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The *Buellia aethalea*-Group in the Greater Sonoran Desert Region with Reference to Similar Species in North America

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Abstract. *Species related to* Buellia aethalea *have been examined from the Greater Sonoran Desert Region. In the region,* B. aethalea s.str. *is a rare montane species. A similar, subalpine species is* B. eganii, *first reported from New Mexico by R. S. Egan, now validly described here. Most common in the* Buellia aethalea-*group is* B. spuria, *a species which does, however, not occur in lowland desert areas of the Sonoran Region.* Buellia stellulata *is similar to* B. spuria, *but differs in thallus chemistry and is restricted to areas along the coast. Although similar in thallus morphology,* B. lacteoidea *is not closely related to the* Buellia aethalea-*group. The new name,* B. maculata, *is introduced for the illegitimate* B. stigmaea. Buellia maculata *is a species with a similar thallus, but not closely related to the* Buellia aethalea-*group and absent from the North American Southwest.* Buellia lepidastra *shows some affinities to the group, but like* B. maculata *is confined to eastern North America.*

Keywords. *Buellia aethalea*-group, Lichen taxonomy, lichenized ascomycetes, saxicolous species, Sonoran Desert, North America.

Species related to *Buellia aethalea* (Ach.) Th. Fr. are often regarded as the core group of the genus *Buellia*. They are potentially significant for the concept of the genus because of a proposal by Moberg et al. (1999) to change the listed type from *B. disciformis* to *B. aethalea*. This proposal has not yet been formally accepted or rejected. Species within the *Buellia aethalea*-group can only be included in *Buellia s.str*. if the proposal to list *Buellia aethalea* as the new type is accepted. Otherwise a new genus name must be suggested to accommodate this group of species. Until a final decision is reached by the committee of fungi, a broad concept of the genus *Buellia* should reasonably be adopted. A suggestion to accommodate species from the *Buellia aethalea*-group into a newly erected genus would inevitably cause confusion and is not reasonable unless the proposal by Moberg et al. (1999) is formally rejected.

Scheidegger (1993) revised the European species included in the *Buellia aethalea*-group. Our revision of saxicolous species with one-septate ascospores from the Greater Sonoran Desert Region also includes several species informally included within that group. This paper focuses on these species and briefly discusses some species not found in the North American Southwest.

In North America, only three species can currently be included as part of the *Buellia aethalea*-group with some certainty: *Buellia aethalea*, *B. spuria*, and *B. stellulata*. Imshaug (1951) referred to these species as part of the ''*stirps spuria*'' and suggested that *B. lacteoidea* may also belong into the group. *Buellia lacteoidea* does not, however, appear to be closely related to *Buellia aethalea* because of several different characters, most notably spores with a distinctly thickened septum. Three other species will be discussed here in the context of the *Buellia aethalea*-group: *Buellia maculata*, a species morphologically similar to *Buellia spuria*, but without the characteristic aeruginose exciple pigment; *Buellia lepidastra*, a species with affinities to the *Buellia aethalea*-group not yet fully resolved; and finally, *B. eganii* is described as superficially similar to *B. aethalea*, but without an aeruginose exciple and lecanoric instead of norstictic acid.

MATERIAL AND METHODS

All specimens were examined with light microscopy using hand- and cryosections. Both conventional bright field microscopy (BF) as well as differential interference contrast (DIC) were used. Selected specimens were also studied with transmission electron microscopy (TEM) according to a protocol described in detail by Bungartz et al. (2002). To improve dehydration and infiltration this

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protocol has been modified according to Bungartz and Nash (2004).

All specimens were spot tested and routinely examined with standardized thin-layer chromatography (Culberson & Johnson 1982; Culberson & Kristinsson 1970; Orange et al. 2001; White & James 1985). If norstictic acid was present, clusters of orange, needle-shaped crystals were formed in KOH. These are best observed in the compound microscope. TLC-plates were interpreted with the computer program WINTABOLITES (Mietzsch et al. 1994), and scanned for permanent record (Egan 2001). In addition a subset of specimens was analysed by Jack A. Elix from the Australian National University in Canberra using standardized high performance liquid chromatography (HPLC, Elix et al. 2003). Even pale UV reactions of the thallus were recorded. UV-fluorescence was only interpreted as negative if the thallus remained dark. Thallus medulla, cortex, and transverse sections of the apothecia were tested with Lugols iodine according to Bungartz et al. (2004*a*).

The thalli frequently contain crystals of various origin. A simple test with H_2SO_4 can be indicative for the presence of Ca-oxalates (Bungartz & Nash 2004), but for all specimens examined here, this reaction was negative and no clusters of needle-shaped crystals were observed.

The terminology referring to spore types is currently in a state of flux and it appears problematic to adopt a single concept. Structurally identical types within *Buellia* s.l. and *Rinodina* s.l. have probably evolved independently (Helms 2003) and it may thus be problematic to refer to these types with the same name. Spore measurements are given according to Nordin (2000). Spore ornamentation follows the terminology of Scheidegger (1993) although the term ''psilate'' was not used because these spores are smooth and therefore lack ornamentation.

Scheidegger (1993) described several diagnostic exciple types illustrated in detail in Bungartz et al. (2004*a*). A protocol by Meyer and Printzen (2000) was followed to identify acetone insoluble pigments. The most common brown pigment appears to be *elachista*-brown, even though the reactions are less obvious than described by Meyer and Printzen (2000).

The terminology of Vobis (1980) and Vobis and Hawksworth (1981) has been adopted to refer to conidiophore types and pycnidium ontogeny. For a detailed discussion of the relevance of conidia and pycnidia as taxonomic characters in *Buellia* s.l. see Bungartz et al. (2004*b*).

References to type material previously examined by Scheidegger (1993) were included even if they were not always available for study. Scheidegger (1993) generally referred to specimens as holo- or isotypes even if a lectotypification might be more appropriate according to current taxonomic practice. In these cases ''*fide* Scheidegger (1993)'' has been included with the specimen citation. Whenever possible specimens were verified and these are then marked by an exclamation mark (!). Of all the material examined, only selected material is cited here. Additional specimen information is available at: http//seinet.asu.edu/collections/selection.jsp.

BUELLIA AETHALEA (Ach.) Th. Fr., Lichenogr. Scand. 1: 604. 1874.

Gyalecta aethalea Ach., Lichenogr. Univ. 669. 1810. TYPE: UNITED KINGDOM. ENGLAND. Durham Co., 54°46′ N, 1°34′ W, ca 67 m [original label data: 'Anglia, Durham'], *Harriman s.n.* (H–Ach 66!, lectotype selected by Foucard et al. 2002; UPS–Ach!, isolectotype; S, isotype).

Lecanora atropallidula Nyl., Flora, Jena 55: 428. 1872. TYPE: FRANCE. PYRENÉES ORIENTALES. Força Real., 400 m, 16 July 1872, *Nylander s.n.* (H-Nyl 28570, holotype *fide* Scheidegger 1993).

Buellia sororia Th. Fr., Lichenogr. Scand. 1: 603. 1874. TYPE: SWEDEN. SÖDERMANLAND. Västermo prästgård, 1872, *Blomberg s.n.* (UPS, lectotype *fide* Scheidegger 1993).

Buellia ocellata var. *tenella* Müll. Arg., Flora, Jena 58: 62. 1875. TYPE: SWITZERLAND. VALAIS. Distelgrat, 1874, *Brun s.n.* (G, holotype *fide* Scheidegger 1993).

Rinodina ocellulata Bagl. & Carest., Atti Soc. Crittog. Ital. 2: 210. 1880. TYPE: ITALY. LOMBARDIA. Vallesia (= Wallis). Varallo. On an arid wall made of diorite, 45°49′ N, 8°15′ E, ca 440 m [original label data: Varallo (Valesia), su di un muro a secco fatto con pietre dioritiche alle scarpie di Valmaggia], 1877, *Carestia s.n.* (= hb. *Critt. Ital.* Ser 2: no. *721*) (MOD, isotype; M-0023752!, isotype).

Lecidea aethaloides Nyl., Flora, Jena 68: 42. 1885. TYPE: FRANCE. PYRENÉES ORIENTALES. Amélie. 11 June 1884, *Nylander s.n.* (H-Nyl 9280, holotype *fide* Scheidegger 1993).

Rinodina atropallidula (Nyl.) Arnold, Flora, Jena 68: 236. 1885.

Lecidea nigerrima Nyl. in Sandst., Abh. Naturw. Ver. Bremen 14: 491. 1898. TYPE: GERMANY. NIEDERSACHSEN. Oldenburg, on roof tiles of the two tile factories along the street from Zwischenahn to Edewecht, 53°10′ N, 8°11′ E, ca 8 m [original label data: Oldenburg, auf Dachziegeln der beiden Ziegeleien an der Chaussee Zwischenahn-Edewecht] *Sandstede s.n.* (= *Arnold, Lich. Exs. 1780*) (M!, lectotype selected here, H-Nyl 5795, isolectotype).

Buellia nigerrima (Nyl.) Arnold, Lich. Exs.. 1780. 1899.

Buellia aethaleoides (Nyl.) H. Olivier, Bull. Acad. Intern. Géogr. Bot 12: 176. 1903.

Buellia baltica Erichsen, Verh. Bot. Ver. Prov. Brandenburg 72: 46. 1930. TYPE: GERMANY. SCHLESWIG-HOLSTEIN. Kreis Plön. Hohwacht, on immersed stones of scree dunes near Strandesberg, supralittoral zone, 54°19′ N, 10°40′60″ E, ca 0 m [original label data: an eingebetteten Steinen der Gerölldünen bei Strandesberg, supralittoral zone], 29 August 1933, *Erichsen s.n.* (HBG, lectotype *fide* Scheidegger 1993: 344, as ''holotype''; S!, isolectotype); Kreis Ekernförde, an Blöcken am Strande bei Aschau, 21 September 1924, Erichsen *s.n.* (= *Lich. Exs. P. Vrang 113,* S!—syntype). NOTE: The specimen mentioned by Scheidegger (1993) as holotype is effectively a lectotype, because the protologue indiscriminately mentions several specimens.

