Phytotaxa 191 (1): 066–080
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.191.1.4

The *Bacidia coprodes* group (Ramalinaceae, Lecanoromycetes, Ascomycota), with special reference to the species in Europe and North America

STEFAN EKMAN[1]
[1] *Museum of Evolution, Uppsala University, Norbyvägen 16, SE-75236 Uppsala, Sweden. Email: stefan.ekman@em.uu.se*

Abstract

This paper aims to clarify taxonomy and nomenclature of the lichen *Bacidia coprodes* and its closest relatives in Europe and North America. *Bacidia coprodes* as treated in recent works was found to consist of three distinct species in Europe and North America, the correct names of which are *B. coprodes* (*s. str.*), *B. notarisiana*, and *B. granosa*. In addition, a fourth species, *B. inornata* (Nyl.) Blomb. & Forssell, was found to be closely related to this group of lichens and is also treated here. The four species can be separated by apothecial and pycnidial pigmentation as well as conidium shape and size. They are closely related to species currently treated in *Bacidia*, *Toninia*, or *Arthrosporum*. Six basionyms, viz. *Bilimbia coprodes*, *Patellaria salevensis*, *Bilimbia subtrachona*, *Lecidea chytrina*, *L. chytrina* var. *hormospora*, and *L. inornata*, are lectotypified. Detailed descriptions and a determination key are provided.

Key words: *Toninia*, *Bacidia trachona*, *Bacidia subcoprodes*, *Bacidia chrysocolla*, *Bacidia clavigera*, *Bilimbia intercedens*, *Bacidia verecundula*, *Catillaria aphana*, *Fellhaneropsis*.

Introduction

When Körber first described *Bilimbia coprodes* for a crustose lichen with black apothecia, brown hypothecium, green epihymenium, and 3-septate ascospores (Arnold 1858), he also noted the remarkable similarity with *B. notarisiana* A. Massal., which had been validly described a few years earlier (Massalongo 1855). In a later treatment, Körber provided a more detailed morphological assessment of *B. coprodes* and clearly distinguished between this lichen and *Biatora trachona* (Ach.) Körb. (originally described as *Verrucaria trachona* Ach.), another lichen with superficially similar morphological characteristics (Körber 1860). Although *B. trachona* always seems to form conspicuous pycnidia, it seldom produces apothecia. However, rare observations of apothecia (e.g., Körber 1855; Zwackh-Holzhausen 1883; Arnold 1884) seem to have caused confusion and led Stizenberger (1868) to unite the two species under the name *Lecidea trachona* (Ach.) Nyl. This collective treatment was followed by most authors for a very long period of time, one notable exception being Lettau (1912), who listed them as separate species and also transferred them to *Bacidia* in accordance with the artificial generic circumscription suggested by Zahlbruckner (1905). *Bacidia coprodes* consequently fell into disuse as a mere synonym of *B. trachona* until Llop & Ekman (2007) pointed out the distinction between them and that they even belong in different families, *B. trachona* in the Pilocarpaceae and *B. coprodes* in the Ramalinaceae. Meanwhile, several additional names of lichens related to *Bacidia coprodes* were published, starting with *Patellaria salevensis* (Müller Argoviensis 1862), soon synonymized with *Lecidea trachona* by Stizenberger (1868), and ending with *Bilimbia pammellii* (Hedrick 1934).

Although *Bacidia coprodes* was recently resurrected and discussed by Llop & Ekman (2007), that treatment did not address the full extent of the taxonomical challenges in the group and was fraught with nomenclatural shortcomings that need attention. The Antarctic material was later investigated by Olech & Czarnota (2009), who recognized two species, *B. subcoprodes* Olech & Czarnota and *B. chrysocolla* Olech *et al.* The purpose of this paper is to further clarify taxonomy and nomenclature of the European and North American members of the *Bacidia coprodes* group and discuss their relationships.

 Accepted by Thorsten Lumbsch: 26 Nov. 2014; published: 30 Dec. 2014

Material and Methods

This study is primarily based on material in the following herbaria: C, E, LD, MA, MSC, TSB, and UPS. In addition, I have examined type material in FH-TUCK, G, H-NYL, L, M, MICH, MU, S, US, VER, W, and ZT. Microscopic characters were investigated either in a 10% aqueous solution of KOH (ascospores, paraphyses) or in pure water (all other characters). Colour reactions of pigments and crystal solubility were observed in K (a 10% aqueous solution of KOH) and N (a 50% aqueous solution of HNO_3). Measurements of quantitative characters are given either as 'minimum value–maximum value' or 'minimum value–arithmetic mean value–maximum value (s= sample standard deviation, N= sample size)'. Lichen substances were screened using High Performance Thin Layer Chromatography according to Arup *et al.* (1993).

I follow the recommendations of McNeill (2014) concerning the indication of holotypes. When it remains unclear whether a specimen should be considered a holotype or just one among several syntypes (the locations of which may currently be unknown), and lectotypification on the available specimen seems premature, such a specimen is simply referred to as a 'type'.

Results

Bacidia coprodes as treated by Llop & Ekman (2007) was found to consist of three distinct species in Europe and North America, the correct names of which are *B. coprodes* (Körb.) Lettau, *B. notarisiana* (A. Massal.) Zahlbr., and *B. granosa* (Tuck.) Zahlbr. In addition, a fourth species, *B. inornata* (Nyl.) Blomb. & Forssell, was found to be closely related to this group of lichens and is treated here. The pigmentation of the proper exciple, hypothecium, hymenium, shape and size of ascospores, pigmentation of the pycnidial wall, and shape and size of the conidia were found to be essential characters for distinguishing among species. Two different and omnipresent pigments seem to be present in the apothecia and pycnidia of the *B. coprodes* group, one greenish (K+ intensifying, N+ purple with the deposition of blue crystals) and one reddish brown (K+ purplish, N+ orange-red) pigment. In addition, an orange-brown (K+ intensifying, N-) pigment is (at least sometimes) present in the hypothecium of *B. notarisiana* and *B. granosa*. These three pigments correspond, respectively, to Bagliettoana-green and Laurocerasi-brown of Meyer & Printzen (2000), and Rubella-orange of Ekman (1996). The latter was included in Arceutina-yellow by Meyer & Printzen (2000).

Discussion

None of the four species treated here belong to *Bacidia s. str.* (the type of which is *B. rosella* (Pers.) De Not.), but are instead closely related to other species currently treated in *Bacidia* (e.g., *B. bagliettoana* (A. Massal. & De Not.) Jatta, *B. illudens* (Nyl.) H. Olivier, *B. subincompta* (Nyl.) Arnold), in *Toninia* (e.g. *T. aromatica* (Sm.) A. Massal., *T. coelestina* (Anzi) Vězda, *T. plumbina* (Anzi) Hafellner & Timdal, *T. verrucarioides* (Nyl.) Timdal), or in *Arthrosporum* (with its single species *A. populorum* A. Massal.) (Ekman 2001). A comprehensive phylogenetic investigation of the Ramalinaceae is needed, however, before the currently used circumscriptions of *Bacidia* and *Toninia* (Timdal 1991, Ekman 1996) can be finally abandoned.

Apart from the four species treated here, the *Bacidia coprodes* group also includes *B. subcoprodes* Olech & Czarnota and *B. chrysocolla* Olech *et al.*, both of which were described from the Antarctica (Olech & Czarnota 2009). I did not investigate the single Antarctic specimen of '*B. coprodes*' listed by Llop & Ekman (2007). I did, however, examine three specimens listed as '*Bacidia trachona*' by Øvstedal (1986) and '*Bacidia* sp. A' by Øvstedal & Lewis Smith (2001), which were found to belong to *Bacidia subcoprodes* Olech & Czarnota (UPS L-016062, L-016063, and L-016064). The latter name is illegitimate, being a younger homonym of *B. subcoprodes* (de Lesd.) Zahlbr., a combination based on *Bilimbia subcoprodes* de Lesd. in Crozals (1924). *B. subcoprodes* Olech & Czarnota differs from the species treated here in having a finely granular thallus, apothecia that become convex and often tuberculate in early stages of development, a thin proper exciple that is often poorly pigmented in the outer parts, a thin hypothecium that is more or less homogeneously red-brown, and pycnidia that consistently produce filiform and curved conidia. *B. chrysocolla* is said to differ from all species treated here in having more or less curved ascospores that are commonly 5-septate. I have not seen material of that species.

Taxonomy

Bacidia coprodes (Körb.) Lettau (1912: 132) (Fig. 1, 4A–C)

Bilimbia coprodes Körber in Arnold (1858: 503). *Lecidea trachona* (Ach.) Nyl. var. *coprodes* (Körb.) Stizenberger (1868: 60). *Lecidea coprodes* (Körb.) Vainio (1883: 12). Type: GERMANY. Bayern: "Ober Wasserzell" [= short for "oberhalb Wasserzell"], 1857, *F. Arnold 652* (lectotype, designated here: M 0157923!; isolectotypes: L 0938376!, UPS L-649434!, UPS L-649435!).

