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Bacidia coprodes—resurrecting a misinterpreted species

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Abstract: *Bacidia coprodes* (Körb.) Lettau, until now treated as a synonym of *Bacidia trachona* (Ach.) Lettau, is resurrected. Morphological, chemical and ecological characteristics place this species close to *Toninia* in the *Ramalinaceae*, but we retain it in *Bacidia* because of uncertainties in the generic taxonomy of this family. *Bacidia coprodes* is fairly widespread on calcareous and enriched siliceous rock in Europe and eastern North America. In North America the species has also been known under the synonyms *Bacidia granosa* (Tuck.) Zahlbr. (basionym: *Lecidea granosa* Tuck.) and *Bacidia pammellii* (Fink) Zahlbr. (basionym: *Bilimbia pammellii* Fink). Morphological and chemical features, together with molecular data, suggest that *B. trachona* does not belong to *Bacidia*, but rather in the *Pilocarpaceae*.

Key words: *Bacidia*, *Bilimbia*, *Pilocarpaceae*, *Ramalinaceae*, *Toninia*

Introduction

The name *Bacidia trachona* (Ach.) Lettau has been used extensively, and for a long time, in a sense inconsistent with the type of the name. In fact, the name has been used for most saxicolous specimens of *Bacidia* s. lat. with three-septate ascospores and a dark hypothecium. The only unbiased description of true *B. trachona* that we are aware of is that provided by Coppins (1992). In an effort to clarify the taxonomy of the entities commonly included in *Bacidia trachona*, we came across the name *Bilimbia coprodes* Körb., described from calcareous rock in central Europe (Körber 1860). The type of this name agrees morphologically with the taxon most commonly misidentified as '*Bacidia trachona*'.

Bacidia trachona was described as *Verrucaria trachona* Ach. by Acharius (1803). The type material in H-ACH consists of thallus with abundant pycnidia but no apothecia, the condition in which this species is mostly found in northern Europe. Except for a few citations of this description (as *Verrucaria trachona* or *Thrombium trachonum* (Ach.) Wallr.), the name seems not to have been much in use until it was taken up by Körber (1854–1855), Nylander (1855), Trevisan (1856), and Nylander (1864) as *Biatora trachona* (Ach.) Körb., *Lecidea vernalis* var. *trachona* (Ach.) Nyl., *Bilimbia trachona* (Ach.) Trev., and *Lecidea trachona* (Ach.) Nyl., respectively. Körber and Nylander cited material collected by Flotow and distributed in Zwackh-Holzhausen's *Lichenes exsiccati* nos. 104 and 117 (published 1851 and 1852, respectively). However, judging from the descriptions provided by these authors, their concept of the species is inconsistent with the type as well as Flotow's material, which corresponds to *B. trachona* s. str. Trevisan (1856), unfortunately, merely listed the name without further details. Körber (1860) formally described *Bilimbia coprodes* collected from calcareous rocks in Germany; although the name had earlier been mentioned briefly by Arnold (1858) in a personal comment provided by Körber. *Bilimbia coprodes* was included by Lettau (1912) in the genus *Bacidia* as *B. coprodes*

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(Körb.) Lettau, following the generic concept of *Bacidia* introduced by Zahlbruckner (1905). This species, like true *B. trachona* when fertile (which was probably unknown to Körber), has three-septate ascospores and a dark hypothecium. It is difficult to trace exactly how the wide concept of *B. trachona* evolved, as the inclusion of *Bilimbia coprodes* was often implicit rather than explicit in taxonomic treatments. The inclusion of Flotow's material in *B. trachona* by Körber (1854–1855) and Nylander (1855) as well as the descriptions provided by these authors probably played an important role in the arising confusion. In addition, the correct description of superficially similar apothecia in true *Bacidia trachona* (as *Lecidea trachona* (Ach.) Nyl.) from the Channel Islands by Leighton (1871) may have confirmed the wide concept of this species applied by European authors. Vainio (1922) was, to our knowledge, the first to explicitly list *Bilimbia coprodes* as a synonym of *Bacidia trachona* (as *Bilimbia trachona*). Zahlbruckner (1926–1927, 1932), however, maintained *Bacidia coprodes* as an independent species. From Lettau (1944) onwards, *B. coprodes* has invariably been treated as a synonym of *Bacidia trachona*.

We propose to resurrect *Bacidia coprodes* (Körb.) Lettau, because it is morphologically and chemically distinct and only distantly related to true *B. trachona*. *Bacidia coprodes* is certainly not congeneric with the type of *Bacidia*, *B. rosella* (Pers.) De Not., but we tentatively maintain it in this genus owing to a lack of credible alternatives.

