatural and taxonomic status of Melaspilea deformis

We borrowed three putative specimens of *Melaspilea deformis* for study: two from MICH (collected in New Hampshire) and one from MSC (collected in Michigan). All keyed to *M. demissa* using Fink (1935), and matched characters with the undetermined material; however, one was later determined by SCT to be *M. constrictella*. For further comparison we examined what we presumed to be type material of *M. deformis* loaned from ASU and G (by GBP), and at G (by PC). These specimens are from the

L. E. Schaerer Exsiccati, No. 283, collected in Bern, Switzerland (as Opegrapha cymbiformis var. deformis). A review of the literature revealed M. deformis to be synonymized with M. gibberulosa (Ach.) Zwackh [now referred to the genus Hazslinszkya (Ertz & Diederich 2015)], first by Zwackh (1862), who cited one of Schaerer's Exsiccati no. 283 in his treatment. According to Redinger (1938), the earliest reference to synonyms of M. gibberulosa, established as Arthonia gibberulosa Ach. (Acharius 1810), is M. deformis (Schaer.) Nyl., originally described as Opegrapha cymbiformis var. deformis Schaer. (Schaerer 1836). Ertz & Diederich (2015) interpreted the name Opegrapha cymbiformis var. deformis as illegitimate, since Schaerer (1836) listed Arthonia gibberulosa as a synonym, and hence the name would automatically be typified by the type of the latter. However, ICN Art. 52 only applies to names that should have been adopted at the same rank and hence *Opegrapha* cymbiformis var. deformis cannot be automatically typified by the type of Arthonia gibberulosa. Instead, one of the synonyms listed at the same rank of variety, viz. Opegrapha verrucarioides var. marmorata Ach. and O. verrucarioides var. megalyna Ach., would automatically typify O. cymbiformis var. deformis. Fortunately, at least one of them also represent M. gibberulosa, as judged from digital images of the types and their annotations in ISTOR: the holotype of O. verrucarioides var. marmorata features the annotation Melanoth. deformis (apparently by Nylander), which refers to an overlooked combination proposed bv Nylander (1856) before recombining the species again as Melaspilea deformis (Nylander 1858). In the latter, Nylander (1858) also lists O. verrucarioides var. marmorata as synonym of M. deformis. We therefore agree with Ertz & Diederich (2015) that the name O. cymbiformis var. *deformis* is illegitimate and synonymous with Melaspilea (Hazslinszkya) gibberulosa, but that it should be automatically typified with the type of O. verrucarioides var. marmorata.

Melaspilea (Hazslinszkya) gibberulosa is a widely distributed European species (e.g. Redinger 1938; Nimis 1993; Llimona & Hladun 2001; Bielczyk et al. 2004; Santesson et al. 2004; Wirth et al. 2013) that is also reported from the USA (Thomson 2003). However, the material referred to in Thomson (2003) was determined by SCT to be M. constrictella. Melaspilea gibberulosa is distinct from the undetermined material by having ascomata that are arthonioid with flat, sunken, black discs bordered by thin, black rims, and smaller spores (Redinger 1938; Thomson 2003). An additional specimen from the Little Carpathians of presentday Slovakia (Zahlbruckner s. n., s. d., US) was also examined.

Specimens examined from Schaerer's Exsiccati no. 283 (Fig. 1) revealed spore heterogeneity among specimens, containing 2-celled spores and 4-6-celled transversely septate spores, suggesting the exsiccati to be a mixture of Melaspilea and Opegrapha material. However, the specimens that do bear the 2-celled trait also match other morphological and anatomical characters described by Redinger (1938) for M. gibberulosa, and Lindsay (1872) for M. deformis, including: thin, pale thallus; short, round-elongate  $(0.2-1.2 \times 0.2-0.4 \text{ mm})$  ascomata with open, blackish brown discs; a lateral, carbonized exciple; and brownish ascomatal tissues as well as the brownish spore colour. Two additional specimens from the exsiccate in G were examined by GBP and found to have the following distinctions from the undetermined material: broadly irregular ascomata  $(0.5-1.0 \times 0.2-0.5 \text{ mm})$  that are immersed to erumpent, compared to prominent to sessile lirellae; distinct paraphyses compared to sometimes indistinct ones in a hymenial gel; smaller asci  $(34-53 \times 10-14 \,\mu\text{m} \text{ compared to})$  $42-85 \times 10-25 \,\mu\text{m}$ ; and smaller, 2-celled, hyaline spores  $(12-17 \times 5-7 \,\mu\text{m}, \text{ compared})$ to  $14-22 \times 6-10 \,\mu\text{m}$ ). Based on these differences, we conclude that the undetermined species is not M. gibberulosa. Fink's description of M. deformis as lirellate appears inconsistent with other treatments of this species, namely Redinger (1938) and Thomson (2003), as well as our own observations.

## Original description of Melaspilea demissa

Melaspilea demissa (as Opegrapha demissa) was originally described by Edward Tuckerman (1872) in a discussion of North American Opegrapha species:

"O. demissa—a description of which is for the present reserved, is marked by larger, rather sunken fruit, scattered over an indistinct pale spot on the bark of Holly, Witch Hazel, and Poison Dogwood in southern Massachusetts (Mr. Willey) and yet larger spores... Thalline features of O. demissa as yet very obscure; but the plant is not parasitic. Ascomata commonly 1 mm in length, scattered and simple, white within. Spores in eights (in clavate thekes) bilocular, and constricted at the middle, brown, 0,016–23 mm. long, 0,006–9 mm. wide. Paraphyses not always indistinct. With iodine, in some specimens, only the tips of gravid thekes shew a slight bluish tinge; but in others, the blue reaction is more marked."