Buellia sororioides Erichsen, Verh. Bot. Ver. Prov. Brandenburg 72: 49. 1930. TYPE: GERMANY. SCHLESWIG-HOLSTEIN. Kreis Lauenburg. On erratic boulders near Buchhorst, 53°22′ N, 10°34′ E, ca 8 m [original label data: Kreis Lauenburg. An erratischen Blöcken bei Buchhorst], 3 October 1926, *Erichsen s.n.* (HBG, lectotype *fide* Scheidegger 1993: 344, as ''holotype''); Kreis Eckernförde. An fränkischen Steingräbern am Strande bei Hemmelmark, 20 July 1925, *Erichsen 18* (= *Lich. Exs. P. Vrang 23,* S!, syntype; US!, syntype); Kreis Plön. Hohwacht bei Strandersberg. An Geröll am Strand, 1933, *Erichsen s.n.* (S!, syntype). NOTE: The specimen mentioned by Scheidegger (1993) as holotype is effectively a lectotype, because the protologue by Erichsen indiscriminately mentions several specimens.

Buellia sororioides f. *dendritica* Erichsen, Verh. Bot. Ver.

TABLE 1. Key characters of the *Buellia aethalea*-group from the Greater Sonoran Desert Region and similar North American species.

Species	Thallus	Hypothallus	Apothecia	Exciple	Spores	Medulla (I−/I+) chemistry
Buellia aethalea	areolate, thin, pale gray to dark gray	usually present, rarely faint or absent	immersed, central, not becoming sessile, disc irregular	*aethalea*-type *cinereorufa*-green present	*Beltraminia*-type i.e., no septum thickening	I+ blue or I−; only norstictic and stictic acid, no atranorin
Buellia spuria	areolate, thin to ± thick; whitish gray to dark gray	often present and strongly developed	emergent, disc circular, frequently with thalline veil	*aethalea*-type *cinereorufa*-green present	*Beltraminia*-type i.e., no septum thickening	I+ blue; atranorin and norstictic and stictic acid
Buellia stellulata	areolate, thin to ± thick; whitish gray to dark gray	often present and strongly developed	emergent, disc circular, frequently with thalline veil	*aethalea*-type *cinereorufa*-green present	*Beltraminia*-type i.e., no septum thickening	I−; atranorin and 2′-*O*-methylperlatolic and/or confluentic acid
SONORAN but possibly not closely related to the *Buellia aethalea*-group						
Buellia eganii	areolate, thick, pale gray to pale brown	often present, but sometimes faint or absent	immersed, lateral, not becoming sessile, disc irregular	*aethalea*-type *cinereorufa*-green absent	*Beltraminia*-type i.e., no septum thickening	I−; lecanoric acid, no atranorin
Buellia lacteoidea	areolate, thin to thick; ivory to pale creamy white, rarely grayish	often present and usually strongly developed	immersed, rarely emergent, disc irregular, usually without thalline veil	*aethalea*-type *cinereorufa*-green present	*Physconia*-type i.e., with septum thickening	strongly I+ blue; atranorin, norstictic, rarely gyrophoric acid
NOT present in the Southwest						
Buellia lepidastra	granular areolate to verrucose, thin to ± thick; dull sordid gray	usually present but not strongly developed	emergent, disc circular, without thalline veil	*aethalea*-type *cinereorufa*-green in outer exciple only	*Beltraminia*-type i.e., no septum thickening	I−; ± norstictic and stictic acid
Buellia maculata	areolate, thin to ± thick; ivory to pale creamy white, rarely grayish	often present and strongly developed	emergent, disc circular, frequently with thalline veil	*aethalea*-type *cinereorufa*-green absent	*Beltraminia*-type i.e., no septum thickening	I+ blue; atranorin and norstictic acid

Prov. Brandenburg 72: 49. 1930. TYPE: GERMANY. SCHLESWIG-HOLSTEIN. Kreis Flensburg. Angeln. On scree along the beach near Birknach [original label data: auf Geröll am Strande bei Birknach], 21 September 1914, *Erichsen s.n.* (HBG, holotype *fide* Scheidegger 1993).

Buellia subatra Erichsen, Hedwigia 70: 218. 1930. TYPE: GERMANY. SCHLESWIG-HOLSTEIN. Kreis Lauenburg. Growing abundantly on a wall of boulders west of Kasseburg, along the way to Friedrichsruh, 53°34′ N, 10°24′ E ca 43 m [original label data: an einem Blockwall westl. von Kasseburg, am Wege nach Friedrichsruh, in Menge], 1 April 1927, *Erichsen s.n.* (HBG, holotype *fide* Scheidegger 1993; S!, two isotypes). NOTE: The material seen by Scheidegger (1993) might better be regarded as a lectotype, but it was not available for study. The specimens in S would then have to be regarded as syntypes.

For additional synonyms see Foucard et al. (2002).

Thallus (Fig. 1A–B) crustose, thin, ± continuous, epilithic; areolate; hypothallus usually distinct, black, between areoles and surrounding thallus; thallus surface matt, usually crusty and gray to pale brown, rarely dark gray, epruinose, phenocorticate; medul-la lacking Ca-oxalate (H_2SO_4−). *Apothecia* lecidei-ne; (0.1–)0.2–0.3(–0.5) mm in diameter; remaining immersed, not becoming sessile, predominantly in

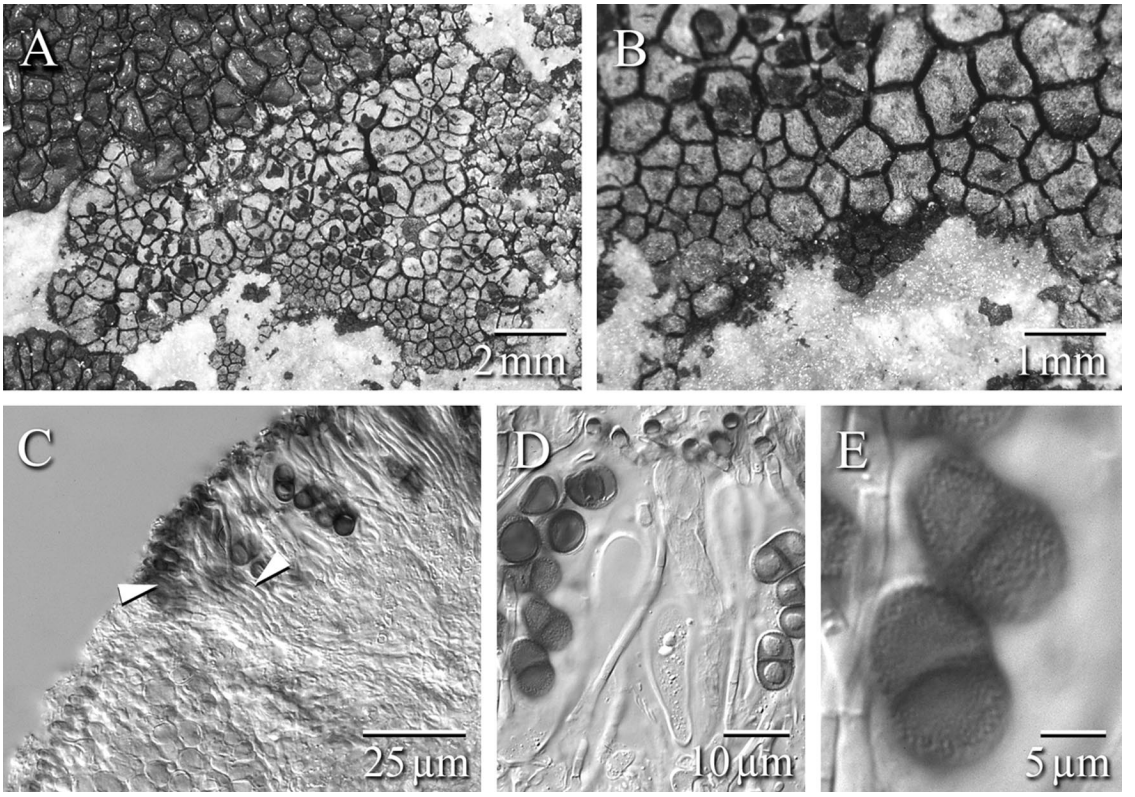

FIGURE 1. *Buellia aethalea* (light micrographs). — A. Areolate thallus with immersed apothecia (*Ryan 23545*). — B. Close-up of areoles with irregular, predominantly central apothecia (*Ryan 23545*). — C. Transverse section of apothecium (arrows indicate the reduced *aethalea*-type exciple; *Nash 25427*). — D. Hymenium with asci, paraphyses, and ascospores (*Ryan 23545*). — E. Microrugulate mature ascospores (*Ryan 23545*).

center of areoles; proper margin indistinct, reduced, inconspicious, black; disc black. These characteristic black spots, resembling tiny buttons, lend the lichen its colloquial name "darkened button lichen." It features epruinose, plane, not becoming convex with age; exciple narrow, poorly differentiated, of *aethalea*-type (Fig. 1C) i.e., inner excipular hyphae narrow, hyaline, prosoplectenchymatous (*textura oblita*), often reduced, similar in structure and orientation to paraphyses, transient with hyaline to pale brown hypothecium (*textura intricata*); outer excipular hyphae parallel, moderately swollen (*textura oblita*) and usually strongly carbonized with various amounts of brown and aeruginose pigments (cf. *elachista*-brown & *cinereorufa*-green, HNO_3+ violet), pigmentation continuous with epihymenium; hymenium hyaline, not inspersed; paraphyses simple to moderately branched, apically swollen, with brown pigment cap (cf. *elachista*-brown) and diffuse, aeruginose pigment (HNO_3+ violet, *cinereorufa*-green). *Asci* 8-spored, clavate, *Bacidia*-type. *Ascospores* (Fig. 1D–E) soon becoming pigmented, initially olive, brown at maturity, broadly ellipsoid, constricted with age, with obtuse ends, not curved, (11.0–) 11.6–[12.8]–14.1(–17.0) × (5.0–)7.2–[8.1]–8.9(–10.0) µm (n = 60); one-septate, proper septum and spore wall narrow, not thickened during spore ontogeny, lateral wall thickenings absent [*Beltraminea* (= *Buellia*)-type]; ornamentation microrugulate. *Pycnidia* rare, urceolate to globose, unilocular, at maturity almost entirely occupied by densely branched conidiophores; conidiogeneous cells mostly terminal, rarely also intercalary (cf. conidiophore-type V); pycnidial ontogeny similar to *Umbilicaria*-type; conidia simple, bacilliform, 5.0–5.5× <1.0 µm (n = 20).