Patellaria salevensis Müller Argoviensis (1862: 400). *Gyalecta salevensis* (Müll. Arg.) Olivier (1911: 192). *Bacidia salevensis* (Müll. Arg.) Zahlbruckner (1926a: 145). *Bilimbia salevensis* (Müll. Arg.) M. Choisy (1953: 177). Type: FRANCE. Rhône-Alpes: Haute-Savoie, ''Längs des Baches oberhalb Les Châbles gegen den Fuss des Piton", 6 June 1856, *J. A. P. Hepp* (lectotype, designated here: G 00053997!; isolectotype: BM 000731134).

Bilimbia subtrachona Arnold (1870: 122). *Bacidia subtrachona* (Arnold) Lettau (1912: 133). Type: AUSTRIA. Tirol: "Dolomit des grossen Rettenstein bei Kitzbühel", 2 August 1869, *F. Arnold* (lectotype, designated here: M 0156514!; isolectotype: M 0012391!).

Lecidea chytrina Stizenberger (1868: 56). *Bilimbia chytrina* (Stizenb.) Arnold (1869: 643). *Bacidia chytrina* (Stizenb.) Zahlbruckner (1926a: 105). Type: GERMANY. Bayern: "Nebelhorn in Allgäu", undated, *H. Rehm* (lectotype, designated here: S L4898!).

Lecidea chytrina var. *hormospora* Stizenberger (1868: 57). *Bilimbia hormospora* (Stizenb.) Arnold (1884: 575). *Bacidia hormospora* (Stizenb.) Lettau (1912: 132). Type: GERMANY. Bayern: "Kalkstein im Rosenthal bei Eichstätt", 27 April 1866, *F. Arnold* (lectotype, designated here: ZT Myc-3656!).

Biatorina seposita Th. Fries (1867: 151). *Bilimbia coprodes* var. *seposita* (Th. Fr.) Th. Fries (1874: 385). *Bacidia coprodes* var. *seposita* (Th. Fr.) Zahlbruckner (1926a: 108). *Bacidia trachona* var. *seposita* (Th. Fr.) H. Magnusson (1945: 312). Type: NORWAY. Troms: "Tromsöe", 17 June 1857, *T. M. Fries* (holotype: UPS L-138582!).

Nomenclature:—Both the name and the diagnosis of *Bilimbia coprodes* were ascribed to Körber by Arnold (1858), the diagnosis being taken directly (with citation marks) from a letter from Körber to Arnold dated 28 Aug 1857. Therefore, the correct author citation is *Bilimbia coprodes* Körber in Arnold (ICN Art. 46.2). The attempt to lectotypify *B. coprodes* by Llop & Ekman (2007) was invalid, as the selected specimen (Arnold, Lich. exs. 333 in M) is not part of the original material, being collected several years after the publication of the name. The lectotype was selected here from among the duplicates of the gathering numbered "652" by Arnold, this number being explicitly cited in the protologue ("oberhalb Wasserzell (652 !)").

The original material of *Biatorina seposita* Th. Fr. consists of a single specimen in UPS, which is considered here as the holotype (ICN Art. 9.N.1). This specimen also bears an annotation by Stizenberger, the wording of which (translated into Swedish) was partially used by Fries in the discussion on relationships with other taxa. A second specimen of *B. coprodes* (cited below) from the type locality of *Biatorina seposita* was collected by Fries in 1864 (i.e., prior to the publication of the name in 1867) and was annotated by him as "*Bilimbia coprode*s Körb. α", bearing no trace of having been associated with the name *Biatorina seposita*.

Thallus crustose, thin, pale green to grey-green to brownish green, finely areolate with warted areoles to more or less granular (particularly when overgrowing bryophytes). Granules, when present, 0.06–0.25 mm diam. *Prothallus* lacking or thin, arachnoid, white (between discrete granules).

Apothecia lecideine, 0.3–0.5–1.2 mm diam. (s=0.2, N=70), rounded to irregularly lobed, at first flat, becoming more or less convex with age, rarely with thin whitish pruina on margin or disc. *Disc* dark purplish brown to black. *Margin* concolorous with disc, often shiny, distinct, slightly raised above disc in young apothecia, soon level with disc, becoming excluded in convex apothecia.

Proper exciple 47–78 µm thick, usually without crystals but pruinose apothecia sometimes with internal, radiating clusters of small crystals that dissolve in N but not K, composed of radiating, mainly dichotomously branched hyphae with thick gelatinous walls and cell lumina not or only slightly constricted at septa; cell lumina 7–12 × 1.5–3 µm in inner part of exciple, gradually wider towards edge, terminal cells up to 5 µm wide; laterally red-brown to greenish black, containing a mixture of a red-brown (K+ purplish, N+ orange-red) and a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals), rim sometimes paler than inner exciple. *Hypothecium* in upper part dark red-brown to greenish black (with a red-brown, K+ purplish and N+ orange-red, and sometimes also a green, K+ intensifying green and N+ purple pigment), concolorous with upper part of exciple, lower part of hymenium gradually merging into paler medulla (visible at least in thin sections). *Hymenium* 50–58–64 µm tall (s=5, N=15),

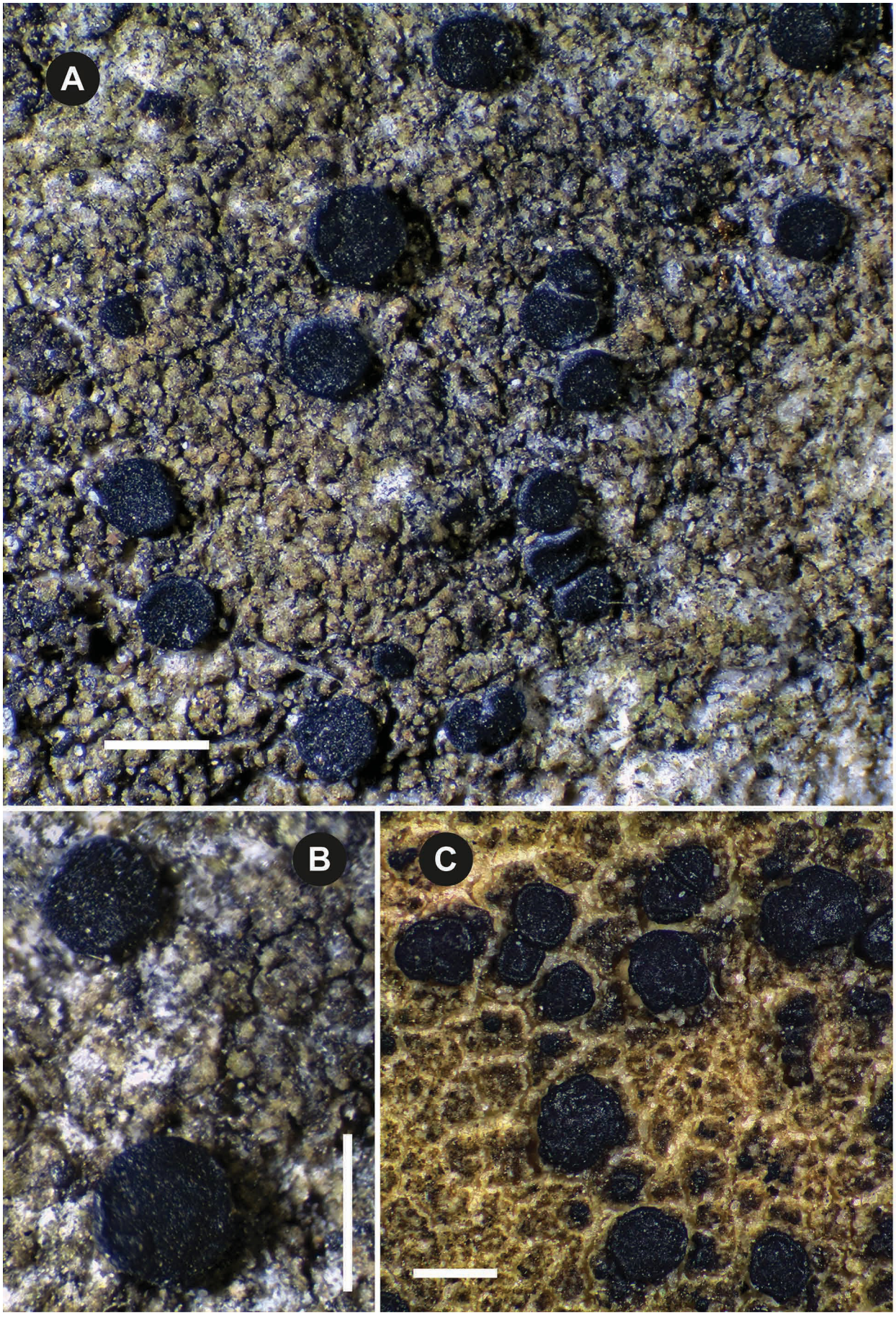

FIGURE 1. *Bacidia coprodes*, thalli with apothecia. **A, B.** Sweden (UPS L-647807). **C.** Sweden (UPS L-103910).—Scales = 0.5 mm.

colourless below, upper part with varying amounts of green pigment, sometimes as a distinct epihymenial layer, sometimes diffusely and unevenly dispersed in upper part. *Paraphyses* abundant, 1.5–2.0–2.8 µm wide in mid-hymenium (s=0.3, N=27), unbranched or sparingly branched in upper part, infrequently anastomosed; apices ± clavate or some not thickened at all, 2.4–3.5–4.9 µm wide (s=0.7, N=48), with or without surrounding gelatinous cap with green pigment. *Asci* clavate, 8-spored, *Bacidia*-type *sensu* Hafellner (1984). *Ascospores* colourless, without perispore or ornamentation, straight or slightly curved, bacilliform or narrowly ellipsoid, sometimes slightly tapering towards one end, with blunt ends, 10–13–20 µm long (s=2, N=40), 2.5–3.1–4.4 µm wide (s=0.4, N=39), with 3 (or exceptionally with 5) septa at maturity.