We interpret "Mr. Willey" as Henry Willey, a student of Tuckerman's who contributed substantially to the understanding of the north-eastern US lichen biota, in particular that of the *Arthoniales* and of Massachusetts. In his posthumous work, *A Synopsis of the North American Lichens* (Tuckerman 1888, edited by Willey), Tuckerman provides a more correct treatment of *M. demissa*. This treatment in full is as follows:

<sup>67</sup>. O. demissa, Tuckerm.; "thallus thin, whitish or obsolete; ascomata minute, elliptical, simple, white within, the disk at length somewhat dilated. Spores 8 in clavate thekes, 2-locular, finally brown, constricted in the middle, 16–23 by 6–9 mic. Paraphyses now distinct." On *Rhus venenata* and other barks. New Bedford, Mass., *Willey*. [Maryland and Virginia, *Dr. Eckfeldt.*] *Genera*, p. 199.

These descriptions appeared to match the south-eastern material well, including the I+ reaction which was also found in all specimens tested. To further explore the potential determination of the south-eastern specimens as *M. demissa*, we examined specimens of *M. demissa* from FH, MICH and US, including type material collected by Willey in New Bedford, Massachusetts. Willey made excellent notes with measurements and drawings of spores, including one drawing of an ascomatal section. Two sets of specimens are considered syntypes: one from FH and labelled "TYPE" includes

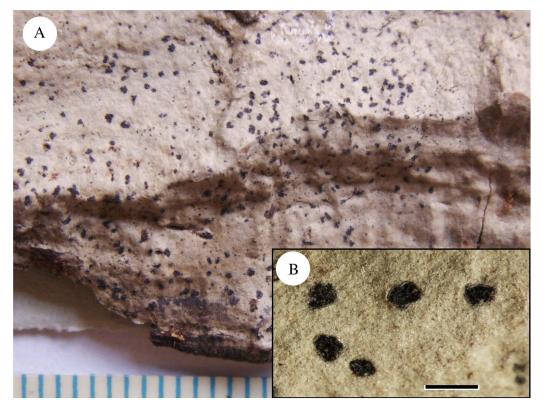


FIG. 1. Melaspilea gibberulosa specimen (Schaerer Exsiccati 283, G barcode G00294512), the original material of *Opegrapha cymbiformis* var. *deformis* which is, however, automatically typified by the type of *O. verrucarioides* var. *marmorata*. A, habit. scale increments = 1 mm; B, detail with apothecia, scale bar = 1 mm. In colour online.

three specimens; another set of three from US is here considered isolectotypes. From the type material, we selected Willev s. n., 1870 [FH] as the lectotype because it contains the most informative notes and drawings (Fig. 2) and it corresponds to the phorophyte (Rhus venenata) first mentioned in Tuckerman's citation. The historical specimens matched the south-eastern material as well as Tuckerman's description, both morphologically (thin thallus with scattered, short lirellae) and anatomically [drawings depicted an ascoma with lateral exciple, brownish tissues, an endophloedal thallus and 2-celled slipper-shaped spores that were hyaline to brownish and measured  $(16-)18-23(-25) \times 7-10(-13) \ \mu\text{m}$  (Fig. 2). Additional specimens of M. demissa from Pennsylvania and Tennessee (US) were also examined and found to match both the type and south-eastern material.

To further compare the south-eastern USA material with the historical material, a multivariate analysis was conducted using PC-ORD (McCune & Mefford 2011). A matrix of 59 specimens and 11 characters as well as ecoregion was created from material examined at NCU and then underwent a cluster analysis to explore the data for groupings (see Appendix). Cluster analysis involved the Sorensen (Bray Curtis) distance measure and the Flexible Beta group linkage method with beta set to -0.25, as recommended in McCune & Grace (2002). Clustering resulted in the south-eastern material grouping with the M. demissa type specimens and others identified as this species in the US collection, further

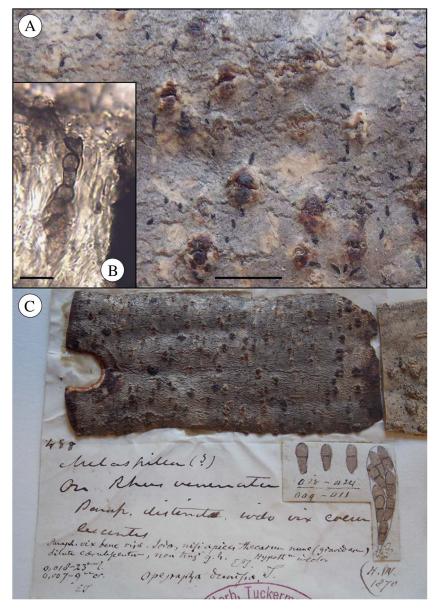
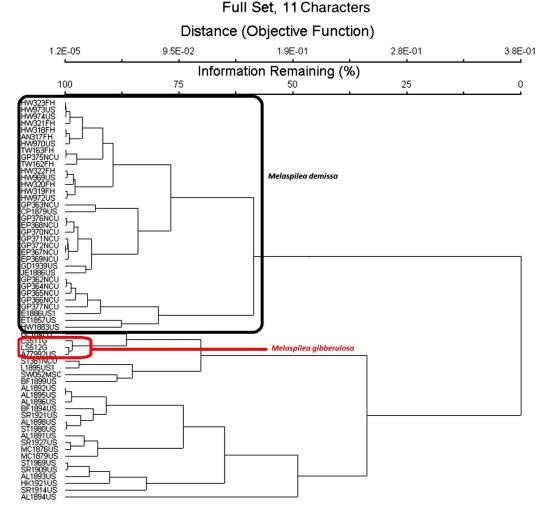


FIG. 2. Melaspilea demissa, lectotype (Willey s. n., 1870, FH). A, thallus, raised areas are lenticels of the phorophyte; B, spores in ascus; C, specimen proposed as lectotype with notes and drawings (Willey s. n., 1870, FH barcode 00377321). Scales: A=5 mm; B=20 μm. In colour online.

supporting the south-eastern material being *M. demissa* (Fig. 3).