Chemistry.—The thallus and medulla react K+ yellow to red (forming crystals), P+ yellow, C−, KC−, CK−. UV− (dark). All Sonoran material examined has an I− medulla; the hymenium reacts amyloid. The Sonoran specimens are characterized by norstictic and connorstictic acid only. Other substances are absent.

Substrate and ecology.—On a variety of hard, siliceous (HCl−) rock substrates.

Distribution (Fig. 6).—Rare, in the Sonoran region currently known only from a few localities at higher elevation.

Notes.—All Sonoran specimens have a hyaline

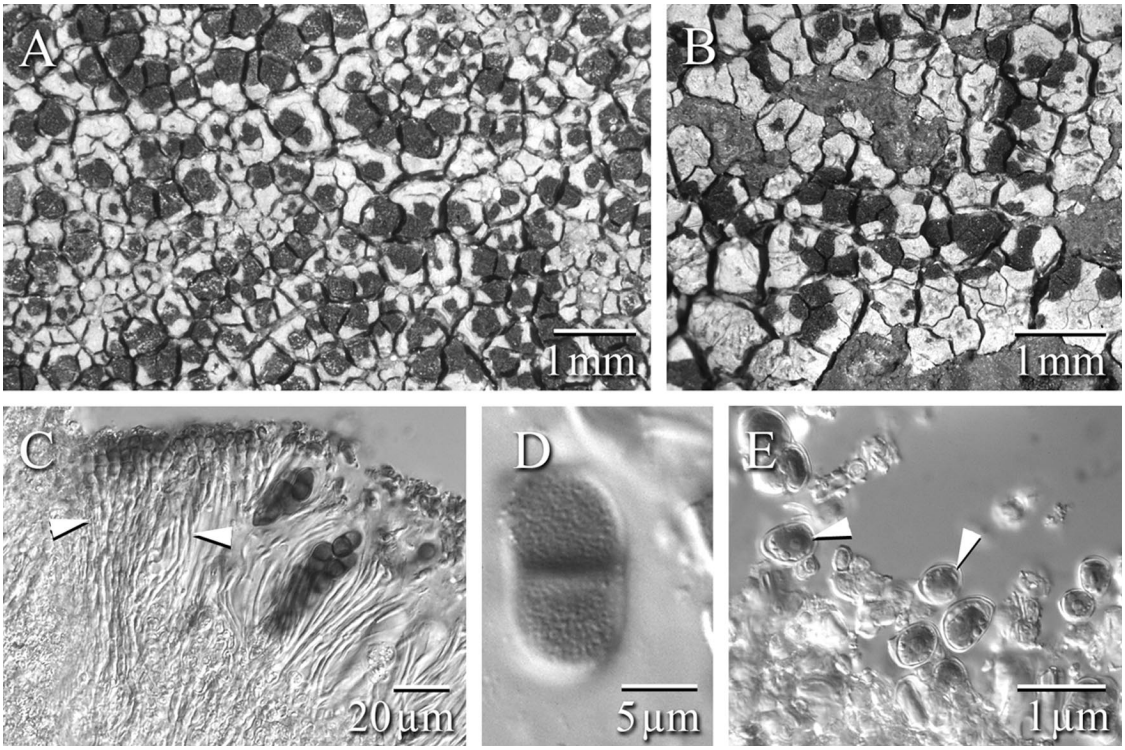

FIGURE 2. *Buellia eganii* (light micrographs). — A. Areolate thallus with immersed apothecia (*Nash 25427*). — B. Close-up of areoles with irregular, predominantly marginal apothecia (*Nordin 5311*). — C. Transverse section of apothecium (arrows indicate the reduced *aethalea*-type exciple; *Nordin 5311*). — D. Microrugulate mature ascospore (*Nordin 5311*). — E. Photobiont cells of *Buellia eganii* (arrows indicate single cells of the alga *Trebouxia*. sp.; *Nordin 5311*).

to faintly brown hypothecium. Scheidegger (1993) reported that hypothecium pigmentation of European specimens varies from hyaline to dark brown. This is rather unusual because *Buellia s.str*. is generally characterized by a dark hypothecium. Scheidegger (1993) reported that medullary reactions with Lugol's iodine vary considerably. All Sonoran specimens are, however, I−.

Additional specimens examined.—EUROPE. FRANCE. PYRENÉES ORIENTALES. *Scheidegger Inv. Nr. 7990, 8293, 8092* (hb. Scheidegger). GERMANY. NIEDERSACHSEN. Kreis Gosslar. *Imshaug 36300* (MSC-76545), *Ullrich s.n.* (MSC-67311). SWEDEN. VÄRMLANDS LAN. *Sundell s.n.* (MSC-40864). SKÅNE. *Almborn s.n.* (ASU). SWITZERLAND. WALLIS. *Scheidegger Inv. Nr. 8554* (hb. Scheidegger).—NORTH AMERICA. U.S.A. ARIZONA. Apache Co. *Nash 26943* (ASU). Cochise Co. *Weber S28044a* (ASU). Coconino Co. *Nash 25427b* (ASU). PIMA CO. *Nash 20716* (ASU). Santa Cruz Co. *Nash 18583* (ASU); *Scheidegger field notes 31–39* (hb. Scheidegger). COLORADO. Clear Creek Co. *Anderson 5292* (ASU). MICHIGAN. Washtenaw Co. *Harris 7687* (MSC-127522). SOUTH DAKOTA. Custer Co. *Wetmore 10338 B* (MSC-68823). Lawrence Co. *Wetmore 8506* (MSC-69496). Pennington Co. *Wetmore 3451* (MSC-68965). WYOMING. Crook Co. *Climbers 11423 A* (MSC-69773).—SOUTH AMERICA. ARGENTINA. CATAMARCA. *Lamb 5587* (MSC-340260).

BUELLIA EGANII Bungartz, *sp. nov.*

Thallus saxicolus, crustaceus, areolatus, crassus, griseus vel badius, fulvus. Hypothallus atratus. Apothecia immersa, lecideina, marginibus propriis tenuibus. Excipulum tenue, fulvo-caeruleum, pigmentum aeruginosum deficiens, carbonaceum. Asci 8-spori. Sporae uniseptatae, ellipsoideae vel oblongae, 12–18 × 6–9 µm. Thallus acidum lecanoricum continens. Similis Buelliae athaleae sed apothecibus lateralibus, thallo crasso et substantia chimica differt.

TYPE: U.S.A. NEW MEXICO. Santa Fe Co. Lake Peak, 18 km NE of Santa Fe, 35°47′47″ N, 105°46′14″ W; alpine tundra; 3,750 m elevation; 14 August 1969; *Egan El-1672* (OMA!, holotype).

The species is named in honor of Robert S. Egan, University of Nebraska at Omaha. He first discovered *B. eganii* working on his Ph.D. dissertation. In his dissertation, Egan called the species *B. lakensis* referring to the type locality Lake Peak, New Mexico. His description was never validly published.

Thallus (Fig. 2A–B) crustose, moderately thick, ± dispersed, epilithic; areolate to subsquamulose; hypothallus absent or, if present, indistinct; thallus surface ± smooth and shiny, or matt, usually pale beige, rarely pale gray, epruinose, phenocorticate;

medulla lacking Ca oxalate (H_2SO_4-). *Apothecia* lecideine; (0.2–)0.3–0.5(–0.7) mm in diameter; remaining immersed, predominantly along margin of areoles; proper margin indistinct, reduced, inconspicious, black; disc black, epruinose, plane, rarely becoming slightly convex with age; exciple narrow, poorly differentiated, of *aethalea*-type (Fig. 2C) i.e., inner excipular hyphae narrow, hyaline, prosoplectenchymatous (*textura oblita*), often reduced, similar in structure and orientation to paraphyses, transient with hyaline to faintly brown hypothecium (pigmentation ± absent, *textura intricata*), outer excipular hyphae parallel, moderately swollen (*textura oblita*) and usually strongly carbonized with various amounts of brown pigments (cf. *elachista*-brown, HNO_3-), pigmentation continuous with epihymenium; hymenium hyaline, not inspersed; paraphyses simple to moderately branched, apically swollen, with brown pigment cap (cf. *elachista*-brown). *Asci* 8-spored, clavate, *Bacidia*-type. *Ascospores* (Fig. 2D) soon becoming pigmented, initially olive, brown at maturity, oblong to ellipsoid, usually not constricted, with obtuse ends, not curved, (12.0–)12.1–[13.7]–15.2(–18.0) × (6.0–)6.3–[7.0]–7.7(–9.0) μm (n = 60); one-septate, proper septum and spore wall narrow, not thickened during spore ontogeny [*Beltraminea* (= *Buellia*)-type]; ornamentation microrugulate. *Pycnidia* rare, urceolate to globose, unilocular, at maturity almost entirely occupied by densely branched conidiophores; conidiogeneous cells mostly terminal, rarely also intercalary (cf. conidiophore-type V); pycnidial ontogeny similar to *Umbilicaria*-type; conidia simple, bacilliform, 4.0–7.0× <1.0 μm (n = 20).