Material and Methods

Specimens provided by herbaria, AAS, ASU, BCN, BG, C, FH, G, LD, M, MA, MU, TSB, UPS, and W, have been examined macroscopically and microscopically. Morphological characteristics were observed on hand-cut sections mounted in distilled water, 10% KOH (K), 33% HNO_3 (N), and lactophenol cotton blue. The nomenclature of apothecial pigments follows Meyer & Printzen (2000). The amyloid reaction of the ascus was studied in the Lugol's solution after pretreatment with K.

The Species

Bacidia coprodes (Körb.) Lettau

Hedwigia **52:** 132 (1912).—*Bilimbia coprodes* Körb., *Par. Lich.*: 166 (1860).—*Lecidea trachona* (Ach.) Nyl. var. *coprodes* (Körb.) Stizenb., *Nova Acta Acad. Leopold.-Carol.* **34** (2)**:** 60 (1867).—*Lecidea coprodes* (Körb.) Vain., *Meddel. Soc. Fauna Flora Fenn.* **10:** 12 (1883).—*Bilimbia coprodes* var. *normalis* Th. Fr., *Lichenogr. Scandin.* **1:** 385 (1874).—*Bilimbia trachona* (Ach.) Trevis. f. *coprodes* (Körb.) Vain., *Acta Soc. Faun. Flor. Fennic.* **53** (1)**:** 233 (1922).—*B. trachona* (Ach.) Lettau f. *coprodes* (Körb.) Lettau, *Feddes Repertorium* **54** (1)**:** 110 (1944); type: Germany, Bayern, Oberbayern, LKr. Eichstätt, 48°52′N, 11°12′E, auf umherliegenden Kalksteinen in der Waldschlucht des Rosenthales bei Eichstätt, 6 xii 1866, *F. Arnold* 333. (M 91507!–lectotype; LD!, W!—isolectotypes).

Patellaria salevensis Müll. Arg., *Mém. Soc. Phys. Hist. Nat. Genève* **16:** 400 (1862).—*Gyalecta salevensis* (Müll. Arg.) Oliv., *Bull. Géogr. Bot.* **21:** 192 (1911).—*Bacidia salevensis* (Müll. Arg.) Zahlbr., *Cat. Lich. Univ.* **4:** 145 (1926); type: Switzerland, "sur un bloc calcaire le long d'un ruisseau qui descend du Salève vers le village de Le Châble", J. A. P. Hepp 580 (G 00053997!—holotype).

Lecidea granosa Tuck., *Proc. Am. Acad. Sci.* **5:** 420 (1862).—*Toninia granosa* (Tuck.) de Lesd., *Bryologist* **24:** 68 (1921).—*Bacidia granosa* (Tuck.) Zahlbr., *Cat. Lich. Univ.* **4:** 203 (1927).—*Bilimbia granosa* (Tuck.) Fink, *Lichen Flora of the United States*: 225 (1935); type: U.S.A., South Carolina, Santee Canal, on brick walls, *H. W. Ravenel* 191 (FH-TUCK!—lectotype).

Bilimbia pammellii Fink in Hendrick, *Mycologia* **26:** 156 (1934).—*Bacidia pammellii* (Fink) Zahlbr., *Cat. Lich. Univ.* **10:** 365 (1939); type: U.S.A., Iowa, The Ledges, Boone Co., 1903, *B. Fink & L. M. Koch* 1407 (MU-L 1397!—lectotype; MICH—isolectotype).

(Figs 1–3)

Thallus crustose, greyish green to pale brownish green, at first granular to warted, then areolate to continuous; with finely granular to warted surface; K ± yellowish, KC −, C −, P −.

Apothecia sessile, pale reddish brown to dark brown or black, (0·15–)0·20–0·75 mm diam.; margin darker than the disc, at first thick, later becoming excluded; disc flat or slightly convex, later becoming convex. *Proper exciple* 40–80 µm thick; prosoplectenchymatous, composed of radiating, branched and anastomosed hyphae with relatively thick gelatinous walls and cell lumina slightly constricted at the septa; innermost cell lumina rectangular *c.* 8 × 2·5 µm, subterminal cells rectangular