As mentioned before, many species of *Melaspilea* superficially resemble *Opegrapha* as both taxa bear thin thalli and small,

usually prominent to sessile, lirellate ascomata with well-developed excipula. This is evident as several *Melaspilea* species were originally placed in *Opegrapha*. During our comparisons we discovered that specimens



### FIG. 3. Cluster diagram of *Melaspilea* specimens examined. See Table in Appendix and text for specimen codes.

of *M. octomera*, a species mostly collected by A. B. Langlois in Louisiana, were actually *Opegrapha astraea* Tuck., a more widespread species that is characterized by a black prothallus and white pruinose lirellae with black excipular margins and multi-septate spores (Tuckerman 1888; Fink 1935). We therefore propose that *M. octomera* be synonymized with *O. astraea*. Further discussion will be presented in a future paper.

A comparison of descriptions of *Melaspilea* and *Opegrapha* in Redinger (1938) and Ryan & Nimis (2004) show some overlap in thallus and ascomatal characters, with a wider variation in *Opegrapha*. Redinger (1938) separated the two genera on the basis of spore and paraphysal characters. He reports *Melaspilea* to have ellipsoid and 1-septate spores and simple paraphyses, whereas in *Opegrapha* spores are multi-septate, fusiform to needleshaped, and paraphyses are branched. Paraphyses are usually difficult to see in *Melaspilea* species, but spore traits of shape, septation and wall thickness (thin in *Melaspilea*, somewhat thickened in *Opegrapha*) are more reliable and provide an easier means of

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200 mi

separating the two genera. *Opegrapha* has been shown to be polyphyletic (Ertz *et al.* 2009; Ertz & Tehler 2011), and *Melaspilea* is well known to be heterogenous (Ryan & Nimis 2004; Sanderson *et al.* 2009). Further study of *Melaspilea* specimens could better resolve the taxonomy of this intriguing genus.

We conclude that the recently collected *Melaspilea* specimens from south-eastern North America bearing a pale tan, matt or shiny thallus and short lirellae are *M. demissa*, and our observations agree with a specimen collected by Gunnar Degelius in the Great Smoky Mountains National Park of eastern Tennessee (*Degelius* s. n., 18 ix 1939, US). The range of this species, from comparison with other material, seems to be widespread in eastern North America.

Here we present a revised treatment of *Melaspilea demissa*, followed by a revised key to North American *Melaspilea* s. lat. from material examined in this study. It is possible that specimens currently identified as *Melaspilea* sp. can now be determined to species with greater confidence using our treatment and key below. Detailed descriptions of the species examined will be presented in a forthcoming paper.

#### The Species

#### Melaspilea demissa (Tuck.) Zahlbr.

#### MycoBank No.: MB395311

Opegrapha demissa Tuck, Gen. Lich.: 199 (1872); type: USA, Massachusetts, Bristol Co., New Bedford, 1870, Willey 488 (FH!—selected here as lectotype).

#### (Fig. 2)

Life form. Crustose, lichenized fungus.

Thallus thin to endoperidermal, as pale to tan, or  $\pm$  shiny stain, continuous, sometimes with a dark prothallus and/or contact lines. *Photobiont Trentepohlia*, endoperidermal; clusters of associated chlorococcoid alga often observed lying on the thallus surface.

Ascomata opegraphoid, scattered to clustered, elliptical to elongate, mostly short black lirellae,  $0.2-1.3 \times 0.2-0.3$  mm, prominent to sessile, straight to curved, usually

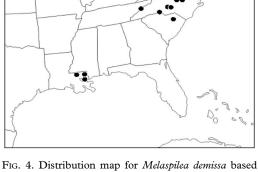


FIG. 4. Distribution map for *Melaspilea demissa* based on specimens examined. Open circle represents type locality of New Bedford, Massachussetts.

unbranched but some may have short branches; disc closed to open, opening in water, blackish brown, epruinose. Exciple carbonized, lateral and extending into the substratum, thickened basally, lined apically and proximally with melanized cells in some specimens. Epihymenium brown to dark brown or absent; hymenium hyaline to brownish, 58-68(-100) µm, gel-like, the gel and brownish coloration dissolving in K, KI+ pale blue; hypothecium pale tan to orangish brown; paraphyses unbranched, thickened with darkened, swollen tips. Asci clavate, abundant, 8-spored. Spores 2-celled, septum slightly constricted or not, one cell often larger, hyaline to light brownish when mature, wall smooth or warty,  $(10-)14-22(-26)\times(-5)6-10(-13)$  µm.

*Chemistry.* Spot tests: thallus K-, C-, PD-, UV+ yellowish. TLC: comparative TLC showed no substances for *Perlmutter* 1284 (including the deeper bark layers) and unknown terpenoids for *Perlmutter* 2073; in

the case of the latter, two distinct and one faint spot were found in the uppermost layers containing the lichen thallus and two distinct spots in the deeper bark layer, suggesting that these spots represent bark substances. If occurring in the uppermost bark layers only (upper of the three spots), it cannot be said with certainty whether the substance originates from the lichen or the bark, but the complete absence of substances in 1284 suggests that these lichens do not contain secondary substances.