Chemistry.—Thallus and medulla C+ pink (fleeting), KC+ pink (fleeting) or C−, KC−, K−, P−. UV+ pale beige to yellow. Thallus cortex and medulla not amyloid; the hymenium reacts amyloid. The thallus is characterized by the presence of lecanoric acid and 5-*O*-methylhiascic acid (confirmed by HPLC).

Substrate and ecology.—On a variety of siliceous (HCl−) rock substrates in subalpine to alpine habitats.

Distribution (Fig. 6).—Currently only known from Lake Peak and Sierra Blanca Peak (New Mexico), Mt. Humphries (San Francisco Peaks, Arizona), and the White Mountains (Arizona).

Notes.—The species is morphologically and anatomically similar to *B. aethalea*, but because of the different chemistry and the absence of *cinereorufa*-green is possibly not closely related.

Additional specimens examined.—NORTH AMERICA. U.S.A. ARIZONA. Apache Co. *Nash 11720* (ASU). Coconino Co. *Nash 36934* (ASU); *Nordin 5311* (UPS). NEW MEXICO. Santa Fe Co. *Egan El-2532* (OMA). Otero Co. *El-1747* (OMA).

BUELLIA LACTEOIDEA de Lesd., Ann. Crypt. Exot. 5: 129. 1932.

TYPE: U.S.A. NEW MEXICO. San Miguel Co. Hermit's Peak, 35°44′39″ N, 105°24′52″ W; on siliceous rock [original label data: Hermit's Peak, roche siliceuse], 3,110 m elevation, 2 July 1930, *Frère Arsène Brouard s.n.* (W!, lectotype selected here; s!, UPS!, isolectotypes). NOTE: The lectotype has been selected here because it can be assumed that the original material was destroyed in World War II.

Thallus (Fig. 3A–B) crustose, thin to moderately thick, ± dispersed, epilithic; areolate; hypothallus conspiciously black, frequently strongly developed and usually between areoles as well as surrounding thallus outline; thallus surface matt, white to whitish gray, rarely beige, epruinose; phenocorticate; medulla lacking Ca oxalate (H_2SO_4-). *Apothecia* lecideine; (0.2–)0.3–0.6(–1.1) mm in diameter; remaining immersed, not becoming sessile (but disc sometimes convex and emerging from surface); proper margin indistinct, reduced, inconspicious, black or rarely masked by thalline veil; disc black, epruinose, plane, often becoming strongly convex with age; exciple narrow, poorly differentiated, of *aethalea*-type (Fig. 3C, F) i.e., inner excipular hyphae narrow, hyaline, prosoplectenchymatous (*textura oblita*), often reduced, similar in structure and orientation to paraphyses, transient with hyaline subhymenium and brown hypothecium (*leptoclinoides*-brown, *textura intricata*), outer excipular hyphae parallel, moderately swollen (*textura oblita*) and usually strongly carbonized with various amounts of brown and aeruginose pigments (cf. *elachista*-brown and *cinereorufa*-green), pigmentation continuous with epihymenium; hymenium hyaline, not inspersed; paraphyses simple to moderately branched, apically swollen, with brown pigment cap (cf. *elachista*-brown) and diffuse, aeruginose pigment (HNO_3+ violet, *cinereorufa*-green). *Asci* 8-spored, clavate, *Bacidia*-type. *Ascospores* (Fig. 3D–E, G–H) soon becoming pigmented, initially olive, brown at maturity, oblong to ellipsoid, usually not constricted, with obtuse ends, not curved, (12.0–)13.5–[15.1]–16.7(–20.0) × (6.0–)6.2–[7.0]–7.9(–9.0) μm (n = 60); one-septate, proper septum soon but only briefly thickened during spore ontogeny (*Physconia*-type); ornamentation rugulate; septum with septal pore canal, simple pore and undifferentiated pore plug; spore wall (Fig. 3G–H) differentiated into cracked, thin perispore (0.10–0.15 μm), narrow intermediate layer (<0.06 μm), thick proper spore wall (0.30–0.47 μm) and thick endospore (0.30–0.57 μm). *Pycnidia* rare, urceolate to globose, unilocular, at maturity

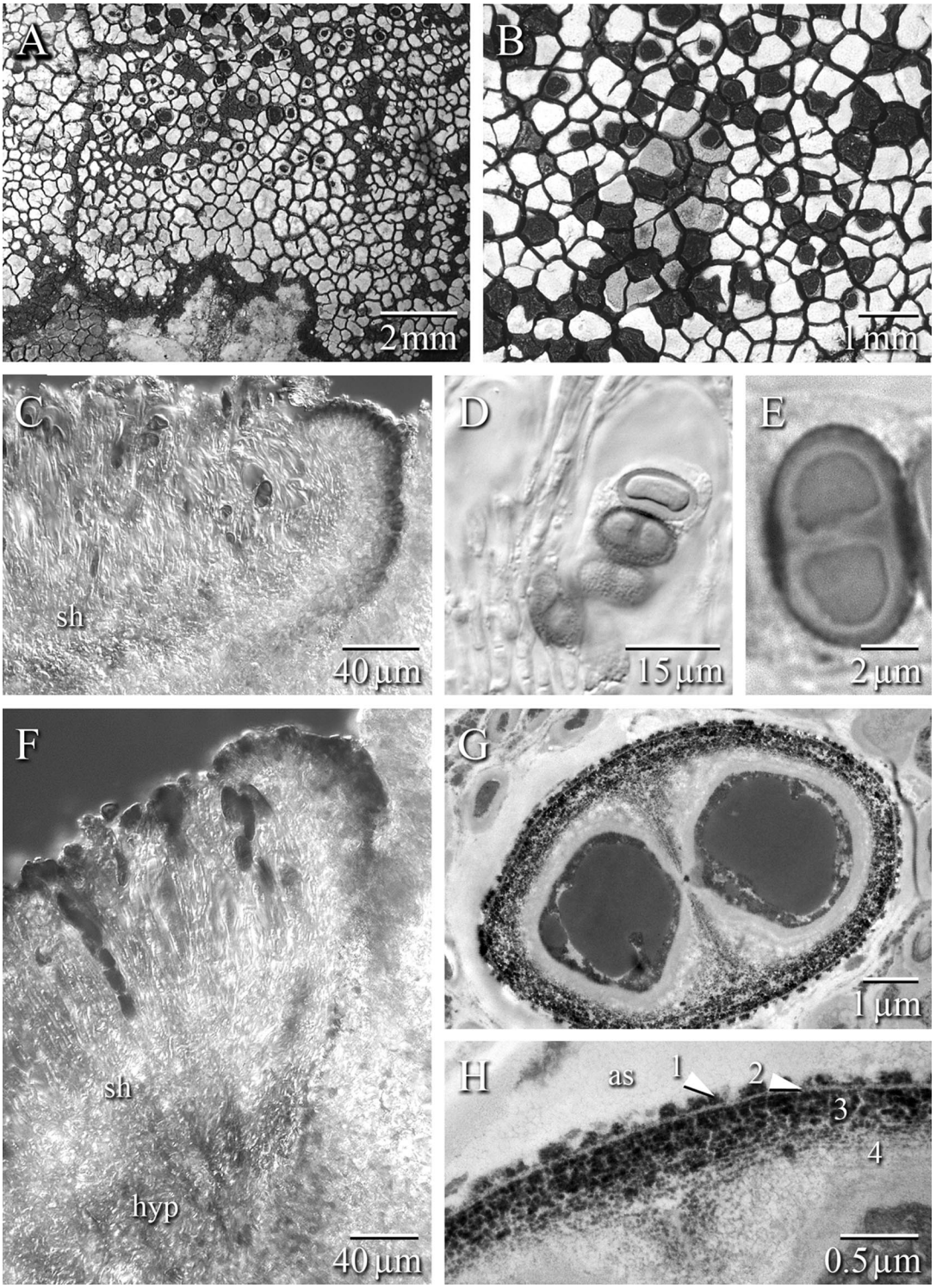

FIGURE 3. *Buellia lacteoidea* [A–F. light micrographs (*Ryan 10885*), G–H. TEM micrographs (*Nordin 5162*)]. — A. Areolate thallus with immersed apothecia. — B. Close-up of areoles with irregular, predominantly marginal apothecia. — C. Transverse section of young apothecium with hyaline subhymenium (sh). — D. Ascus with immature ascospores. — E. Premature ascospore with a ± thickened septum. — F. Transverse section of older apothecium with a hyaline subhymenium (sh) and dark hypothecium (hyp). — G. Mature ascospore. — H. Spore wall of mature ascospore: (as) ascus wall; (1) perispore; (2) intermediate layer; (3) proper spore wall; (4) endospore.

almost entirely occupied by densely branched conidiophores; conidiogeneous cells mostly terminal, rarely also intercalary (cf. conidiophore-type V); pycnidial ontogeny similar to *Umbilicaria*-type; conidia simple, bacilliform, 2.5–4.5 × 1.5–2.0 μm (n = 20).

Chemistry.—The thallus and medulla usually react K+ yellow to red (forming crystals), P+ yellow, C− (rarely C+ pink), KC− (rarely KC+ pink), CK−. UV+ pale ivory (if gyrophoric acid is present). The medulla reacts very strongly amyloid and this reaction can even be observed if specimens are tested directly on the thallus cortex. The hymenium also reacts amyloid. Specimens generally contain atranorin, norstictic, and connorstictic acid. Additionally gyrophoric acid may also be present. The following HPLC-artifacts were observed: haematommic acid, methyl β-orsellinate.

Substrate and ecology.—On a variety of hard siliceous (HCl−) rock substrates.

Distribution (Fig. 6).—Only known from western North America; not a typical desert species, but frequent at higher elevation (montane).