Pycnidia often present, semi-immersed in thallus except for a dark brown to blackish ostiolar region, 50–100 µm diam., unilocular, with a brown (K+ purplish, N+ orange-red) pigment (but no green pigment) in upper part; inside of cavity lined with conidiophores terminated by cylindrical conidiogenous cells, 4–8 × 1.5–2.5 µm. *Conidia* acrogenously formed, usually (1) short-bacilliform, narrowly ellipsoid, or tear-shaped, straight, non-septate, 3–10 × 1.5–2.8 µm, or sometimes (2) filiform, curved, non-septate, 6–20 × 0.8–1.0 µm.

Chemistry:—No lichen substances detected.

Habitat and distribution:—On limestone or other base-rich types of rock, usually in shade, such as crevices or overhangs. Some mountain specimens (judging from associated species) seem to be collected in moist habitats in more or less full sun. The species is known from highlands and mountains throughout much of Europe: Italy, Montenegro, France, Austria, Germany, Scotland, Norway (incl. Bear Island in the Svalbard Archipelago), Sweden, and Finland. Reports from Hungary, Romania, and northern Spain by Llop & Ekman (2007) have not been re-investigated. Occurrences in central, western, and northern Europe span from high to fairly low elevations, whereas the few known finds from southern Europe always seem to be at high elevations. In addition, there is a single known find from the Black Hills of South Dakota in the United States. *B. coprodes* is likely to be overlooked in other parts of the northern United States and Canada. Wirth *et al.* (2013) pointed out that the species has not been observed in Germany for over a century.

Notes:—*B. coprodes* is characterized by the hypothecium being as dark as or darker than the surrounding proper exciple (Fig. 4A–C). Pycnidia with the straight and wide type of condia are by far the most common. In some specimens, however, pycnidia contain narrow, filiform and curved conidia. These specimens do not seem to have any other distinguishing features, but rather represent a random sample from the variation within *B. coprodes*. Therefore, they are treated here as part of the variation within *B. coprodes*.

Bacidia coprodes can be confused with *B. notarisiana* and *B. granosa*, both of which constantly have filiform conidia and a hypothecium that is paler than the surrounding exciple. It can also be confused with poorly developed forms of *Toninia aromatica*, which, however, tends to produce rounded, sometimes pruinose squamules with irregular maculae.

There are a few deviating specimens that I have excluded from *B. coprodes* as treated above and which may represent undescribed species. Two rock-inhabiting specimens from Ben Lawers in Scotland (E 00425707 and E 00425708) are very similar to *B. coprodes* in most respects, except that ascospores are longer (19–26 um) and frequently 5- or 7-septate at maturity. A specimen overgrowing dying cyanophilic lichens and collected in Härjedalen, Sweden (UPS L-649189), is also similar to *B. coprodes*, except that ascospores are narrowly bacilliform (15–25 × 1.5–2.5 um) and the proper exciple dominated by green pigment. Finally, a corticolous specimen from Toledo in Spain (MA-Lichen 7145) deviates from *B. coprodes* in having a microsquamulose thallus, apothecia with a tall hymenium (60–75 um) and producing mainly 1-septate ascospores (but some 3-septate).

Selected specimens examined:—AUSTRIA. Niederösterreich: "In monte Sonntagsberg prope Rosenau", undated, *P. P. Strasser* in Krypt. exs. (Vindob.) 657 (LD, UPS L-649467). FINLAND. Tavastia australis: Tammela par., "Mustiala", 1870, *A. Kullhem* (UPS L-648011). GERMANY. Bayern: "Am Wege zum Bahnhof bei Eichstätt", November 1873, *F. Arnold* (LD). "In der Waldschlucht des Rosenthales bei Eichstätt", 6 December 1866, *F. Arnold* in Arnold: Lich. exs. 333 (LD, UPS L-168564). ITALY. Abruzzi: L'Aquila, "Gran Sasso, above Rifugio Duca degli Abruzzi, 2200 m," 9 August 1996, *P. L. Nimis & M. Tretiach* (TSB 24544). MONTENEGRO. Plav: "In the mountain pass Čakor, W of Peć, alt. 1850 m", 8 July 1979, *S. Svane 4229-1* (C). NORWAY. Troms: "Tromsö, Flöjfjeldet", 23 June 1864, *T. M. Fries* (UPS L-138583). SVALBARD AND JAN MAYEN. Bjørnøya, "Mt. Misery", 24 July 1868, *T. M. Fries* (UPS L-650772). SWEDEN. Västergötland: Österplana par., "Kinnekulle, nedanför Högkullen, åt söder", 20 September 1859, *F. Graewe* (LD, UPS L-647788). Närke: Lerbäck par., "Ödeskärr", 1869, *P. J. Hellbom* (UPS L-647778). Östergötland: Väversunda par., "Omberg, Väfversunda", 1873, *P. G. E. Theorin* (LD, UPS L-647807). Värmland: Filipstad par., "Pajsberg vid Yngen", 1867, *J. G. Lagergren* (UPS L-647811). Hälsingland: Skog par., Holmsveden, Sagberg kalkbrott", 12 August 1991, *Å. Ågren 268* (UPS L-54892). Härjedalen: Tännäs par., "Funnesdalen", 1867, *P. J.*

Hellbom (UPS L-171930). Jämtland: Kall par., "Skutån", undated, *S. Almquist* (UPS L-647836). Åre par., "Rennberg", August 1873, *S. Almquist* (UPS L-171901). Lule lappmark: Gällivare par., "Vastenjaure, Puoltaketjejauratj", 9 August 1965, *G. Gilenstam 1218a* (UPS L-103910). Lycksele lappmark: Tärna par., "Björkfors, Mortsbäcken", 19 July 1924, *A. H. Magnusson 8413* (UPS L-171922). Torne lappmark: Jukkasjärvi par., "Nuolja, 1000 m", 2 August 1921, *A. H. Magnusson 6200a* (UPS L-171926). UNITED KINGDOM. Angus (VC 90): "Caenlochan Glen (N side): valley of Glasallt Burn", 7 August 1989, *B. J. Coppins 13370 & O. L. Gilbert* (E 00425705). UNITED STATES OF AMERICA. South Dakota: Lawrence Co., "Black Hills, near Bridalveil Falls in Spearfish Canyon (5 mi south of Spearfish), in deeply shaded east-west gulch, 4300 ft", 12 August 1960, *C. M. Wetmore 9377A* (LD, MSC 0097749).

Bacidia notarisiana (A. Massal.) Zahlbruckner (1926a: 131) (Fig. 2, 4E)

Bilimbia notarisiana A. Massalongo (1855: 46). Type: ITALY. Liguria: Genova, "Genova, nella salita di Mt Cucco", undated, *F. Baglietto* (holotype: VER!; isotype: ZT!).

Nomenclature:—The invalidly published herbarium name *Coniangium notarisianum* was coined by Francesco Baglietto and appears on the label of the type material of *Bilimbia notarisiana*. The duplicate specimen in ZT was probably sent directly to Stizenberger by Baglietto and bears no sign of having been studied by Massalongo. The only specimen seen by Massalongo, in VER, is considered here as the holotype.

Thallus crustose, thin, pale green to grey-green, finely areolate with warted areoles. *Prothallus* lacking.

Apothecia lecideine, 0.2–0.3–0.5 mm diam. (s=0.1, N=50), rounded to irregularly lobate, at first flat, becoming more or less convex with age, without pruina. *Disc* beige-brown to black, often piebald. *Margin* concolorous with disc or darker than disc, often shiny, distinct, slightly raised above disc in young apothecia, soon level with disc, becoming excluded in convex apothecia.