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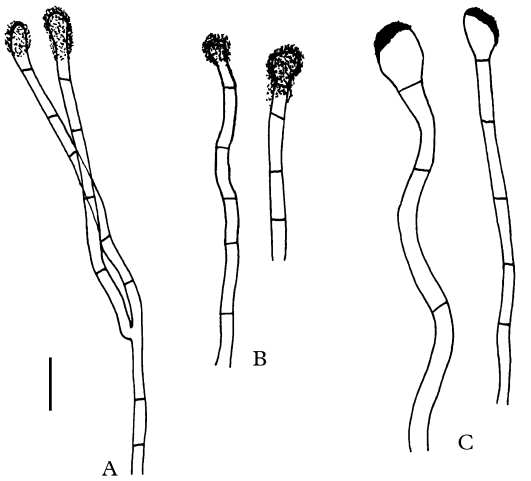


FIG. 1. Paraphyses. A, *Bacidia coprodes*, Norway; B, *B. coprodes*, Italy; C, *Toninia mesoidea*; D, conidiogenous cells and bacilliform conidia. Scale=8 μm.

4 × 2 μm, apical cells globose, 3–5 μm wide; lateral part dominated by a greyish to blackish green pigment (Bagliettoana-green, reacting K+ green; N+ violet, with the deposition of blue-violet crystals that turn green with K, and dissolve after successive applications of HCl and K), gradually merging into the medulla, which is dominated by a reddish brown pigment (Laurocerasi-brown, reacting K+ purplish red, N − and C+ intensifying red colour and finally bleaching). *Hymenium* 45–60 μm tall, colourless below, without distinct epithecium but upper part with varying amounts of the green pigment as in the excipulum. *Hypothecium* paraplectenchymatous, pale greenish to reddish brown, *c.* 10 μm thick. *Paraphyses* straight, simple or rarely forked, not or slightly anastomosed; upper cells globose, up to 2–3(–4) μm wide (Fig. 1A & B), with thin gelatinous cap surrounding the upper cells that usually contain green pigment. *Asci* clavate, 8-spored, 35–45 × 7–12 μm; *Bacidia*-type, sometimes with I+ darker blue area surrounding the conical I − axial mass (*Biatora*-type, Hafellner 1984). *Ascospores* colourless, straight, narrowly ellipsoid to fusiform, slightly asymmetrical and tapering towards one end, (1–)3-septate, 11–20(–23) × 2·4–4·3(–5) μm, without perispore or ornamentation (Fig. 2A).

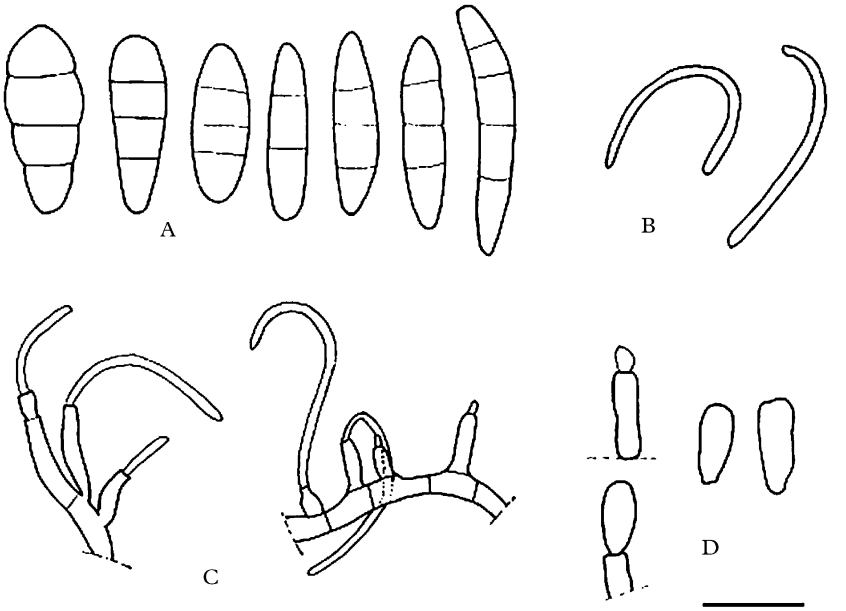


FIG. 2. *Bacidia coprodes*. A, ascospores; B, filiform conidia; C, conidiophores, conidiogenous cells and filiform conidia; D, conidiogenous cells and bacilliform conidia. Scale=8 μm.