Notes.—Buellia lacteoidea has often been confused with *B. spuria*. The two species are superficially similar. Imshaug (1951) suggested that these species can be distinguished by the hyaline hypothecium of *B. lacteoidea*. This suggestion is misleading. *Buellia lacteoidea* is the only species currently known from the Sonoran Region with a differentiation of a hyaline subhymenium and a pigmented hypothecium. Although the hypothecium of young specimens of *B. lacteoidea* is only faintly colored, this pigmentation becomes stronger with age. If mature apothecia are sectioned for comparison, *B. lacteoidea* may thus easily be confused with *B. spuria*. The species can, nevertheless, be distinguished by the hypothecium and by the spore ontogeny and position of the apothecia. In *B. lacteoidea* apothecia generally remain immersed and often become deformed by adjoining areoles. Young apothecia of *B. spuria* are also immersed but eventually emerge from the thallus and become distinctly sessile. *Buellia lacteoidea* has spores with a brief phase when a distinctly thickened median septum can be distinguished. No wall or septum thickenings are present during the spore ontogeny of *B. spuria*. Both species have a medulla reacting with Lugol's iodine, but the reaction is much stronger and more persistent in *B. lacteoidea*.

Additional specimens examined.—NORTH AMERICA. MEXICO. BAJA CALIFORNIA. *Nash 14739* (ASU). U.S.A. ARIZONA. Apache Co. *Hertel 40155* (M). Cochise Co. *Darrow 4208, Nash 14579, Nordin 5162* (UPS). Coconino Co. *Hertel 40297* (M). Gila Co. *Nash 6649* (M). Graham Co. *Nash 16630* (ASU). Greenlee Co. *Nash 10642b* (ASU). Pima Co. *Hertel 40013* (M);. Santa Cruz Co. *Nash 18582* (ASU). COLORADO. Boulder Co. *Anderson 9287* (ASU). NEW MEXICO. Catron Co. *Nash 22588* (ASU). Sierra Co. *Nash 7110* (ASU). San Miguel Co. *Imshaug 9940* (MSC-335171). SOUTH DAKOTA. Custer Co. *Wetmore 7219* (MSC-65895). Pennington Co. *Wetmore 6450* (M-0061340); *Imshaug 8034 A* (MSC-65968). UTAH. Garfield Co. *Nebecker 2166* (ASU).

BUELLIA SPURIA (Schaer.) Anzi, Cat. Lich. Sondr. 87. 1860.

Lecidea spuria Schaer., Lich. Helvet. Spicil. Sect. 3: 127. 1828. TYPE: SWITZERLAND. KANTON ZÜRICH. On granitic alpine boulders growing with *Lecidea atro-alba* [original label data: *Ad saxa granitica,* Schleicher, 1823 sub *Lecidea atro-alba*; Hepp, Flechten Europas Nr. 33, auf Alpenfindlingen bei Zürich], collected by *Schleicher s.n.,* distributed by Hepp, *Lich. Helvet. Exs. 33* (BERN, neotype, selected by Scheidegger 1993; M-0023903!, isoneotype; BM-000660170!, isoneotype).

Catolechia lactea A. Massal., Ricerch. Auton. Lich. 84. 1852. TYPE: ITALY. VENETO. Monte Bolca. On basalt, 45°36′ N, 11°11′ E, ca 791 m [original label data: *ad basaltica*], 1849, *Massalongo s.n.* (MOD, holotype *fide* Scheidegger 1993).

Buellia italica var. *lactea* A. Massal, Schedul. Critic. 9: 193. 1856.

Buellia italica var. *recobarina* A. Massal., Sched. Crit. 9: 163. 1865. TYPE: ITALY. Living on rock in the vicinity of Voltri [original label data: Vive sulli rupe nelle vicinanze di Voltri], *Massalongo s.n.* (W, isotype *fide* Scheidegger 1993).

Buellia lactea var. *olivaceofusca* Anzi, Atti. Soc. Ital. Sci. Natur. 9: 252. 1866. TYPE: ITALY. TOSCANA. On micaschist from the mountain Pisano [original label data: Sul micaschisto nel monte Pisano] *Anzi s.n.* (TO, holotype; W, isotype *fide* Scheidegger 1993).

Buellia italica var. *insularis* Bagl., Nuov. Giorn. Bot. Ital. 3: 264. 1871. TYPE: ITALY. SARDINIA. Orri, *Baglietto s.n.* (G, isotype *fide* Scheidegger 1993).

Lecidea exilis Kremp., Verh. zool.-bot. Ges. Wien 26: 444. 1876. *non* Kremp. Verh. zool.-bot. Ges. Wien 30: 340. 1880. TYPE: PERU. LIMA. Circumnavigation of the World by S.M. Donau 1868–1871, *Barrania s.n.* (M-0023771!). NOTE: The type material is a specimen named by Krempelhuber as *Lecidea excilis* Kremp. (Verh. zool.-bot. Ges. Wien 30: 340. 1880). Mayrhofer recognized the name as illegitimate and annotated the specimen as *Buellia krempelhuberi* Zahlbr. (*vidi* H. Mayrhofer, Graz, 1983). The specimen was examined by Elix and Wrardlaw using HPLC and contains: atranorin (major), chloroatranorin (major), norstictic acid (minor), stictic acid (major), cryptostictic acid (minor).

Buellia exilis (Kremp.) Müll. Arg., Flora 70: 61. 1887.

Buellia liguriensis de Lesd., Bull. Soc. Bot. France 101(5–6): 225. 1954. TYPE: ITALY. LIGURIA. Spotorno. On rock. [original label data: *Liguria occid.: Spotorno; rupicola, specim. orig.*]; January 1953, *Sbarbaro s.n.* (US!, lectotype selected here). NOTE: The original material was probably destroyed in World War II.

Buellia lactea (A. Massal.) Körb., Parerg. Lich.: 183. 1860.

Buellia olivaceofusca (Anzi) Zahlbr., Cat. Lich. Univ. 7: 385. 1931.

Buellia norstictica Imshaug ined. NOTE: Name never validly published. Two specimens deposited in M collected by Imshaug and Harris on the East Falkland Islands belong to *Buellia spuria* (UTM Grid 21F VC 4373, Port

William: Outcrops on Engineer Point headland, The Narrows, 50 ft. (15 m) 19 January 1968. *Imshaug 40617*; UTM Grid 21F VC 3472, Stanley: Empetrum-heath & outcrops on Tumbledown Mountain, 500–700 ft. (150–215 m) 3 January 1968, *Imshaug 39675*).

Thallus (Fig. 4A–B) crustose, thin to moderately thickened, ± continuous, epilithic; areolate; hypothallus conspiciously black, in most specimens strongly developed and growing between areoles, rarely only surrounding thallus outline; thallus surface matt, usually white to whitish gray, rarely dark gray, epruinose, phenocorticate; medulla lacking Ca-oxalate (H_2SO_4-). *Apothecia* lecideine; (0.2–)0.3–0.4(–0.5) mm in diameter; immersed to adnate, rarely sessile; proper margin thin, ± persistent, rarely excluded with age, black or color masked by grayish remains of necrotic thalline material (thalline veil); disc black, epruinose, plane, rarely becoming slightly convex with age; exciple narrow, poorly differentiated, of *aethalea*-type (Fig. 4C) i.e., inner excipular hyphae narrow, hyaline, prosoplectenchymatous (*textura oblita*), often reduced, similar in structure and orientation to paraphyses, transient with deep reddish brown hypothecium (*leptoclinoides*-brown, *textura intricata*), outer excipular hyphae parallel, moderately swollen (*textura oblita*) and usually strongly carbonized with various amounts of brown and aeruginose pigments (cf. *elachista*-brown and *cinereorufa*-green), pigmentation continuous with epihymenium; hymenium hyaline, not inspersed; paraphyses simple to moderately branched, apically swollen, with brown pigment cap (cf. *elachista*-brown) and diffuse, aeruginose pigment (HNO_3+ violet, *cinereorufa*-green). *Asci* 8-spored, clavate, *Bacidia*-type (Fig. 4E, H). *Ascospores* (Fig. 4D, F–G) soon becoming pigmented, initially olive, brown at maturity, oblong to ellipsoid, usually not constricted, with obtuse ends, not curved, (11.0–)11.9–[13.3]–14.8(–18.0) × (5.0–)5.9–[6.7]–7.4(–8.0) μm ($n = 60$); one-septate, proper septum and spore wall narrow, not thickening during spore ontogeny [*Beltraminea* (= *Buellia*)-type]; ornamentation microrugulate, or absent in some specimens; septum with septal pore canal, simple pore and undifferentiated pore plug; spore wall (Fig. 4I) differentiated into smooth to fissured, thin perispore (0.18–0.23 μm), narrow intermediate layer (<0.03 μm), thick proper spore wall (0.32–0.50 μm) and thin endospore (0.10–0.16 μm). *Pycnidia* rare, urceolate to globose, unilocular, at maturity almost entirely occupied by densely branched conidiophores; conidiogeneous cells mostly terminal, rarely also intercalary (cf. conidiophore-type V); pycnidial ontogeny similar to the *Umbilicaria*-type; conidia simple, bacilliform, 4.5–6.0 × 0.5–1.0 μm ($n = 20$).

Chemistry.—The thallus usually reacts K+ yellow to red (forming crystals), P− or + yellow, C−, KC−, CK−. UV− (dark). The thallus medulla is amyloid, but the reaction is only observed if the solution is directly applied to the medulla, not the cortex. The hymenium reacts amyloid. Atranorin and chloroatranorin and artifacts generated by the hydrolysis of atranorin (haematommic acid and methyl β-orsellinate) have been detected by HPLC. In addition, norstictic and connorstictic acid are regularly present and several other depsidones can also be reported: stictic with constictic acid and cryptostictic, hypostictic, and methylstictic acid (detected by HPLC).