Proper exciple 34–60 µm thick, without crystals; composed of radiating, mainly dichotomously branched hyphae with thick gelatinous walls and cell lumina not or only slightly constricted at the septa; cell lumina 10–17 × 1.5–2.5 µm in inner part of exciple, gradually wider towards edge, terminal cells up to 5 µm wide; dark red-brown or blackish green, with a mixture of a red-brown (K+ purplish, N+ orange-red) and a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals), rim sometimes paler than inner exciple. *Hypothecium* pale to medium orange-brown throughout (with a red-brown, K+ purplish and N+ orange-red pigment and, at least in paler versions, an orange-brown, K+ intensifying, N- pigment), distinctly paler than and contrasting with exciple. *Hymenium* 47–55–62 µm tall (s=5, N=15), colourless below, upper part with varying amounts of green pigment, which is diffusely and unevenly dispersed in upper part, often concentrated to vertical streaks. *Paraphyses* abundant, 1.2–1.5–1.7 µm wide in mid-hymenium (s=0.1, N=30), unbranched or sparingly branched in upper part, infrequently anastomosed; apices ± clavate, 1.6–3.3–4.7 µm wide (s=0.9, N=30), with or without surrounding gelatinous cap with green pigment. *Asci* clavate, 8-spored, *Bacidia*-type *sensu* Hafellner (1984). *Ascospores* colourless, without perispore or ornamentation, straight or slightly curved, short-bacilliform, narrowly ellipsoid, or fusiform, sometimes slightly tapering towards one end, with blunt or slightly pointed ends, 11–14–19 µm long (s=2, N=30), 2.6–3.3–3.9 µm wide (s=0.3, N=30), with 3 septa at maturity.

Pycnidia often present, semi-immersed in thallus except for a blackish ostiolar region, 30–80 µm diam., unilocular, with a red-brown (K+ purplish, N+ orange-red) pigment (but no green pigment) in upper part; inside of cavity lined with conidiophores terminated by cylindrical or narrowly ampulliform conidiogenous cells, 5–8 × 1.2–1.6 µm. *Conidia* acrogenously formed, filiform, more or less curved, non-septate, 8–16 × c. 1.0 µm.

Chemistry:—No lichen substances detected.

Habitat and distribution:—Apparently on calcareous rock, sometimes in anthropogenic settings (e.g., cement constructions). Currently known only from low or moderate elevations in northern Italy, but is likely to be more widespread in the Mediterranean region.

Notes:—Very similar to *B. granosa*, differing from this in the warted thallus surface never becoming microsquamulose, the consistent lack of a dark prothallus, and the lack of green pigment in the pycnidial wall. Both species differ from *B. coprodes* in the hypothecium being distinctly paler than the surrounding proper exciple (Fig. 4E–F).

Additional specimens examined:—ITALY. Friuli-Venezia Giulia: Udine, "Alto Friuli presso Bueris, 250 m, su vecchio muretto d'arenaria," 10 November 1983, *P. L. Nimis* (TSB 3769). Liguria: Genova, "Quarto, ad maceriam, herba tectam," 20 November 1936, *C. Sbarbaro* (UPS L-160570). Genova, "Val Bisagno, S. Pantaleo", June 1946, *C. Sbarbaro* (UPS L-634654).

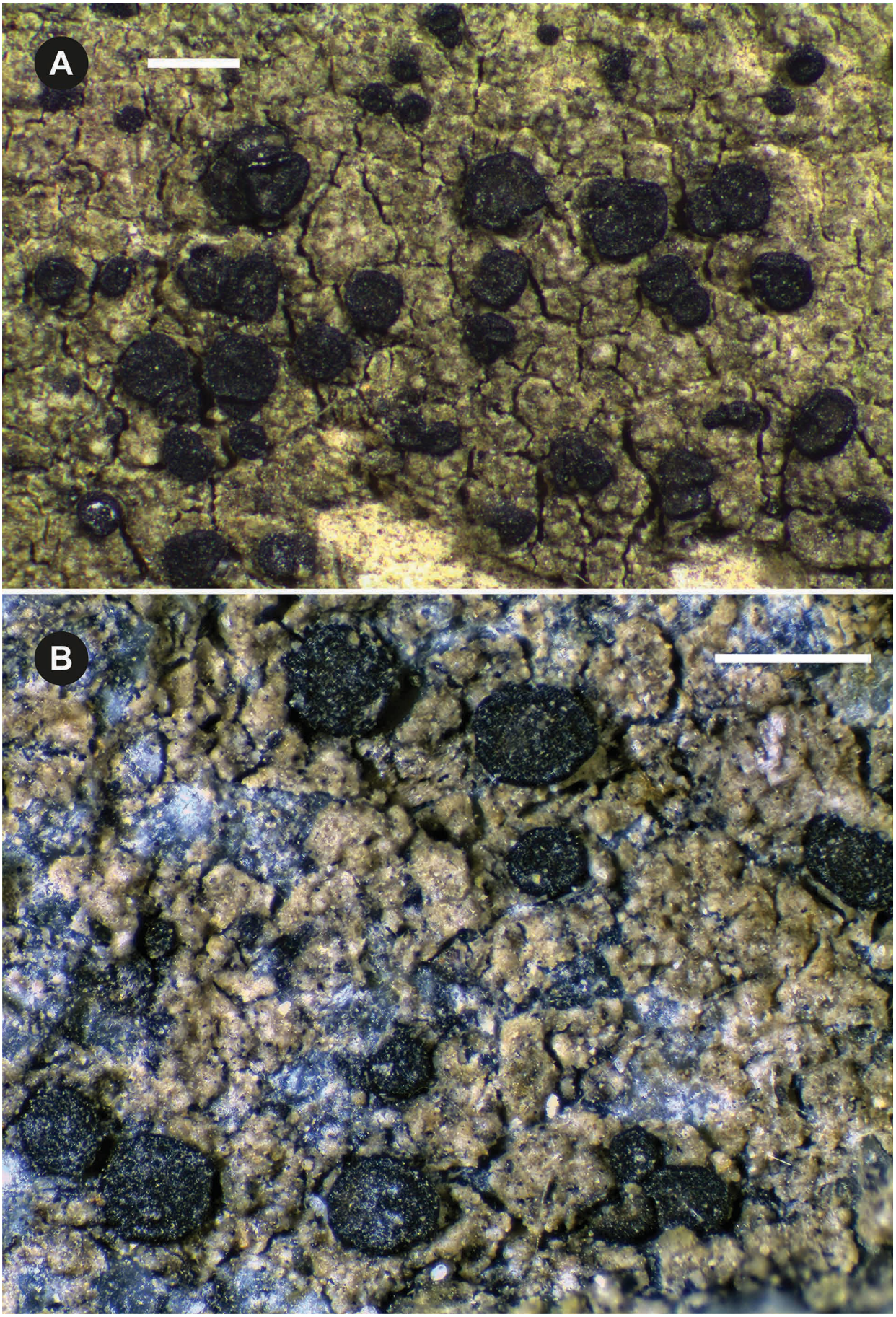

FIGURE 2. *Bacidia notarisiana*, thalli with apothecia. **A.** Italy (UPS L-634654). **B.** Italy (TSB 3769).—Scales = 0.5 mm.

Bacidia granosa (Tuck.) Zahlbruckner (1926b: 203) (Fig. 3A, 4F)

Lecidea granosa Tuckerman (1862: 420). *Toninia granosa* (Tuck.) Bouly de Lesdain (1921: 68). *Bilimbia granosa* (Tuck.) Fink (1935: 225). Type: UNITED STATES OF AMERICA. South Carolina: Berkeley Co., "Santee Canal, on brick walls", H. W. Ravenel 191 (lectotype, selected by Ekman 1996: FH-TUCK 00060062!).

Lecidea trachonopsis Nyl. in Nylander & Crombie (1883: 64). - *Bacidia trachonopsis* (Nyl.) Zahlbruckner (1926a: 157). Type: CHINA. Shanghai: "prope Shanghai", 1862, *A. C. Maingay* (H-NYL 18967!)

Bilimbia pammellii Fink in Hedrick (1934: 156). *Bacidia pammellii* (Fink) Zahlbruckner (1939: 365). Type: UNITED STATES OF AMERICA. Iowa: Boone Co., "The Ledges, sandstone", 27 July 1903, *B. Fink* (lectotype, selected by Ekman 1996: MU L1397; isolectotype: MICH 68325!).

Nomenclature:—Fink should be cited as the author of *Bilimbia pammellii*, as both the name and validating description were ascribed to him (ICN Art. 46.2). The ascription of the validating description to Fink was made by Hedrick (1933) with the statement "the descriptions were prepared by Dr. Fink". This is considered here as 'internal evidence' in the sense of Art 46.7, as the two papers (Hedrick 1933, 1934) have the same title and author and are parts of the same publication in the sense of Art 35.5.

Thallus crustose, thin to rather thick, pale green to grey-green, finely areolate; areoles ± effigurate with warted surface or becoming ± microsquamulose with age. *Prothallus* lacking or sometimes present, forming a thin, dark line along edge of thallus.