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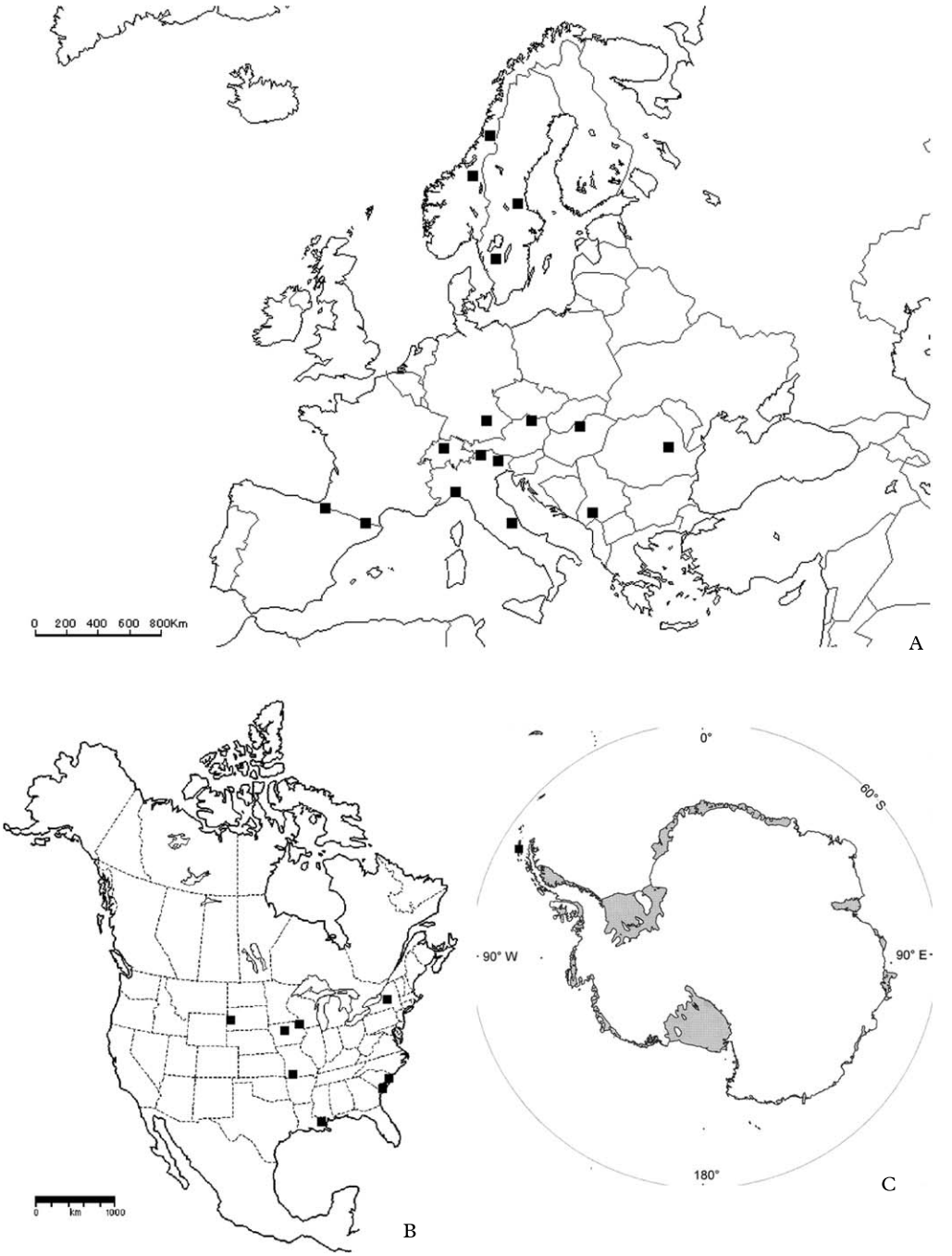


FIG. 3. World distribution of *Bacidia coprodes*. A, Europe; B, North America; C, Antarctica.

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Pycnidia usually present, immersed in the thallus except for a dark brown to blackish ostiole, 50–100(–150) µm diam., unilocular; wall paraplectenchymatous, colourless, on the inside covered by colourless, irregularly rectangular conidiophorous cells, 4–6 × 1–2 µm, terminated by colourless, cylindrical to flask-shaped conidiogenous cells, 4–8 × 1–2 µm. *Conidia* acrogenous, of two types: (1) filiform, curved to sigmoid, non-septate, 15–20 × *c.* 1 µm (Fig. 2B & C), (2) bacilliform to drop-shaped, non-septate, 5–8 × 2–2.5 µm (Fig. 2D).

Chemistry. No secondary substances have been detected by TLC.