Substrate and ecology.—On a variety of siliceous (HCl−) rock substrates.

Distribution (Fig. 6).—Common and widely distributed throughout the Northern Hemisphere. In the Sonoran Region not a typical desert species, but frequent at higher elevations (montane).

Notes.—For comparison with *B. lacteoidea*, see notes on that species. *Buellia stellulata* is morphologically similar, but consistently has a non-amyloid medulla and contains 2′-*O*-methylperlatolic acid instead of norstictic acid.

Additional specimens examined.—EUROPE. FRANCE. LANGUEDOC. *Vězda s.n.* (MSC-77231). ITALY. LIGURIA. *Sbarbaro s.n.* (MSC-146477), *Sbarbaro s.n.* (MSC-146480).—CENTRAL AMERICA. CUBA. LA HABANA. *Imshaug 24742* (MSC-348151), *Imshaug 25013* (MSC-348113).—NORTH AMERICA. MEXICO. BAJA CALIFORNIA. *Nash 34365* (ASU). BAJA CALIFORNIA SUR. *Nash 30404* (ASU). CHIHUAHUA. *Nash 31199* (ASU). DURANGO. *Nash 13936* (ASU). SINALOA. *Nash 12169* (ASU). SONORA. *Wetmore 71688* (MIN); *Ryan 21626* (ASU). U.S.A. ARIZONA. Apache Co. *Nash 10545* (ASU). Cochise Co. *Hertel 40054* (M). Coconino Co. *Zschau s.n.* (ASU). Gila Co. *Biringer 115* (ASU). Graham Co. *Nash 36053* (ASU). Greenlee Co. *Nash 10642a* (ASU). Navajo Co. *Nash 11185* (ASU). Pima Co. *Biringer 40* (ASU); *Hertel 39914a* (M). Santa Cruz Co. *Darrow 4259* (ASU). Yavapai Co. *Nash 6337* (ASU). COLORADO. Jefferson Co. *Weber 18939* (MSC-54263), *Erdman 18939* (MSC-54263). LOUISIANA. Natchitoches Co. *Tucker 17480* (SBBG, MSC-141381). MONTANA. Gallatin Co. *Nash 21672* (ASU). NEW MEXICO. Socorro Co. *Nash 22538* (ASU). TEXAS. Brewster Co. *Wetmore 19408* (MIN). SOUTH DAKOTA. Custer Co. *Wetmore 7583B* (MSC-69458). TEXAS. Jeff Davis Co. *Nash 6563* (MIN). WASHINGTON. Whatcom Co. *Ryan 7856* (ASU).—SOUTH AMERICA. ARGENTINA. CATAMARCA. *Lamb 5525* (MSC-354199), *5504* (MSC-340263). TUCUMAN. *Lamb 5354* (MSC).

BUELLIA STELLULATA (Taylor) Mudd, Manual Brit. Lich. 216. 1861.

Lecidea stellulata Taylor in Mack., Flora Hibernica 2: 118. 1836. TYPE: IRELAND: *possibly* in Kerry Co. Kerry Mountains, near Carrig East, 51°55′ N, 09°37′ W *or in* Cork Co. Caha Mountains. Carrigmount, 51°47′ N, 09°14′ W [original label data: Carig Mountain] *Taylor ex hb. Borrer s.n.* (BM-000660158!, lectotype selected by Foucard et al. 2002). NOTE: Foucard et al. (2002, p. 71) used the spelling ''Craig Mountain'' when selecting the lectotype. This must be an error. The spelling ''Craig'' was never used by Taylor and no such place apparently exists in Ireland (S. Louwhoff, lichen curator at BM, pers. comm.). Taylor (1836, p. 216) wrote in the protologue: ''. . . on silicious and aluminious rocks in the Kerry Mountains . . . .'' The lectotype collected by Borrer (BM-000660158) is annotated in Tay-

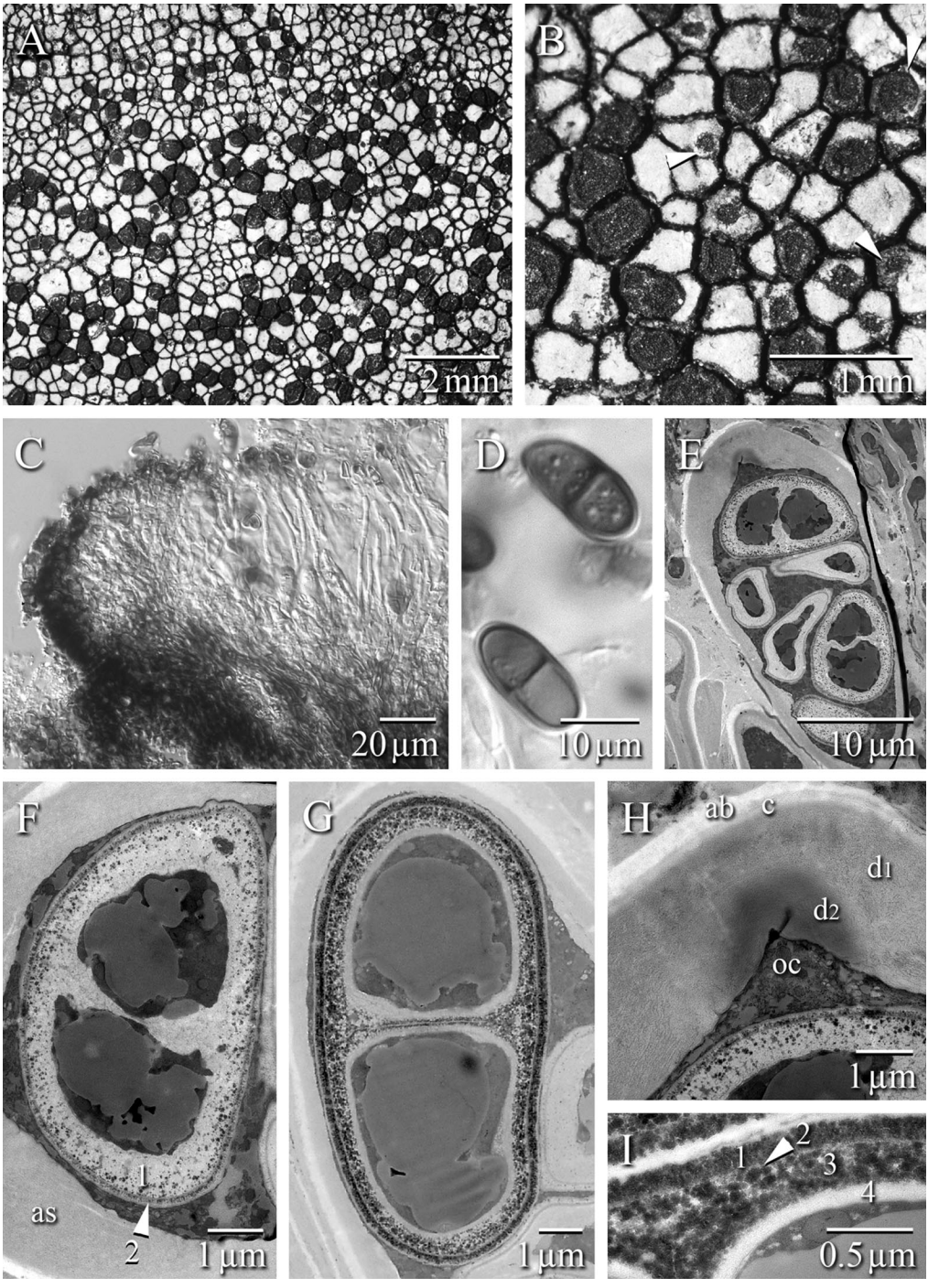

FIGURE 4. *Buellia spuria* [A–D. light micrographs (*Nash 10755*), E–I. TEM micrographs (*Nash 35879*)]. — A. Areolate thallus with immersed to slightly sessile, circular apothecia. — B. Close-up of areoles with ± immersed apothecia, some with a thalline veil (arrows). — C. Transverse section of an apothecium. — D. Mature ascospores. — E. Immature ascus. — F. Immature ascospore: the endospore and proper spore wall not yet fully differentiated (1), but the perispore (2) is clearly visible; (as) ascus wall. — G. Mature ascospore. — H. *Bacidia*-type ascus (for designation of the different layers see Bellemère 1994): The a- and b-layer (ab) are barely visible and cannot reliably be distinguished (possibly as a result of fixation artifacts); (c) outer electron opaque c-layer; (d1) d1-layer i.e., the outer tholus, which is distinctly laminated (in light microscopy this outer part stains deep blue with Lugol's iodine); (d2) d2-layer i.e., the inner tholus, which is not layered and ± homogeneous (not staining in Lugol's iodine); (oc) ocular chamber. — I. Spore wall of a mature ascospore: (1) perispore; (2) intermediate layer; (3) proper spore wall; (4) endospore.

lor's handwriting as ''*Lecidea stellulata* Tayl. Carig Mountain from Dr. Taylor in herb. Borrer''. Research for the type locality yielded little conclusive information. The label possibly refers to a mountain near East Carrig, a village northeast of Kenmare, Kerry Mountains, County Kerry. It is also possible that Taylor referred to Carrigmount, a peak in County Cork (close to the border of County Kerry).

Buellia candidula Arnold, Verh. zool. bot. Ges. Wien 22: 291. 1872. TYPE: ITALY. TRENTINO (= SOUTH TIROL). On boulders above Gries [original label data: An Blöcken oberhalb Gries], *Arnold s.n.* (M, holotype).

Buellia microstellulata Imsh. ined. NOTE: Imshaug never published this name. The specimens at MSC from South America (Juan Fernandez) belong to *B. stellulata*.