Apothecia lecideine, 0.2–0.3–0.6 mm diam. (s=0.1, N=75), rounded to irregularly lobate, at first flat, becoming more or less convex with age, without pruina. *Disc* black. *Margin* concolorous with disc, distinct, slightly raised above disc in young apothecia, soon level with disc, becoming excluded in convex apothecia.

Proper exciple 37–56 µm thick, without crystals; composed of radiating, mainly dichotomously branched hyphae with thick gelatinous walls and cell lumina not or only slightly constricted at septa; cell lumina 7–12 × 1.5–3 µm in inner part of exciple, gradually wider towards edge, terminal cells up to 5 µm wide; dark red-brown or blackish green, with a mixture of a red-brown (K+ purplish, N+ orange-red) and a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals), rim sometimes paler than inner exciple. *Hypothecium* pale orange-brown to medium red- or purple-brown throughout (with a red-brown, K+ purplish and N+ orange-red pigment and, at least in paler versions, an orange-brown, K+ intensifying, N- pigment), distinctly paler than and contrasting with exciple. *Hymenium* 44–54–67 µm tall (s=6, N=32), colourless below, upper part with unevenly distributed green pigment, which is often concentrated to vertical streaks. *Paraphyses* abundant, 1.2–1.5–2.0 µm wide in mid-hymenium (s=0.2, N=55), unbranched or sparingly branched in upper part, infrequently anastomosed; apices ± clavate, 2.0–3.2–5.4 µm wide (s=0.9, N=70), with or without surrounding gelatinous cap with green pigment. *Asci* clavate, 8-spored, *Bacidia*-type *sensu* Hafellner (1984). *Ascospores* colourless, without perispore or ornamentation, straight or slightly curved, short-bacilliform, narrowly ellipsoid, or fusiform, sometimes slightly tapering towards one end, with blunt or slightly pointed ends, 11–15–28 µm long (s=3, N=72), 2.6–3.3–4.2 µm wide (s=0.3, N=72), with 3 septa at maturity.

Pycnidia often present, semi-immersed in thallus except for a blackish ostiolar region, 30–80 µm diam., unilocular, with a mixture of a red-brown (K+ purplish, N+ orange-red) and a sordid green (K+ intensifying, N+ purple) pigment in upper part; inside of cavity lined with conidiophores terminated by cylindrical or narrowly ampulliform conidiogenous cells, 5–8 × 1.0–2.0 µm. *Conidia* acrogenously formed, filiform, more or less curved, non-septate, 7–20 × 0.5–1.0 µm.

Chemistry:—No lichen substances detected.

Habitat and distribution:—On sandstone or limestone rocks, sometimes on man-made substrates such as brick, probably mostly or always in shade, at low elevations. Currently known from the continental eastern United States, Cuba, Bermuda, and coastal eastern China.

Notes:—Very similar to *B. notarisiana* (see that species).

Additional specimens examined:—UNITED STATES OF AMERICA. Iowa: Clayton Co., "Bixby, north of Edgewood", 8 September 1961, *H. A. Imshaug 28034A* (MSC 0097748). Fayette Co., 3 December 1895, *B. Fink* in Cummings, Williams & Seymour: Decades of North American Lichens 245 and Cummings, Williams & Seymour: Lichenes Boreali-Americani 186 (LD, MSC 0143353, MSC 0132953); 1895, *B. Fink* (UPS L-649436, L-649437). Fayette Co., "Echo Valley State Park, east of West Union", 30 October 1965, *C. Wetmore 13629* (MSC 0097750). Jackson Co., "Maquoketa Caves Park, northwest of Maquoketa", 9 September 1961, *H. A. Imshaug 28087* (MSC 0097751). Jones Co., "Wapsipinicon, south of Anamosa", 9 September 1961, *H. A. Imshaug 28116* (MSC 0097747). Louisiana: Orleans par., "graveyard in New Orleans", 1851, *J. Hale* (FH-TUCK 00060061). Michigan: Alpena Co., "limestone sinkholes c. 3 mi N of Long Rapids", 3 August 1974, *R. C. Harris 9347* (MSC 0097752). Missouri: Taney

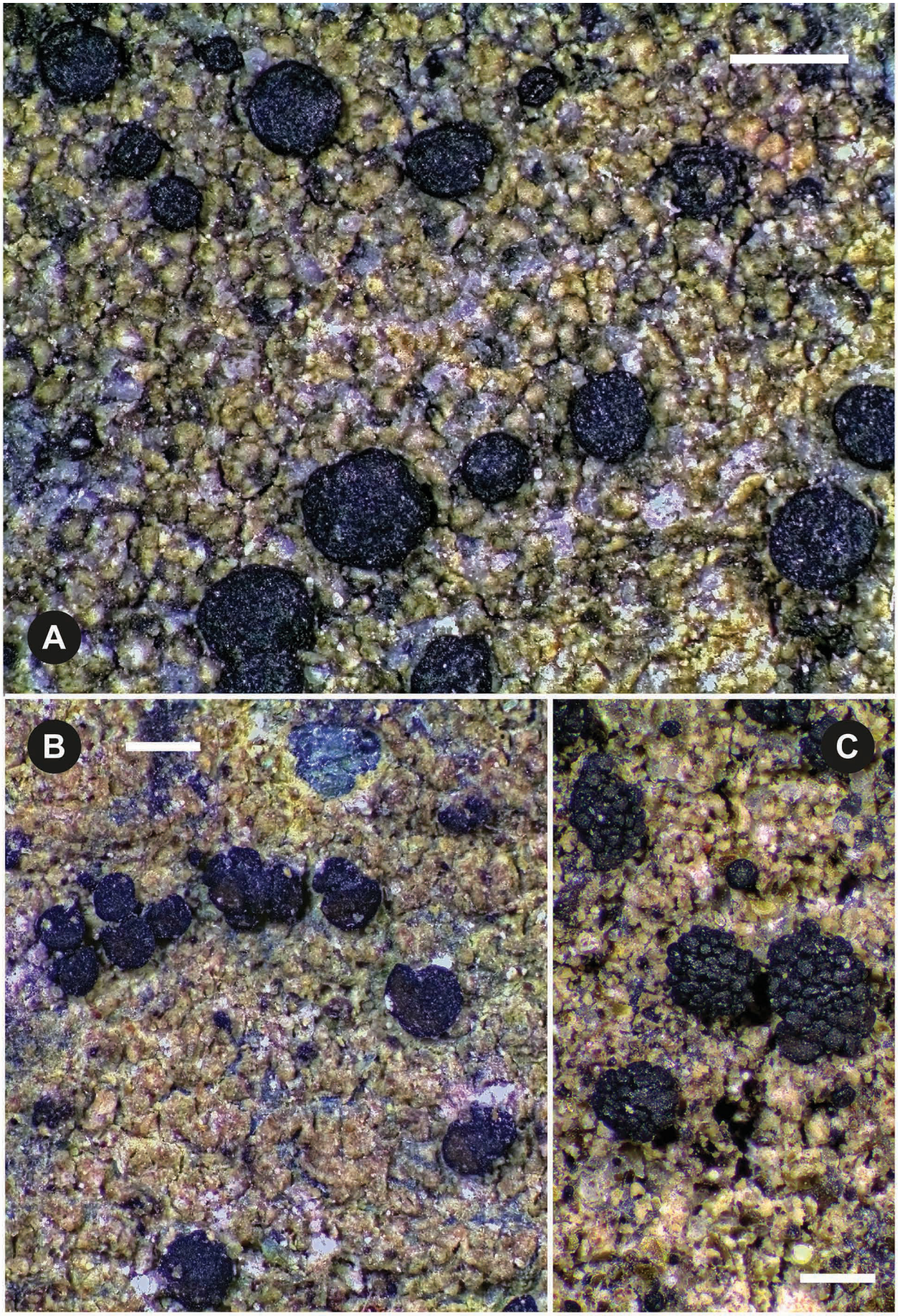

FIGURE 3. *Bacidia granosa* and *B. inornata*, thalli with apothecia. **A.** *B. granosa*, U.S.A. (MSC 0097751). **B.** *B. inornata*, Sweden (UPS L-649188). **C.** *B. inornata*, Sweden (UPS L-637820).—Scales = 0.5 mm.

Co., "Mark Twain National Forest, Hercules Glades, 1 mile north of Persimmon Hollow", 30 August 1991, *C. M. Wetmore 68454* (LD). South Carolina: undated, *H. W. Ravenel* (FH-TUCK 00060063). Charleston Co., "Charleston, brick wall", 1853, *H. W. Ravenel 385* (FH-TUCK 00060064). BERMUDA. "The Flatts, on limestone", April 1916, *A. B. Hervey* (MSC 0097745). CUBA. Wright: Lichenes Cubae 236 (UPS L-662824).