*Distribution.* Appears to be widespread in eastern USA, found in DC, IA, LA, MA, MD, NH, NC, SC, PA, TN, VA, WI (Fig. 4).

*Ecology.* Corticolous on smooth bark of understorey stems and branches in shaded forests.

### Key to North American Melaspilea species

This key was developed from a comparison of specimens attributed to *Melaspilea* s. lat. in several North American herbaria. The nomenclature of several species has been adjusted according to the recent study by Ertz & Diederich (2015). The following taxa were found to be misidentifications and are excluded from this key: *M. gibberulosa, M. lentiginosula, M. mesophlebia* and *M. octomera. Melaspilea interjecta* was recently reported from a collection in Oregon (Villella *et al.* 2013) and is herein included. Detailed descriptions of taxa in this key other than *M. demissa* will be presented in a subsequent publication.

1	Lichenicolous; hypothecium colourless
2(1)	Apothecia arthonioid (round to irregular; erumpent), 0.2–0.4 mm diam.; on <i>Pyrenula</i>
3(2)	Apothecia $0.3-0.9 \times 0.1-0.2$ mm; disc closed, with lirella tips blunt or short-acute; spores $15-21 \times 6-9 \mu$ m; on <i>Pyrenula, Thelotrema</i> or <i>Trypethelium</i>
4(1)	Saxicolous, western USA
5(4)	Apothecia arthonioid (round to irregular, erumpent to sessile).6Apothecia opegraphoid (lirellate, sessile).9
6(5)	Apothecia large, $(0.4-)0.8-1.0 \text{ mm}$ diam
7(6)	Throughout eastern USA; apothecia not erumpent, $0.4-1.2 \text{ mm}$ diam.; spores $12-17 \times 6.0-8.5 \mu \text{m} \dots \dots$
	(Glyphis maculosa Fr., Melaspilea angulosa Nyl.)

8(6)	Apothecia $0.2-0.8 \text{ mm}$ diam., erumpent; hypothecium brown; spores $14-18 \times 7.5-12.5 \mu \text{m} \dots \dots$
	(Arthonia proximella Nyl., Melaspilea proximella (Nyl.) Nyl. ex Norrlin)
9(5)	Apothecia sometimes heaped; hypothecium colourless; spores $12-17 \times 4.5-6.5 \mu\text{m} \dots \dots$
	Apothecia not heaped; hypothecium brown or colourless; spores $12-24 \times 6 \cdot 0 - 12 \cdot 5 \mu m \dots 10$
10(9)	Exciple thin
	Exciple thick, at least basally

#### Conclusions

This study revealed that the south-eastern USA material collected in recent surveys is Melaspilea demissa. We have reviewed the type material, from which a lectotype was selected and is presented here. From a wider study of additional species in comparison with the recent south-eastern collections, we have amassed sufficient morphological and anatomical information to develop a key to North American Melaspilea species, primarily sorted by habit (lichenized or lichenicolous), substratum (saxicolous or corticolous), ascomatal features (mainly shape as either arthonioid or opegraphoid, as well as size), spore dimensions, and geography. We present this key to aid the identification of Melaspilea specimens in current and future North American lichen surveys.

However, it should be re-emphasized that *Melaspilea* is a heterogenous taxon in strong need of revision. The ascomatal morphology of the arthonioid taxa and opegraphoid taxa appears so distinct as to suggest separate or multiple lineages, even within these morphological groups. To best resolve the accuracy of *Melaspilea* taxonomy, we recommend molecular study of this problematic taxon. Until then, we hope that the arthonioid and opegraphoid crustose lichens studied here can be appropriately identified and included in biodiversity assessments.

#### **Specimens Examined**

Specimen information is presented here in abridged form. Full specimen records are available online on websites of the Smithsonian Institution's National Herbarium (US) (http://botany.si.edu/), Uppsala's Natural History Museum (UPS) (http:// 130.238.83.220:81/home.php), Conservatoire et Jardin botaniques de la Ville de Genève (G) (http://www.ville-ge.ch/cjb/), and on the Consortium of North American Lichen Herbaria web portal (for all other listed holdings) (http://lichenportal.org/).

Melaspilea amota Nyl. USA: Florida: Lake Co., N of Eustis, Rapp 716 (MICH); Alachua Co., Gainesville, Rapp s. n. (FLAS). Louisiana: Natchitoches Parish, Bayou Millieu, Langlois s. n. (US); Point Coupee Parish, Chenal, Langlois 775 (US); St. Martinville/Lafayette Parish border, Bayou Tortue, Langlois s. n. (LSU, MICH, NY, US); Iberville Parish, Tucker 13394 (LSU, SBBG).

Melaspilea arthonioides (Fee) Nyl. Locality unknown, Anonymous s n., s. d. (G) (as Lecidea arthonioides, type). USA: Florida: Lake Co., north of Eustis on tree trunk, 12 vii 1928, Rapp s. n. (MICH); Monroe Co., Pumpkin Key, iv 1921, Kelly s. n. (US); Seminole Co., Sanford, Rapp; Lichenes Exs. 238 (FLAS, NEB, VT, US), ix 1921, Rapp s. n. (US). Iowa: Fayette Co., Fayette, vii 1894, Fink s. n. (US). Iowa: Fayette Co., Fayette, vii 1894, Fink s. n. (US). Louisiana: East Baton Rouge Parish, Baton Rouge, Tucker 7297 (US), Tucker 21224 (SBBG); Iberville Parish, Tucker 13345 (LSU, SBBG). Massachusetts: Hampshire County, Hadley, 17 vii 1899, Tuckerman s. n. (US). Minnesota: Yellow Medicine Co., Granite Falls, Fink 32A (MICH). Missouri: Franklin Co., Meramec State Park, Buck 49642 (NY); Taney Co., Mark Twain National Forest, Harris 47747 (NY); Washington Co., Pea Ridge Conservation Area, *Harris* 47910-A (NY).