Buellia rinodina Malme ined. NOTE: A specimen in Krempelhuber's herbarium no. *3847* (M-0061371!) is annotated as ''*Buellia rinodina* Malme (*Lecidea squamulata* Fée)'', but this name was apparently never published. The specimen was collected by Glaziou in 1869 in Brazil, Rio de Janeiro. It clearly belongs to *B. stellulata*.

The following species have been treated as synonyms of *B. stellulata*, but do not belong to this taxon:

Buellia minutula (Körb.) Arn., Flora 53: 215. 1870. NOTE: Imshaug (1951) suggested that *Buellia minutula* is synonymous with *B. stellulata*. Hafellner, however, examined the specimen seen by Imshaug and annotated it as the type of *Karschia minutula* (unpublished annotation of a specimen seen in M).

Buellia maritima (A. Massal.) Bagl. in A. Massal., Schedul. Critic. 8: 150. 1856.—*Catolechia maritima* A. Massal., Framm. Lich.: 22. 1855. NOTE: Scheidegger (1993) included *B. maritima* (= *C. maritima*) as synonym, but the type is identical with *Buellia subalbula* according to Bungartz and Nash (2004).

Thallus (Fig. 5A–B) crustose, thin to moderately thickened, ± continuous, epilithic; areolate; hypothallus black, conspicious, in most specimens strongly developed and growing between areoles, rarely only surrounding thallus outline; thallus surface matt to ± shiny, usually white to whitish gray, rarely dark gray, epruinose, phenocorticate; medulla lacking Ca-oxalate (H_2SO_4-). *Apothecia* lecideine; (0.2–)0.3–0.4(–0.5) mm in diameter; immersed to adnate, rarely sessile; proper margin thin, ± persistent, rarely excluded with age, black or color masked by grayish remains of necrotic thalline material (thalline veil); disc black, epruinose, plane, rarely becoming slightly convex with age; exciple narrow, poorly differentiated, of *aethalea*-type (Fig. 5C) i.e., inner excipular hyphae narrow, hyaline, prosoplectenchymatous (*textura oblita*), often reduced, similar in structure and orientation to paraphyses, transient with deep reddish brown hypothecium (*leptoclinoides*-brown, *textura intricata*), outer excipular hyphae parallel, moderately swollen (*textura oblita*) and usually strongly carbonized with various amounts of brown and aeruginose pigments (cf. *elachista*-brown and *cinereorufa*-green), pigmentation continuous with epihymenium; hymenium hyaline, not inspersed; paraphyses simple to moderately branched, apically swollen, with brown pigment cap (cf. *elachista*-brown) and diffuse, aeruginose pigment (HNO_3+ violet, *cinereorufa*-green). *Asci* 8-spored, clavate, *Bacidia*-type (Fig. 5D). *Ascospores* (Fig. 5E–F) soon becoming pigmented, initially olive, brown at maturity, oblong to ellipsoid, usually not constricted, with obtuse ends, not curved, (8.0–)8.7–[9.9]–11.1(–13.0) × (4.5–)4.8–[5.5]–6.1(–7.0) μm (n = 60); one-septate, proper septum and spore wall narrow, not thickened during spore ontogeny, lateral wall thickenings absent [*Beltraminea* (= *Buellia*)-type]; ornamentation microrugulate, or absent in some specimens; septum with septal pore canal, simple pore, and undifferentiated pore plug; spore wall (Fig. 5G) differentiated into smooth, thin perispore (<0.06 μm), indistinct intermediate layer (<0.01 μm), thick proper spore wall (0.53–0.68 μm) and moderately thickened endospore (0.12–0.26 μm). *Pycnidia* rare, urceolate to globose, unilocular, at maturity almost entirely occupied by densely branched conidiophores; conidiogeneous cells mostly terminal, rarely also intercalary (cf. conidiophore-type V); pycnidial ontogeny similar to *Umbilicaria*-type; conidia simple, bacilliform, 3.5–4.0 × 0.5–1.0 μm (n = 20).

Chemistry.—The thalli typically react K+ yellow (sometimes weakly), P− or P+ faintly yellow, C−, KC−, CK−. UV− (dark). Thallus cortex and medulla are not amyloid but the hymenium reacts with Lugol's. Atranorin and 2′-*O*-methylperlatolic and/or confluentic acid are characteristic for this species.

Substrate and ecology.—On hard siliceous rock (generally HCl−), especially near the coast.

Distribution (Fig. 6).—Scheidegger (1993) suggested that this species occurs ''On sun exposed, calcareous or siliceous rocks in southern or central Europe''. The type specimen was, however, collected at an oceanic hillsite, in southwestern Ireland, not central or southwestern Europe. According to the British Lichen Flora (Orange et al. 1992), the species is most typical ''On hard, rocks and pebbles, mainly maritime in the xeric supralittoral. N. & W. Britain, Ireland. N. & C. Europe.'' Sheard (1964) also emphasized the coastal distribution of the species. It is very unlikely that the species extends far inland into southern or central Europe and Scheidegger's (1993) reference thus appears somewhat misleading. Reports of *B. stellulata* from inland localities should carefully be re-examined. It is possible that these specimens have been misidentified.

In the Sonoran Region, only specimens from coastal areas of California and Baja California are

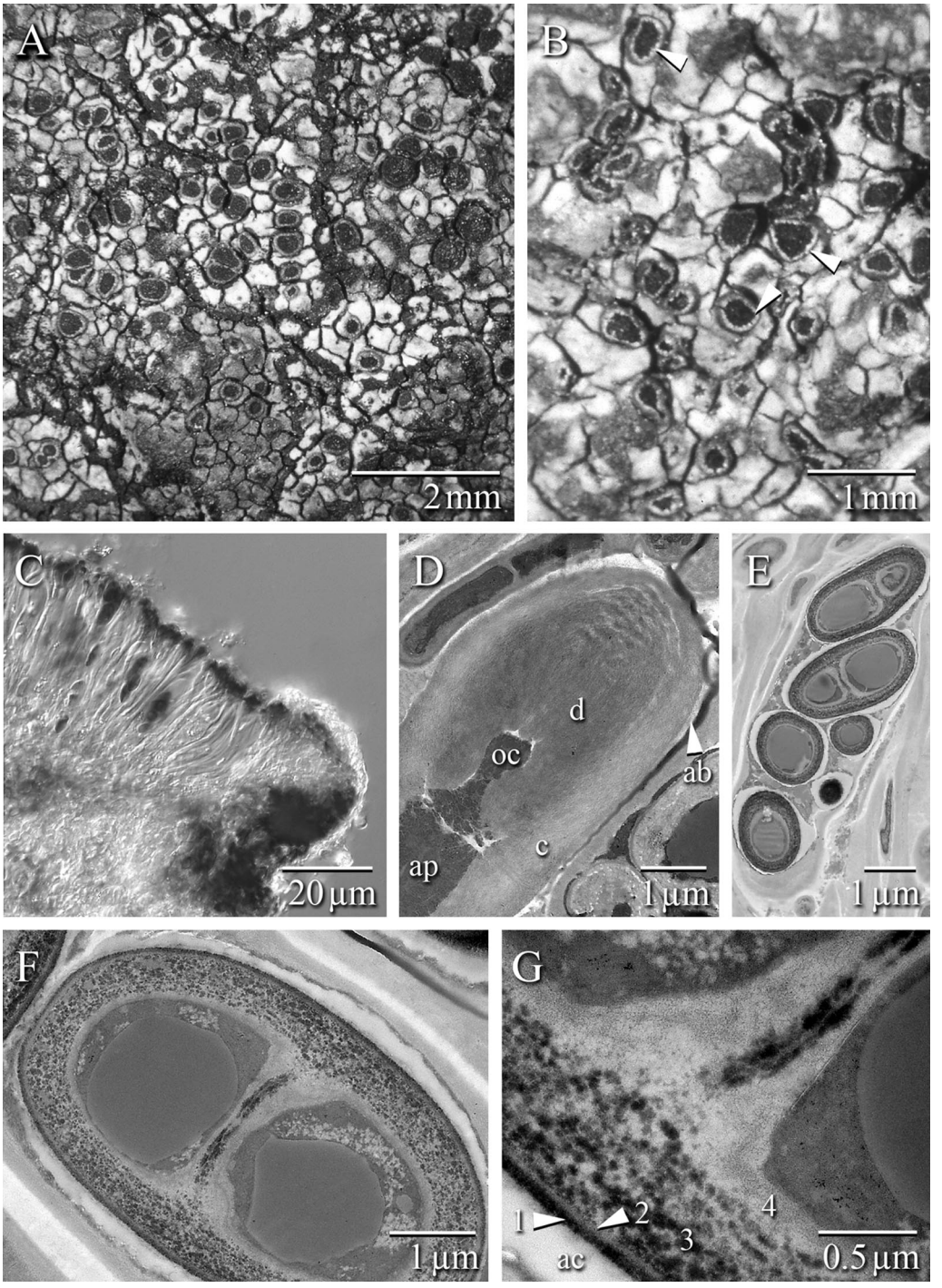

FIGURE 5. *Buellia stellulata* [A–C. light micrographs (*Ryan 31282a*), D–G. TEM micrographs (*Nash 38464*)]. — A. Areolate thallus with immersed to slightly sessile, circular apothecia. — B. Close-up of areoles with ± immersed apothecia, some with a thalline veil (arrows). — C. Transverse section of an apothecium. — D. Immature *Bacidia*-type ascus (for designation of the different layers see Bellemère 1994): spores have not yet formed within the ascoplasm (ap); the ocular chamber (oc) is tear-drop shaped; the innermost layer of the tholus (d) is layered but not yet distinctly differentiated into a d1- and d2-layer; the c-layer (c) is thick and forms the main ascus wall; a- and b-layer (ab) are barely visible and cannot be reliably distinguished (possibly as a result of fixation artifacts). — E. Ascus with mature ascospores. — F. Mature ascospore. — G. Spore wall of a mature ascospore: (ac) ascus wall; (1) perispore; (2) intermediate layer; (3) proper spore wall; (4) endospore.