Bacidia inornata (Nyl.) Blomb. & Forssell in Nordstedt et al. (1880: 81) (Fig. 3B–C, 4D)

Lecidea inornata Nylander (1874: 11). Type: FINLAND. Tavastia australis: "Padasjoki, Nyystölä, kiven reunalla", 1872, *E. Lang* a.k.a. *E. A. Vainio* (lectotype, designated here: TUR-V 20450!; isolectotype: H-NYL 17944).

Nomenclature:—Nylander clearly saw TUR-V 20450, as he mentions in the diagnosis that the specimen was growing "cum *Verrucaria gibbosula*", a note that only appears on the material in TUR-V. The small piece in H-NYL (17944) probably represents a part of Vainio's original collection that Nylander kept for his own herbarium. As the TUR-V specimen is more abundant, it is selected here as the lectotype.

Thallus crustose thin, pale green to grey-green, almost granular or finely areolate, with ± smooth, warted, or scurfy surface. *Prothallus* thin, white, arachnoid, visible along edge of thallus and between discrete areoles.

Apothecia lecideine, 0.2–0.3–0.7 mm diam. (s=0.1, N=30), rounded or irregularly lobed, flat, somewhat convex with age, without pruina, often becoming tuberculate by regeneration of several young apothecia from aging apothecia. *Disc* yellow-brown to red-brown to black, sometimes piebald. *Margin* darker than or concolorous with disc, matt, distinct, slightly raised above disc in young apothecia, soon level with disc, persistent.

Proper exciple 44–72 µm thick, without crystals; composed of radiating, mainly dichotomously branched hyphae with thick gelatinous walls and cell lumina not or only slightly constricted at septa; cell lumina 7–12 × 2–2.5 µm in inner part of exciple, gradually wider towards edge, terminal cells up to 8 µm wide; blackish purple-brown or blackish green, with a mixture of a red-brown (K+ purplish, N+ orange-red) and,in the upper lateral parts, a sordid green pigment (K+ intensifying green, N+ purple with the deposition of blue crystals), rim concolourous with inner exciple. *Hypothecium* in upper part dark red-brown, concolourous with proper exciple or slightly paler, in lower part medium to dark red-brown, concolourous with or paler than upper part of hypothecium (all parts with a red-brown, K+ purplish and N+ orange-red pigment). *Hymenium* 32–39–46 µm tall (s=4, N=15), colourless or dilute red-brown, upper part also with unevenly distributed spots of red-brown and sordid green pigment. *Paraphyses* abundant, 1.2–1.4–1.6 µm wide in mid-hymenium (s=0.2, N=15), unbranched or sparingly branched in upper part, not anastomosed; apices ± clavate, 2.0–2.9–3.9 µm wide (s=0.6, N=30), with or without surrounding gelatinous cap with red-brown or green pigment. *Asci* clavate, 8-spored, *Bacidia*-type *sensu* Hafellner (1984). *Ascospores* colourless, without perispore or ornamentation, straight, bacilliform or short-acicular with blunt ends, 11–15–19 µm long (s=2, N=30), 1.9–2.1–2.3 µm wide (s=0.1, N=30), with (0–)3(–5) septa at maturity, septa apparently forming late during ascospore development.

Pycnidia often present, sessile to stipitate, 60–90 µm diam., unilocular; wall with a red-brown (K+ purplish, N+ orange-red) pigment; inside of cavity lined with conidiophores terminated by cylindrical or narrowly ampulliform conidiogenous cells, 6–8 × 1.0–1.2 µm. *Conidia* acrogenously formed, bacilliform to narrowly ellipsoid, straight, non-septate, 4–7 × 1.2–1.5 µm.

Chemistry:—No lichen substances detected.

Habitat and distribution:—*B. inornata* inhabits acid, preferably soft and easily weathering rocks and boulders in humid and shady situations, often near water. Currently known from a few places in Sweden, Finland, Wales, and Scotland.

Notes:—*B. inornata* is similar to *B. coprodes* in the pigmentation of the proper exciple and hypothecium as well as conidium shape. *B. inornata* can be distinguished, however, on account of the tuberculate apothecia (Fig. 3C), thinner hymenium, more red-brown and less green pigment in the epihymenium (Fig. 4D), narrower ascospores, and (when present) sessile to stipitate pycnidia. Ascospores are poorly developed in the type material, which is probably why Nylander (1874) incorrectly described the ascospores as acicular and 32–36 × 1–1.5 µm. In the otherwise excellent description of this species by Vainio (1922: 166), ascospore shape and size were taken unaltered from Nylander's original description ("*secund. Nyl. l. c.*"), possibly because Vainio also had problems finding mature ascospores. Symptomatically, the hand-written notes by Vainio on the envelope of the TUR-V specimen contain details about almost every aspect of the morphology of the species with the exception of ascospores. Apart from the descriptions by Nylander and Vainio, the only other description of this poorly known species was provided by Foucard (1990: 83). First reported from Sweden (Västergötland) by Magnusson (1955), but that specimen is *Micarea marginata* (UPS L-200622, determined by B. J. Coppins).

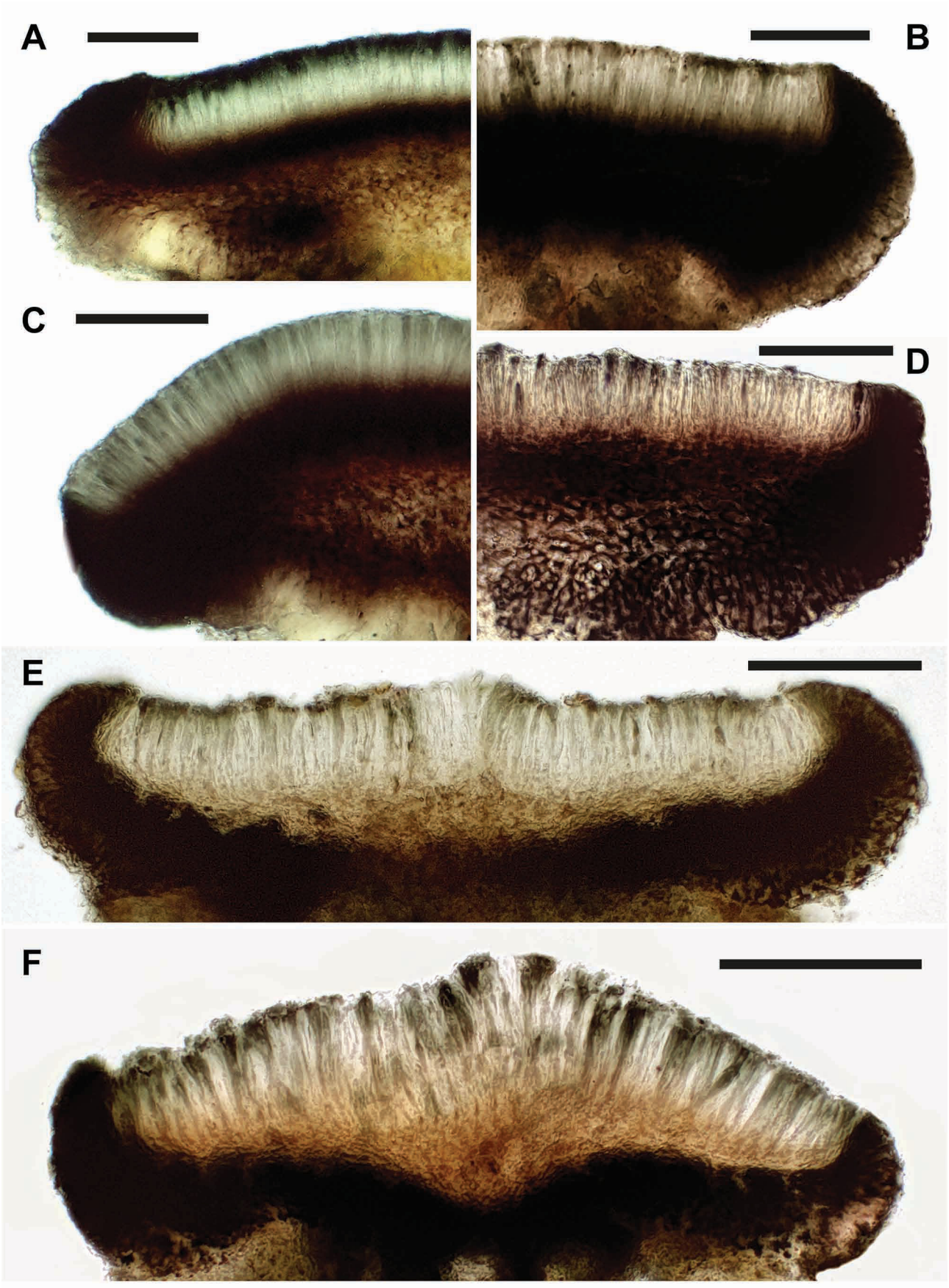

FIGURE 4. Sections of apothecia. **A.** *Bacidia coprodes*, Sweden (UPS L-647836). **B.** *B. coprodes*, Germany (ZT Myc-3656, lectotype of *Lecidea chytrina* var. *hormospora*). **C.** *B. coprodes*, Norway (UPS L-138582, holotype of *Biatorina seposita*). **D.** *B. inornata*, U.K. (E 00425709). **E.** *B. notarisiana*, Italy (UPS L-634654). **F.** *B. granosa*, U.S.A. (UPS L-649436).—Scales = 100 µm.