Melaspilea cinerascens (Willey) Fink. USA: Louisiana: Langlois s. n., s. d. (MICH).

Melaspilea constrictella (Stirt.) A. L. Sm. USA: Louisiana: Langlois 1766 (US). Michigan: Alpena Co., 8 miles SW of Alpena on Populus, 1974, Wang 964 (MSC). Wisconsin: Sawyer Co., Flambeau River State Forest on Pinus strobus, Hale 2081 (WIS).

Melaspilea cupularis Müll. Arg. USA: Louisiana: St. Martinville Parish, St. Martinville, Langlois s. n. (MICH).

Melaspilea demissa (Tuck.) Zahlbr. USA: District of Columbia: Takoma Park on Rhus, Williams, Decades of American Lichens 284 (DUKE, FH, ISC, MICH, US). Iowa: Clayton County, 1894, Fink s. n. (MICH); Fayette County, 1894, Fink s. n. (MICH). Louisiana: St. Tammany Parish, Abita, 26 xi 1891, Langlois s. n. (US); Washington Parish, Tucker 28427C (LSU). Massachusetts: Bristol County, New Bedford, Willey s. n., 1870 "On Rhus venenata", "On Ash", Willey s. n., 1862-1898, "On Holly", Willey s. n., 1862-1898 "On Rhus venenata", Willey s. n., 1862-1898, "On Witchhazel" (syntype collection, FH and US), Willey s. n., 1881 "On Cherry", Willey s. n., 1884 "On Rhus copallina", Willey s. n., 1862-1898 (US), Willev 239, New Bedford, Bristol Co. (MIN). New Hampshire: Coos Co., Jefferson, Willey s. n., s. d. (MICH); White Mountains, Willey s. n., s. d. (MICH). North Carolina: Gaston County, Crowder's Mountain, Green s. n., s. d. (MICH); Orange County, Mason Farm Biological Reserve, Perlmutter 827 (on Viburnum), 912 (on Viburnum), 929 (on Prunus), 1456 (on Cornus), 1470 (on hardwood sapling) (all NCU); Randoph Co., Purgatory Mt. on hardwood trunk, 25 ix 2011, Rivas Plata s. n., (NCU); Ridges Mt. on Prunus, 24 ix 2011, Rivas Plata s. n. (2 specimens, NCU); Wake Co., Turnipseed Nature Preserve, Perlmutter 2073 (on Ilex), 2325 (on Ilex), 2344 (on Prunus), 2345 (on Ilex), 2604 (on Prunus). Pennsylvania: 1886, Eckfeldt s. n. (US); Lehnert, s. n., s. d. (MICH). South Carolina: 1886, Eckfeldt s. n. (US); Darlington Co., Black Creek watershed on Aralia, Perlmutter 1495 (NCU); Florence Co., Back Swamp on Ilex, Perlmutter 1571 (NCU). Tennessee: Sevier County, Great Smoky Mountains National Park, 18 ix 1939, Degelius s. n. (US). Virginia: Grayson Co., Jefferson National Forest on hardwood trunk, Perlmutter 1284 (NCU).

Melaspilea epigena Müll. Arg. USA: Louisiana: East Baton Rouge Parish, Centurion Place subdivision, lichenicolous on Reimnitzia santensis, Tucker 15903 (LSU).

Melaspilea gibberulosa (Ach.) Zwackh. [now Hazslinszkya gibberulosa (Ach.) Körb.] Switzerland: Bern: on St. Peter's island on *Juglans, Schaerer* s. n., s. d. 507734 (ASU), G00294511 and G00294512 (G), NEB00032057 (NEB) (as *Opegrapha cymbiformis* f. *deformis*, syntype collection).—Slovakia: Little Carpathians: Zahlbruckner s. n., s. d., (US).

Melaspilea maculosa (Fr.) Mull. Arg. Locality unknown. Ref.: K. Vetensk. Acad. Handl. 1820: 44 (1820), Anonymous s. n., s. d., L-104319, 182909 (as Glyphis maculosa, holotype, UPS). USA: Florida: Seminole Co., Sanford, Rapp 238 (MICH); Escambia Co., Big Lagoon State Recreation Area, Platt 52 (LSU, NCU). Louisiana: Bois Levert, 26 xii 1898, Langlois s. n. (US); St. Martinville Parish, St. Martinville, Langlois 776 (US), on Celits, Langlois 857 (MICH), Langlois 1033 (MICH, SBBG); East Baton Rouge Parish, Baton Rouge, on Fraxinus, Tucker 11951 (ASU, BRY, DUKE, FLAS, MIN, MSC, OMA, SBBG, TENN, WIS); Burden Research Plantation, on Fraxinus, Tucker 17252 (NCU); Ben Hur Farm, on Fraxinus, Tucker 21332 (US); West Feliciana Parish, S. Tucker 12821 (LSU).

Melaspilea proximella (Nyl.) Nyl. ex Norrlin. [now Melaspileella proximella (Nyl.) Ertz & Diederich] USA: New Hampshire:Coos Co., Jefferson, 1883, Willey s. n. (US). Vermont: 1879, Pringle s. n. (US).