Distribution and ecology. *Bacidia coprodes* is a saxicolous species, growing primarily on calcareous rock, but it has also been found on enriched siliceous rock. The species occurs from sea level to the alpine belt (0–2200 m a.s.l.). The known distribution includes Europe from the Mediterranean region to Scandinavia (Fig. 3A), eastern and central North America (Fig. 3B), as well as Antarctica (South Shetland Islands) (Fig. 3C). From Antarctica, it has previously been reported as '*Bacidia* sp. A' by Øvstedal & Lewis Smith (2001: 102).

Discussion

Bacidia granosa (Tuck.) Zahlbr. (with the synonym *B. pammellii* (Fink in Hedrick) Zahlbr.) was tentatively treated as a different species from *B. coprodes*, on account of 'pycnidial characters', namely the conidial types described above by Ekman (1996). However, closer examination has revealed that the two types of conidia, although never mixed in the same thallus, occur in different individuals in close geographic proximity without other morphological differences. Type 1 conidia (Fig. 2B & C) are the most widespread, whereas we have observed type 2 conidia (Fig. 2D) only in some European samples.

Bacidia coprodes is distinguished from other species currently included in *Bacidia* by a combination of a relatively thick, continuous to cracked thallus, a dark reddish brown inner exciple and hypothecium, straight and narrowly ellipsoid to fusiform ascospores, and in being restricted to rock habitats. It is similar to other species currently included in *Bacidia*, viz. *B. auerswaldii* (Hepp ex Stizenb.) Mig., *B. circumspecta* (Nyl. ex Vain.) Malme, *B. igniarii* (Nyl.) Oksner and *B. subincompta* (Nyl.) Arnold, which are similar in spore shape and apothecial pigments but are restricted to bark habitats. *Bacidia coprodes* is also similar to several species currently treated in *Toninia*, most notably species of group 3 of Timdal (1992: 28–29), and keys out as *T. mesoidea* (Nyl.) Zahlbr. in Timdal's key. However, *T. mesoidea* differs from *B. coprodes* in lacking green pigment in the exciple and in having wider ascospores. Furthermore, *B. coprodes* and the corticolous species mentioned above differ from most members of Timdal's group 3 by the presence of a sharply delimited pigmented cap surrounding the apical cell of the paraphyses in the *Toninia* sp. (Fig. 1). The placement of *B. coprodes* in *Bacidia* is tentative. *Bacidia* and *Toninia*, as currently accepted, are probably both polyphyletic (Ekman 2001). The species of *Bacidia* mentioned above are likely to be more closely related to taxa in *Toninia* than in *Bacidia* s. str., and we could have chosen instead to include *B. coprodes* in *Toninia*. However, the taxonomy in *Bacidia*, *Toninia*, and related genera is currently in a very unstable state and significant changes in generic delimitations are expected. Therefore, to ensure that we do not impose unnecessary nomenclatural change by transferring the species to another genus, the delimitation of which might change soon, we have chosen to keep the species in *Bacidia* for the time being.

Bacidia coprodes differs from *Bacidia trachona* in ascus structure, paraphyses, pycnidia, conidia, chemistry, and ecology. The two species are not at all similar, except at a very superficial level. The asci of *B. coprodes* are *Bacidia*-type, whereas the asci of *B. trachona* are *Byssoloma*-type (*sensu* Hafellner 1984), with a dark tube structure in the tholus. The paraphyses of *B. coprodes* are simple, not or only slightly anastomosed,

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whereas in *B. trachona* they are branched and anastomosing. The pycnidia of *B. coprodes* are small, immersed, and always globose with a narrow ostiole. The pycnidia of *B. trachona*, on the other hand, are big and sessile. They are at first closed and globose, but later open and gape widely with the conidial mass exposed and looking like a drop of liquid, with a byssoid structure surrounding the insertion area with the thallus. Two kinds of conidia are known in *B. coprodes*, acicular, curved to sigmoid and bacilliform. *Bacidia trachona* has only bacilliform conidia, which are smaller than the ones found in *B. coprodes*. The species differ chemically: *B. trachona* containing argopsin, reacting P+orange-red, whereas no substances have been found in *B. coprodes* (despite the fact that the thallus sometimes reacts weakly dull yellowish with KOH). While *B. coprodes* belongs in the *Ramalinaceae sensu* Ekman (2001), morphological and chemical features, as well as molecular data, place *B. trachona* in the *Pilocarpaceae* (Andersen & Ekman 2005). The morphology and delimitation of this family have been discussed by Lücking *et al.* (1994) and Lücking (1999).