Additional specimens examined:—SWEDEN. Härjedalen: Tännäs par., "1.2 km N of Ramundbergsvallen, the W side of the stream Sveån", elev. 825 m, 62°43'N 12°22'E, 3 June 2007, *M. Svensson 1030* (UPS L-649188). Jämtland: Åre par., "Handöl, Handöl rapids, E river bank S of the suspension bridge and N of the small hill with boulders c. 400 m SSW of the suspension bridge", elev. 570–620 m, 63.23°N 12.45°E, 31 July 1993, *A. Nordin, B. Owe-Larsson & G. Thor 136* (UPS L-637820). Ångermanland: Nordingrå par., "Omne, p. 255, NO-sluttning, vittrad sten på hylla i skugga", 15 July 1958, *S. Sundell 1474* (UPS L-200623). UNITED KINGDOM. Camarthen (VC 44): "13 km N of Llandovery: Allt Rhyd-y-gross NNR, wood SE of Cribyn Du, on sheltered underhang on rock face by stream", 24 July 1981, *B. J. Coppins 8597 & R. G. Woods* (E 00425712). Mid-Perth (VC 88): "Aberfeldy, Moness Wood, on shaded rocks under trees, by river", 6 April 1986, *B. J. Coppins 11270* (E 00425710). "Crieff, Drummond Park, Drummond Wood, shaded boulder near stream", 9 August 1978, *B. J. Coppins 3617* (E 00425711). "Allt na Ceardaich, Killin, base of shaded acid-stone wall, 175 m", 25 January 1991, *A. M. Fryday 2024* (E 00425709).

Key

The key below includes saxicolous, lichenized members of the Ramalinaceae with brown pigment in the proper exciple and hypothecium, a green (K+ intensifying, N+ purple) pigment in the epihymenium, and 3-septate, bacilliform, ellipsoid, or fusiform ascospores shorter than 30 µm. All taxa keyed out below have an ascus apex with a more or less conical ocular chamber and likewise conical axial body (more or less '*Bacidia*-type' in the sense of Hafellner 1984). The part of the key dealing with species of *Toninia* has been adapted from Timdal (1991). Note that Hitch *et al.* (2009), unlike Timdal (1991), treat *T. fusispora* as a species separate from *T. aromatica*, mainly on account of ascospore shape.

In addition to the species keyed out below, attention should be paid to other similar species with more or less brown proper exciple and hypothecium and green epihymenium, and septate ascospores, viz. *Bacidia bagliettoana* (A. Massal. & De Not.) Jatta, *Bacidia illudens* (Nyl.) H. Olivier, *Toninia coelestina* (Anzi) Vězda, and *T. cretica* Timdal. All of these species inhabit soil, detritus, or moribund bryophytes, and never occur directly on rock. Ascospores mostly tend to be longer than in the species treated here, often longer than 25 µm. Furthermore, 5–7-septate ascospores are frequent in *B. bagliettoana*, *B. illudens*, and *T. coelestina*. *Bilimbia sabuletorum* (Schreb.) Arnold and *B. microcarpa* (Th. Fr.) Th. Fr. are also frequently misidentified as members of the *Bacidia coprodes* group. *Bilimbia*, however, is characterized by stout paraphyses and excipular hyphae and distinctly thick-walled asci. *B. sabuletorum* and *B. lobulata*, the most widespread species of that genus, are also characterized by a finely warted epispore. Finally, members of the *B. coprodes* group may be confused with an undescribed species of *Fellhaneropsis* currently known from shaded siliceous rocks in a few sites in central Sweden and one in central Germany. This species also has black apothecia with a well developed and persistent proper margin, 3-septate ascospores and a dark brown hypothecium. Unlike members of the *B. coprodes* group, however, this species has abundant pycnidia with very long and filiform conidia, a dark-amyloid tube structure in the axial body, somewhat constricted ascospore septa, and a micareoid photobiont.

1. Thallus thin, continuous and finely areolate, of discontiguous areoles with warted surface, or granular (granules then up to 0.25 mm wide) 2
- Thallus composed of discrete or contiguous, up to 4 mm wide and flat to moderately convex, pale grey to dark brown squamules with pruinose or epruinose surface 6

2. Ascospores broadly ellipsoid, at least 5 µm wide ..... *T. mesoidea*
- Ascospores less than 4.5 µm wide (members of the *Bacidia coprodes* group) 3

3. Hymenium up to c. 45 µm, colourless to dilute red-brown; epihymenium with mixed red-brown and green pigment; ascospores mostly c. 2 µm wide; pycnidia sessile or stalked; conidia bacilliform to narrowly ellipsoid, straight ..... *B. inornata*
- Hymenium mostly taller than 45 µm, colourless and with green pigment in epihymenium and sometimes in vertical streaks; ascospores ≥ 2.5 µm wide; pycnidia immersed; conidia filiform, bacilliform, narrowly ellipsoid, or tear-shaped, straight or curved 4

4. Hypothecium at least in upper part dark red-brown to greenish black, concolorous with or darker than inner exciple; conidia either filiform and curved or short-bacilliform to narrowly ellipsoid to tear-shaped, straight ..... *B. coprodes*
- Hypothecium evenly pale orange-brown to medium red-brown, paler than and distinctly contrasting with red-brown to blackish green inner exciple; conidia filiform, curved..... 5

5. Areoles somewhat effigurate, with age forming minute squamules; prothallus, when present, forming a black line; pycnidial wall

with mixture of green and red-brown pigment ..... *B. granosa*
- Areoles warted, never becoming effigurate or microsquamulose; prothallus absent; pycnidial wall with red-brown pigment only ..... *B. notarisiana*

6. Squamules with irregular pale flecks; upper part of hymenium with green pigment only ..... *T. aromatica* (incl. *T. fusispora*)
- Squamules without irregular pale flecks; upper part of hymenium dominated by red-brown pigment ..... *T. verrucarioides*

Additional names

The following observations were made on types of three names that I came across during the course of this revision.

***Bilimbia clavigera* Zahlbruckner (1903: 180)**
Bacidia clavigera (Zahlbr.) Zahlbruckner (1926a: 107). Type: CROATIA. Split-Dalmatia: Hvar, "Insel Lesina, am Wege von Lesina nach Cittavecchia, an Kalkfelsen", November 1902, *J. Lütkemüller* (W!).

Zahlbruckner (1903) considered his new species to be closely related to *Bacidia coprodes*. The type material in W, from the island Hvar off the Dalmatian coast in Croatia, is probably *Toninia aromatica* with a poorly developed thallus consisting of scattered small whitish squamules.

***Bilimbia trachona* var. *intercedens* Arnold (1873: 505)**
Bilimbia intercedens (Arnold) Arnold (1877: 570). *Bacidia trachona* var. *intercedens* (Arnold) Zahlbruckner (1926b: 209). Type: AUSTRIA. Tirol: "*Larix*-Rinde, Waldrast in Tirol", August 1872, *F. Arnold* (UPS L-664328!).

Original material could not be located in M. The type specimen in UPS was probably sent from Arnold to T. M. Fries. This specimen was labelled "*Bilimbia* --/n. sp" and annotated "a me adhuc denominanda" (= "should still be named by me") by Arnold, and surely represents the taxon later described as *Bilimbia trachona* var. *intercedens* Arnold. This taxon was the only taxon in *Bilimbia* described as new from the area in question, and the locality data fully agree with the material discussed in detail by Arnold (1873: 511–512). The type material of *Bilimbia trachona* var. *intercedens* in UPS belongs to *Bacidia verecundula* (Th. Fr.) H. Magn., which was originally described as *Bilimbia verecundula* Th. Fries (1874: 387). Note that Arnold (1877), when combining his taxon to species level, put forward the idea of a close relationship with *Bacidia verecundula*, possibly after having communicated with Fries on the matter. Also note that *Patellaria intercedens* Müll. Arg., on which *Bacidia intercedens* (Müll. Arg.) Zahlbr. is based, is a different taxon.

***Bilimbia subcoprodes* de Lesd. in Crozals (1924: 107)**
Bacidia subcoprodes (de Lesd.) Zahlbruckner (1932: 409). Type: FRANCE. Provence-Alpes-Côte d'Azur: Var, "Giens", February 1924, *A. de Crozals* (US 01138555!).

The type material in US is *Catillaria aphana* (Nyl.) Coppins. Most ascospores are 1-septate, although some are non-septate and some 3-septate. This variation in ascospore septation is often observed in that species.