Melaspilea tribuloides (Tuck.) Müll. Arg. [now Melanographa tribuloides (Tuck.) Müll. Arg.] USA: Alabama: Mobile Co., Mobile, 1876, Curtis s. n. (US). Florida: Duval Co., Ft. George, Calkins s. n. (MICH); Seminole Co., Sanford, Rapp 2751 (US). Louisiana: Catahoula Parish, Sicily Island Wildlife Management Area, on Pyrenula (as Melanotheca) cruenta, Tucker 27467B (LSU); East Baton Rouge Parish, Forest Park, on Pyrenula cruenta, Tucker 9997 (NCU, SBBG); East Feliciana Parish, Idlewild Research Plantation, on Pyrenula (as Melanotheca), Tucker 18437B (MICH, MIN, MSC, OMA, SBBG); St. Tammany Parish, Fontainebleau State Park, on Pyrenula (as Melanotheca) cruenta, S. Tucker 18374 (SBBG). North Carolina: 1879, Curtis s. n. (US).

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# Appendix. PC-ORD Matrix of North American *Melaspilea* specimens examined including type material of *M. demissa* and *M. gibberulosa* (the latter from Europe)

Specimens are coded with the following scheme: collector's initials followed by the last three letters of the specimen barcode or, if not available, the collection year followed by herbarium acronym. Traits are categorized as either C (category) or Q (quantitative). Measurements are expressed as sample mean  $\pm$  SD with the sample size in parenthesis, but are analyzed using PC-ORD by the mean only.

	Characters*										
Specimens	C HABIT	C CONTLN	C ASCTYP	Q ASCLEN	C ASCEMR	C HYMINS	C PARAPH	C SPOSEP	Q SPOLEN	Q SPOWID	Region† C REGION
HW323FH	1	0	2	$0.65 \pm 0.26 \ (n=8)$	3	1	1	1	$19.4 \pm 1.5 \ (n=5)$	$8.2 \pm 0.8 \ (n=5)$	1
HW322FH	1	1	2	$0.70 \pm 0.17 \ (n=8)$	3	1	1	1	$20.4 \pm 1.7 \ (n = 5)$	$8.5 \pm 1.2 \ (n=5)$	1
HW321FH	1	0	2	$0.73 \pm 0.13 \ (n=8)$	3	1	2	1	$19.8 \pm 2.3 \ (n=7)$	$9.4 \pm 1.0 \ (n=7)$	1
HW318FH	1	0	2	$0.50 \pm 0.12 \ (n=8)$	3	1	2	1	$17.3 \pm 2.6 \ (n=8)$	$8.9 \pm 0.9 (n = 8)$	1
HW319FH	1	1	2	$0.65 \pm 0.16 \ (n=8)$	3	1	2	1	$19.0 \pm 1.9 \ (n=5)$	$8.5 \pm 1.2 \ (n=5)$	1
HW320FH	1	1	2	$0.65 \pm 0.20 \ (n=8)$	3	1	2	1	$21 \cdot 1 \pm 1 \cdot 5 \ (n = 5)$	$8.5 \pm 1.2 \ (n=5)$	1
TW163FH	1	0	2	$0.4 \pm 0.13 \ (n=8)$	3	1	2	1	$18.4 \pm 1.4 \ (n=5)$	$8 \cdot 3 \pm 0 \cdot 4 \ (n = 5)$	2
BF164FH	1	0	2	$0.40 \pm 0.08 \ (n=8)$	3	1	1	1	$14.8 \pm 0.8 \ (n=5)$	$5.8 \pm 0.9 \ (n=5)$	14