Selected specimens examined. **Antarctica:** *South Shetland Islands*: Livingston Island, Byers Peninsula, between Chester Cone and Sealers Hill, 62.63°S, 61.07°W, 25–50 m, on small stones scattered over sparsely vegetated black ash plain, 1981, *R. I. L. Smith* 3836 (AAS).—**Austria:** *Niederösterreich*: Ad saxa umbrosa calcarea in monte Sonntagberg prope Rosenau, *P. P. Strasser* (LD); an kalktrofen Sandstein in der Grater von Kronstein nach Reckwinkl, iv 1891, unknown collector (W); auf Kalk in Wassergespreng nächst Kaltenleutgeben, iv 1891, unknown collector (W).—**Germany:** *Baden-Württemberg*: an Sandsteinfelsen bei Heidelberg, *W. Ahles* (BG). *Bayern*: Eichstätt, Kalksteine im Laubwalde des Rosenthales bei Eichstätt, 1867, *F. Arnold* (LD); Eichstätt, Kalksteine im Laubwalde um Wege zum Bahnhofe bei Eichstätt, xi 1873, *F. Arnold* (LD); Oberbayern, LKr. Eichstätt, 48°52′N, 11°12′E, Kalkstein im Rosenthales bei Eichstätt, xii 1875, *F. Arnold* (M).—**Hungary:** Sáros, Singlércom, supra saxa calcarea, 1879, *Lojka* (W).—**Italy:** *Abruzzi*: prov. L'Aquila, Gran Sasso, above Rifugio Doca degli Abruzzi, alpine veg., limestone/dolomite, 2200 m, 9 viii 1996, *P. L. Nimis & M. Tretiach* (TSB). *Alto Friuli*: presso Bueris (Udine), 250 m, su vecchio muretto d'arenaria, 10 xi 1983, *P. L. Nimis* (TSB). *Liguria*: Quarto (Genova), infra Montem Jasce ad immam maceram, herbis tectam, 1937, *C. Sbarbaro* (BCN, UPS). *Veneto*: auf Kalkfelsen am Rohrmooser Back, auf Dolomites am südlichen Abhang aus Sergschrofens (W).—**Norway:** *Nordland*: Hattfjelldal, lower part of valley Elsdal, near river Elsvasselva, along tributary creek, *c.* 290 m, on humid rock, 1988, *A. Botnen* 1828 (BG). *Sør-Trøndelag*: Roeros, Skaarhammerdal, 7 viii 1912, *E. P. Vrang* (LD).—**Romania:** Annos Doppe bei Sinaia Sauslein, 1897, *Loillesberger* (W).—**Serbia and Montenegro:** *Montenegro*: in the mountain pass Čakor, W of Peć, 1850 m, 8 vii 1979, *S. Svane* (C).—**Spain:** *Girona*: Ripollès, Vall de Núria, Fontalba, 31TDG29, calcària compacta, 2100–2200 m, 18 vii 1986, *P. Navarro-Rosinés* (BCN). *Navarra*: Isaba, Macizo de Añelarra, Larra, 30TXN7857, 2000 m, cueva cerca del Anie, *J. Etayo* (MA).—**Sweden:** *Närke*: Örebro, Blomskog, S. of Ängebäck, on a rock wall in shade, 7 ix 1969, *S. W. Sundell* (LD). *Dalarna*: Boda, Styggforsen, 1880, *P. G. Theorin* (LD).—**United States of America:** *Iowa*: Fayette, on shaded calcareous rocks, 3 xii 1895, *B. Fink* [Cummings, Williams & Seymour, *North American Lichens* no. 245] (LD). *Louisiana*: graveyard in New Orleans, 1851, *Hale* (FH-TUCK). *Missouri*: Taney County, Mark Twain Nat. For., Hercules Glades, 1 mile north of Persimmon Hollow, on south-west facing slope with patchy open calcareous rock outcrops and juniper, oak, hickory and persimmon, 1991, *C. M. Wetmore* [68454] (LD). *New York*: Jamesville, 1870, *H. Willey* (FH-TUCK). *South Carolina*: Charleston, brick walls, 1853, *H. W. Ravenel* (FH-TUCK); on mortar, *H. W. Ravenel* (FH-TUCK). *South Dakota*: Black Hills, Lawrence County, near Bridalveil Falls in Spearfish Canyon (5 miles south of Spearfish), in deeply shaded east-west gulch, 4300 ft, 1960, *C. M. Wetmore* [9377A] (LD).

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