Acknowledgements

I am grateful to the curators listed in the Material and Methods for providing essential loans of herbarium material, to Brian Coppins for directing my attention to British specimens that proved to belong to *B. coprodes* and *B. inornata*, and to Francesco Di Carlo for hospitality during a visit to the Massalongo herbarium in Verona. The Swedish Taxonomy Initiative is thanked for financial support (grant no. 146/07 1.4).

References

Arnold, F. (1858) Die Lichenen des fränkischen Jura. *Flora (Jena)* 41: 473–508.

Arnold, F. (1869) Lichenologische Ausflüge in Tirol. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 19: 605–656.

Arnold, F. (1870) Lichenologische Fragmente VII. *Flora (Jena)* 53: 121–124.

Arnold, F. (1873) Lichenologische Ausflüge in Tirol. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 23: 485–534.

Arnold, F. (1877) Lichenologische Ausflüge in Tirol. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 27: 533–570.
Arnold, F. (1884) Die Lichenen des fränkischen Jura. *Flora (Jena)* 67: 549–596.
Arup, U., Ekman, S., Lindblom, L. & Mattsson, J.-E. (1993) High performance thin layer chromatography (HPTLC), an improved technique for screening lichen substances. *The Lichenologist* 25: 61–71. http://dx.doi.org/10.1017/S0024282993000076
Bouly de Lesdain, M. (1921) Lichenes Prope Habanam in insula Cuba anno 1914 a cl. Fratre Arsene Brouard lecti. *The Bryologist* 24: 68–69. http://dx.doi.org/10.2307/3238000
Choisy, M. (1953) Catalogue des Lichens de la région lyonnaise. *Bulletin mensuel de la Société Linnéenne de Lyon* 22: 177–192.
Crozals, A. de (1924) Les lichens du Massif des Maures. *Annales de la Société d'Histoire Naturelle de Toulon* 10: 88–116.
Ekman, S. (1996) The corticolous and lignicolous species of Bacidia and Bacidina in North America. *Opera Botanica* 127: 1–148.
Ekman, S. (2001) Molecular phylogeny of the Bacidiaceae (Lecanorales, lichenized Ascomycota). *Mycological Research* 105: 783–797. http://dx.doi.org/10.1017/S0953756201004269
Fink, B. (1935) *The lichen flora of the United States*. University of Michigan Press, Ann Arbor, 426 pp.
Foucard, T. (1990) *Svensk skorplavsflor*a. Stenström Interpublishing, Stockholm, 306 pp.
Fries, T.M. (1867) Nya skandinaviska laf-arter. *Botaniska Notiser* 1867: 151–155.
Fries, T.M. (1874) *Lichenographia Scandinavica. Pars secunda.* Berling, Uppsala, pp. 325–639
Hafellner, J. (1984) Studien in Richtung einer natürlicheren Gliederung der Sammelfamilien Lecanoraceae und Lecideaceae. *Beiheft zur Nova Hedwigia* 79: 241–371.
Hedrick, J. (1933) New genera and species of lichens from the herbarium of Bruce Fink I. *Mycologia* 25: 303–316. http://dx.doi.org/10.2307/3754098
Hedrick, J. (1934) New genera and species of lichens from the herbarium of Bruce Fink II. *Mycologia* 26: 153–166. http://dx.doi.org/10.2307/3754037
Hitch, C.J.B., Timdal, E. & James, P.W. (2009) Toninia A. Massal. (1852). *In*: Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A, Gilbert, O.L., James, P.W. & Wolseley, P.A. (Eds.) *The lichens of Great Britain and Ireland*. The British Lichen Society, London, pp. 895–903.
Körber, G.W. (1855) *Systema lichenum Germaniae.* Part 2. Trewendt & Granier, Breslau, 458 pp.
Körber, G.W. (1860) *Pargerga lichenologica.* Part 2. Eduard Trewendt, Breslau, 501 pp.
Lettau, G. (1912) Beiträge zur Lichenographie von Thüringen. *Hedwigia* 52: 81–264.
Llop, E. & Ekman, S. (2007) Bacidia coprodes – resurrecting a misinterpreted species. *The Lichenologist* 39: 251–257. http://dx.doi.org/10.1017/s0024282907006779
Magnusson, A.H. (1945) New or otherwise interesting Swedish lichens. XII. *Botaniska Notiser* 1945: 304–314.
Magnusson, A.H. (1955) New or otherwise interesting Swedish lichens. XV. *Botaniska Notiser* 108: 292–306.
Massalongo, A.B. (1855) *Symmicta lichenum novorum*. Verona, 136 pp.
McNeill, J. (2014) Holotype specimens and type citations: General issues. *Taxon* 63: 1112–1113. http://dx.doi.org/10.12705/635.7
Meyer, B. & Printzen, C. (2000) Proposal for a standardized nomenclature and characterization of insoluble lichen pigments. *The Lichenologist* 32: 571–583. http://dx.doi.org/10.1006/lich.2000.0294
Müller Argoviensis, J. (1862) Principes de classification des lichens et énumération des lichens des environs de Genève. *Memoires de la Société de Physique et d'Histoire Naturelle de Genève* 16 (2): 343–435.
Nordstedt, O., Wittrock, W.B., Kjellman, F.R., Blomberg, O.G. & Forssell, K.B.J. (1880) *Points-förteckning. Enumerantur plantae Scandinaviae. 4. Characéer, alger och lafvar.* Lund, 116 pp.
Nylander, W. (1874) Addenda nova ad Lichenographiam europaeam. Continuatio septima decima. *Flora (Jena)* 57: 6–16.
Nylander, W. & Crombie, J.M. (1883) On a collection of exotic lichens made in Eastern Asia by the late Dr. A. C. Maingay. *Journal of the Linnean Society, Botany* 20: 48–69. http://dx.doi.org/10.1111/j.1095-8339.1883.tb00184.x
Olech, M. & Czarnota, P. (2009) Two new Bacidia (Ramalinaceae, lichenized Ascomycota) from Antarctica. *Polish Polar Research* 30: 339–346. http://dx.doi.org/10.4202/ppres.2009.18
Olivier, H. (1911) Etude synoptique et géographique des Lécidés de la flore d'Europe. *Bulletin de Géographie Botanique* 20: 157–209.
Øvstedal, D.O. (1986) Lichens and lichen parasites from the British-Swedish-Norwegian Antarctic expedition 1949-52 to Dronning Maud Land. *Cryptogamie Bryologie et Lichénologie* 7: 63–70.
Øvstedal, D.O. & Lewis Smith, R.I. (2001) *Lichens of Antarctica and South Georgia. A guide to their identification and ecology.* Cambridge

University Press, Cambridge, 411 pp.
Stizenberger, E. (1868) ["1867"] Lecidea sabuletorum Flörke und die ihr verwandten Flechten-Arten. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* 34 (2): 1–84.
Timdal, E. (1991) A monograph of the genus Toninia (Lecideaceae, Ascomycetes). *Opera Botanica* 110: 1–137.
Tuckerman, E. (1862) Observations on North American and other lichens. *Proceedings of the American Academy of Arts and Sciences* 5: 383–422.
http://dx.doi.org/10.2307/20021278
Vainio, E.A. (1883) Adjumenta ad Lichenographiam Lapponiae Fennicae. *Meddelanden af Societas pro Fauna et Flora Fennica* 10: 1–230.
Vainio, E.A. (1922) Lichenographia Fennica II. Baeomyceae et Lecideales. *Acta Societatis pro Fauna et Flora Fennica* 53 (1): 1–340.
Wirth, V., Hauck, M. & Schultz, M. (2013) *Die Flechten Deutschlands*. Ulmer, Stuttgart, 1244 pp.
Zahlbruckner, A. (1903) Vorarbeiten zu einer Flechtenflora Dalmatiens II. *Österreichische Botanische Zeitschrift* 53: 147–153, 177–185, 239–246, 285–289, 332–336.
http://dx.doi.org/10.1007/bf01791220
Zahlbruckner, A. (1905) Ascolichenes. Liefereung 3. *In:* Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesonderen den Nutzpflanzen 1(1*)*. Engelmann, Leipzig, pp. 97–144.
Zahlbruckner, A. (1926a) *Catalogus lichenum universalis 4(1)*. Gebrüder Borntraeger, Leipzig, pp. 1–160.
Zahlbruckner, A. (1926b) *Catalogus lichenum universalis 4(2)*. Gebrüder Borntraeger, Leipzig, pp. 161–320.
Zahlbruckner, A. (1932) *Catalogus lichenum universalis 8(3)*. Gebrüder Borntraeger, Leipzig, pp. 321–480.
Zahlbruckner, A. (1939) *Catalogus lichenum universalis 10(3)*. Gebrüder Borntraeger, Leipzig, pp. 321–480.
Zwack-Holzhausen, W. von (1883) *Die Lichenen Heidelbergs*. G. Weiss, Heidelberg, 82 pp.