AN317FH	1	0	2	$0.68 \pm 0.15 \ (n=8)$	3	1	2	1	$18.0 \pm 1.5 \ (n=5)$	$9 \cdot 2 \pm 0 \cdot 9 \ (n = 5)$	1
TW162FH	1	0	2	$0.53 \pm 0.16 \ (n=8)$	3	1	2	1	$20.4 \pm 1.7 \ (n = 5)$	$8 \cdot 2 \pm 0 \cdot 8 \ (n = 5)$	2
HW969US	1	1	2	$0.74 \pm 0.21 \ (n=7)$	3	0	1	1	$19.8 \pm 1.8 \ (n=6)$	$8.5 \pm 1.5 \ (n=6)$	1
HW972US	1	1	2	$0.76 \pm 0.19 \ (n=7)$	3	1	1	1	$18.7 \pm 1.7 \ (n=5)$	$8 \cdot 2 \pm 0 \cdot 8 \ (n = 5)$	1
HW970US	1	0	2	$0.70 \pm 0.20 \ (n=7)$	3	1	1	1	$17.8 \pm 1.4 \ (n=6)$	$8.5 \pm 0.0 \ (n=6)$	1
HW974US	1	0	2	$0.80 \pm 0.32 \ (n=7)$	3	1	1	1	$19.8 \pm 0.9 \ (n=6)$	$8.8 \pm 0.7 \ (n=6)$	1
HW973US	1	0	2	$0.58 \pm 0.19 \ (n=8)$	3	1	1	1	$19.6 \pm 2.9 \ (n=4)$	$8 \cdot 1 \pm 1 \cdot 6 \ (n = 4)$	1
GP362NCU	1	0	2	$0.75 \pm 0.21$ (n = 6)	3	0	2	1	$17.9 \pm 2.9 (n = 5)$	$7.4 \pm 0.8 (n = 5)$	3
GP363NCU	1	1	2	$0.50 \pm 0.10 \ (n=5)$	3	0	1	1	$21.0 \pm 1.6 \ (n=8)$	$10.2 \pm 0.9 \ (n=8)$	3
GP364NCU	1	0	2	$1 \cdot 1 \pm 0 \cdot 5 \ (n = 7)$	3	0	2	1	$17.0 \pm 2.1 (n = 9)$	$7.7 \pm 0.9 (n = 9)$	3
GP377NCU	1	0	2 2	$0.46 \pm 0.09 \ (n=5)$	3	1	2	1	$17.2 \pm 1.8 (n = 8)$	$8.5 \pm 1.2$ (n = 8)	4
GP365NCU	1	1	2	$0.64 \pm 0.31 \ (n=7)$	3	0	2	1	$16.7 \pm 2.0 \ (n=6)$	$7.8 \pm 0.8 \ (n=6)$	3
GP366NCU	1	0	2	$0.73 \pm 0.21$ $(n = 7)$	3	1	2	1	$16.3 \pm 1.2 (n = 3)$	$7.3 \pm 1.3 (n = 3)$	3
GP375NCU	1	0	2	$0.42 \pm 0.12 \ (n=6)$	3	1	2	1	$18.4 \pm 1.6 \ (n = 10)$	$9.7 \pm 1.3 \ (n = 10)$	2
GP376NCU	1	0	2	0.40 (n = 1)	3	1	1	1	$19.8 \pm 1.7$ (n = 10)	$9.7 \pm 1.4 \ (n = 10)$	2
GP370NCU	1	0	2	$0.35 \pm 0.09 \ (n=8)$	3	1	1	1	$18.5 \pm 3.6 (n = 9)$	$8.9 \pm 1.3 (n = 9)$	3
GP371NCU	1	0	2	$0.54 \pm 0.26 (n = 7)$	3	0	1	1	$18.5 \pm 3.0 (n = 9)$	$9.5 \pm 1.3 (n = 9)$	3
GP372NCU	1	0	2	$0.45 \pm 0.13$ $(n = 4)$	3	0	1	1	$19.4 \pm 3.0 (n = 9)$	$9.3 \pm 2.1 \ (n=9)$	3
EP368NCU	1	0	2	$0.68 \pm 0.19 \ (n=6)$	3	1	1	1	$19.6 \pm 1.8 \ (n=6)$	$9.6 \pm 1.6 (n = 6)$	3
EP367NCU	1	0	2	$0.53 \pm 0.13 \ (n=4)$	3	0	1	1	$19.8 \pm 1.4 \ (n=6)$	$8 \cdot 8 \pm 0 \cdot 7 \ (n = 6)$	3
EP369NCU	1	0	2	$0.48 \pm 0.15 \ (n=5)$	3	0	1	1	$19.7 \pm 2.6 \ (n=5)$	$10.5 \pm 0.8 \ (n=5)$	3
ST381NCU	2	0	2	$0.33 \pm 0.13 \ (n=8)$	3	0	1	1	$13.1 \pm 1.5 \ (n=4)$	$7 \cdot 0 \pm 0 \cdot 4 \ (n = 4)$	9
SW052MSC	1	0	2	$0.25 \pm 0.07 (n = 2)$	3	0	1	1	$11.8 \pm 1.2$ $(n = 4)$	$5.8 \pm 0.8 (n = 4)$	6

#### Appendix. (Continued)

Specimens	Characters*										
	C HABIT	C CONTLN	C ASCTYP	Q ASCLEN	C ASCEMR	C HYMINS	C PARAPH	C SPOSEP	Q SPOLEN	Q SPOWID	Region† C REGION
LS511G	1	0	1	$0.64 \pm 0.21 \ (n=5)$	2	0	1	1	$15.0 \pm 1.7 \ (n=6)$	$6.5 \pm 0.7 \ (n=6)$	12
LS512G	1	0	1	$0.58 \pm -0.08 \ (n=5)$	2	0	1	1	$12.8 \pm 0.9 \ (n=6)$	$6.5 \pm 0.7 \ (n=6)$	12
AL1892US	1	1	1	$0.55 \pm 0.12$ (n = 8)	2	1	1	1	$16.8 \pm 1.0 \ (n=6)$	$8.5 \pm 0.3 (n=6)$	9
AL1895US	1	1	1	$0.58 \pm 0.09 (n = 8)$	2	1	1	1	$16 \cdot 1 \pm 2 \cdot 5 \ (n = 6)$	$8.5 \pm 0.3 (n=6)$	9
AL1896US	1	1	1	$0.58 \pm 0.15$ (n = 8)	2	1	1	1	$18.7 \pm 1.4 \ (n=4)$	$8.9 \pm 0.8 \ (n=4)$	9
ST1969US	1	0	1	$0.88 \pm 0.16$ (n = 8)	2	0	1	1	$23.0 \pm 1.7$ $(n = 4)$	$11.5 \pm 0.8 (n = 4)$	9
SR1909US	1	0	1	$1.18 \pm 0.26 \ (n=8)$	2	0	1	1	$22.5 \pm 2.6 \ (n=4)$	$11 \cdot 1 \pm 1 \cdot 0 \ (n = 4)$	10
BF1899US	1	0	1	$0.54 \pm 0.09 \ (n=8)$	3	1	1	1	$11.9 \pm 0.00 \ (n=3)$	$6.8 \pm 1.7 \ (n=3)$	8
ET1857US	1	0	1	$0.6 \pm 0.06 (n = 6)$	2	1	1	1	$16.2 \pm 1.0 \ (n=4)$	$7.7 \pm 1.0 \ (n=4)$	1
BF1894US	1	0	1	$0.56 \pm 0.10 \ (n=7)$	2	0	1	1	$17.8 \pm 1.0 \ (n=4)$	$8.5 \pm 0.0 \ (n=4)$	7
HK1921US	1	1	1	$2.08 \pm 0.38 \ (n=6)$	2	0	1	1	$22 \cdot 1 \pm 2 \cdot 4 \ (n = 4)$	$9.8 \pm 0.8 \ (n=4)$	11
SR1921US	1	0	1	$1.08 \pm -0.30$ (n = 8)	2	0	1	1	$17.4 \pm 0.8 (n = 4)$	$8.9 \pm 0.8 \ (n=4)$	10
L1895US1	1	1	2	$0.74 \pm 0.24 \ (n=8)$	3	0	1	1	$13.2 \pm 0.8 \ (n=4)$	$6.0 \pm 1.0 \ (n=4)$	9
GD1939US	1	0	2	$0.45 \pm 0.05 (n = 6)$	3	0	1	1	$19.1 \pm 1.6 (n = 4)$	$8 \cdot 1 \pm 0 \cdot 8 \ (n = 4)$	4
AL1891US	1	0	2	$0.42 \pm 0.42 (n = 5)$	3	0	1	1	$19.0 \pm 1.4 \ (n=2)$	$7.5 \pm 0.7(n-2)$	10
JE1886US	1	0	2	$0.56 \pm 0.14$ (n = 8)	3	1	1	1	$19.7 \pm 2.6 (n = 5)$	$9.9 \pm 0.8 (n = 5)$	5
AZ7992US	1	0	1	$0.51 \pm 0.11 \ (n=8)$	3	0	1	1	$13.6 \pm 1.4 \ (n=4)$	$6.8 \pm 0.0 \ (n=4)$	12
E1886US1	1	0	1	$0.57 \pm 0.10 \ (n=7)$	3	0	1	1	$16.9 \pm 1.0 \ (n=5)$	$7.7 \pm 0.9 \ (n=5)$	3
SR1914US	1	0	1	$1.19 \pm 0.3 \ (n=7)$	1	0	1	2	$22 \cdot 1 \pm 2 \cdot 4 \ (n = 4)$	$5.5 \pm 0.8 \ (n=4)$	10
AL1893US	1	0	2	$1.05 \pm 0.14$ (n = 8)	2	0	1	1	$20.0 \pm 1.6 (n = 4)$	$10.7 \pm 2.5 (n = 4)$	9
AL1898US	1	1	1	$1.34 \pm 0.35 (n = 8)$	2	0	1	1	$18.7 \pm 2.4 \ (n=4)$	$8.1 \pm 1.6 \ (n=4)$	9
ST1980US	1	0	1	$1.15 \pm 0.25 \ (n=8)$	2	0	1	1	$19.0 \pm 3.3 (n = 5)$	$9.9 \pm 1.4 \ (n=5)$	9
AL1894US	1	0	1	$0.88 \pm 0.41 \ (n=6)$	3	1	1	2	$32.3 \pm 0.0 \ (n=2)$	$6 \cdot 0 \pm 1 \cdot 2 \ (n = 2)$	9
CP1879US	1	0	1	$0.34 \pm 0.05 \ (n=7)$	3	0	1	1	$20.5 \pm 2.5 (n = 3)$	$10.5 \pm 4.8 \ (n=3)$	1
HW1883US	1	0	1	$0.25 \pm 0.06 \ (n=4)$	3	0	1	1	$14.6 \pm 2.3 \ (n=6)$	$6 \cdot 4 \pm 1 \cdot 6 \ (n = 6)$	1
SR1927US	2	0	2	$0.60 \pm 0.17 \ (n=7)$	3	0	1	1	$16 \cdot 2 \pm 1 \cdot 2 \ (n = 2)$	$8.5 \pm 0.0 \ (n=2)$	10
MC1879US	2	0	2	$0.50 \pm 0.14 \ (n=6)$	3	0	1	1	$17.5 \pm 1.6 \ (n = 6)$	$8 \cdot 2 \pm 1 \cdot 4 \ (n = 6)$	13
MC1876US	2	0	2	$0.47 \pm 0.16 \ (n=6)$	3	0	1	1	$17.1 \pm 2.6 \ (n = 8)$	$6.8 \pm 1.4 \ (n=8)$	10

\*Characters are as follows: HABIT = lichenized (1) or lichenicolous fungus (2), CONTLN = contact lines absent (0) or present (1), ASCTYP = ascomatal type (1 = arthonioid, 2 = opegraphoid), ASCLEN = ascomatal length or diameter (mm), ASCEMR = ascoma emergence (1 = immersed, 2 = erumpent, 3 = sessile), HYMINS = hymenium inspersion (0 = not inspersed), 1 = inspersed), PARAPH = paraphyses (1 = not thickened, 2 = thickened), SPORSEP = spore septation (1 = one-septate, 2 = multiseptate), SPOLEN = spore length ( $\mu$ m), SPOWID = spore width ( $\mu$ m), REGION = EPA Level III ecoregion.;

tEcoregions are numbered as follows: 1 = Northeastern Coastal Zone (Massachusetts), 2 = Southeastern Plains (South Carolina), 3 = Piedmont (North Carolina), 4 = Blue Ridge (Tennessee, Virginia), 5 = Ridge and Valley (Pennsylvania), 6 = Northern Lakes and Forests (Michigan), 7 = Driftless Area, 8 = Glaciated Plains (Minnesota), 9 = Mississippi Alluvial Plain (Louisiana), 10 = South Coastal Plain (Alabama, Florida), 11 = South Florida Coastal Plain (Florida), 12 = European Broadleaf Forest (Switzerland, Slovakia), 13 = Northeastern Highlands (New Hampshire, Vermont), 14 = Mid Atlantic Coastal Plain (North Carolina).

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