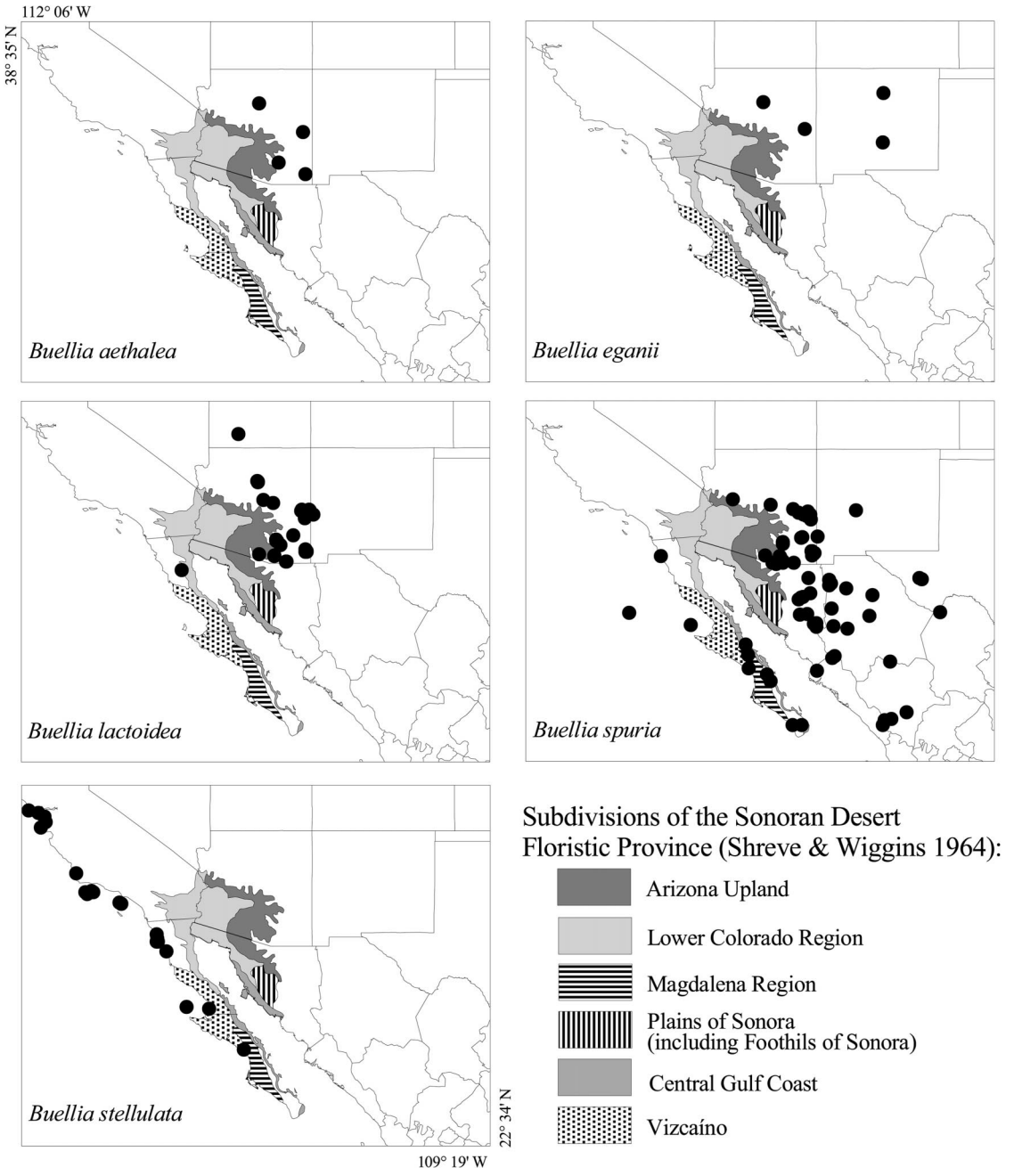

FIGURE 6. Distribution of species treated here in the Greater Sonoran Desert Region (Floristic Provinces according to Shreve & Wiggins 1964).

currently known. Specimens from inland localities of the Sonoran Region identified as *B. stellulata* mostly belong to *B. spuria*. Along the coast, specimens of *B. stellulata* have also been confused with *B. fimbriata* (Tuck.) Sheard or *B. cerrusata* Llimona & Werner. Both names are synonyms of *B. tesserata* Körb. (Rico et al. 2003). *Buellia stellulata* is superficially similar to the maritime *B. tesserata*, but the two species can reliably be distinguished by their distinctly different chemistry (*B. stellulata*: 2′-*O*-methylperlatolic vs. *B. tesserata*: divaricatic acid and related substances). *Buellia tesserata* is also characterized by a more distinctly coarse spore ornamentation (rugulate rather than microrugulate) and the absence of the exciple pigment *cinereorufa*-green from its apothecia. *Buellia stellulata* has a dense, black hypothallus that forms a distinct thallus outline often extending between the areoles.

Buellia tesserata has a fimbriate prothallus, usually not extending between the areoles (i.e., not forming a hypothallus).

Additional specimens examined.—NORTH AMERICA. MEXICO. BAJA CALIFORNIA. *Nash 26116* (ASU); *Kalb 24673b* (hb. Kalb). BAJA CALIFORNIA SUR. *Nash 39773* (ASU). U.S.A. CALIFORNIA. Del Norte Co. *Nash 11532* (ASU). Los Angeles Co. *Weber L-42106* (COLO); *Nash 32099* (ASU). Marin Co. *Weber 8159* (COLO). San Luis Obispo Co. *Riefner L-86315* (COLO). San Mateo Co. *Ryan 21975*. Santa Barbara Co. *Ryan 31283* (ASU). Santa Cruz Co. *Herre L-78271* (COLO).—SOUTH AMERICA. CHILE. JUAN FERNANDEZ ISLANDS. *Imshaug 38014*.—AUSTRALASIA. NEW ZEALAND. SOUTH ISLAND. Marlborough Co. *Nash 19784b* (ASU).

Additional species discussed here:

BUELLIA LEPIDASTRA(Tuck.) Tuck., Syn. N. Americ. Lich. 2: 90. 1888.

Lecidea lepidastra Tuck., Am. Journ. Sci., ser. 2, 25: 249. 1858. TYPE: U.S.A. VERMONT. Windham Co. Brattleborough. On granite, *Frost s.n.* (FH!, lectotype selected here; MICH!, two isolectotypes). NOTE: Three type specimens collected by Frost in Vermont are mounted together with several other collections on a sheet at FH with the number *3276*. The specimen in the lower right corner has a red sticker with the word ''type''. The protologue does not specify a specimen as the holotype and the specimen labeled ''type'' is selected here as the lectotype.

A specimen in M (M-0023904!) is not part of the type, but erroneously labeled as such. The original label reads ''*Buellia lepidastra* Tuck., Willey, Massachusetts''. Both the collector ''Willey'' as well as the locality ''Massachusetts'' have been crossed out and annotated in a different handwriting as: ''*Lecidea lepidastra* Tuck., Americ. J. Arts and Sci. ser. 2, 25: 429 (1888). Vermont: Brattleborough, *Mr. Frost* [Windham County] 42°51′03″ N, 72°33′30″ W.'' It is very unlikely that Frost or Tuckerman would have erroneously labeled this collection and later changed the label data. It is much more likely that the original data are correct and the specimen collected by Willey is not part of the type collection. The specimens collected by Willey were mentioned by Tuckerman when he transferred the species into *Buellia*, but only the collection by Frost is mentioned in the protologue of *Lecidea lepidastra* Tuck. This specimen, not the Willey collection, must therefore be selected as the lectotype.

Additional specimens examined.—NORTH AMERICA. U.S.A. ALABAMA. Unknown Co. *Peters s.n.* (FH). ILLINOIS. Jackson Co. *Hatcher 63* (MSC-146975). MASSACHUSETTS. Norfolk Co. *Willey s.n.* (BM-000660157); *Willey 572, 660* (FH). Hampshire Co. *Tuckerman s.n.* (FH). SOUTH CAROLINA. Chester Co. *Green 106* (M-0061352).

BUELLIA MACULATA Bungartz, *nomen novum pro Buellia stigmaea* Tuck., Syn. N. Americ. Lich. 2: 90. 1888. *non* Körb., Syst. Lich. German.: 226. 1855.

TYPE: U.S.A. PENNSYLVANIA. Chester Co. *Michener 209 ex Tuckerman sheet 3281* (FH!, lectotype selected here; US!, isolectotype). NOTE: The species name *B. stigmaea* Tuck. is illegitimate because it must be considered a later homonym of *B. stigmatea* Körb. due to the extremely similar spelling of the species epithet: ''*stigmaea*'' vs. ''*stigmatea*'' (Art. 53.3. ICNB, Greuter et al. 2000). The original epithet ''*stigmaea*'' literally means ''with stains''. The new epithet ''*maculata*'', meaning ''speckled'', has been chosen here to refer to Tuckerman's original name. The protologue mentions specimens from several localities and a lectotype is therefore selected here.

Additional specimens examined.—NORTH AMERICA. U.S.A. ILLINOIS. Union Co. *Hatcher 47* (MSC-0005815). MARYLAND. Baltimore Co. *Plitt 28, 400a* (MSC-0005812, msc-0005813). MASSACHUSETTS. Barnstable Co. *Brodo 4203* (MSC-0005806, MSC-0005807, MSC-0005808). NEW YORK. Suffolk Co. *Brodo 2672* (MSC-0005811, MSC-0005810, MSC-0005809). NORTH CAROLINA. Stanley Co. *Culberson 5054* (MSC-0005816). TENNESSEE. Hamilton Co. *Calkins s.n.* (MSC-0005814).

KEY TO THE SPECIES

1. Young spores with distinct septum thickening (*Physconia*-type); layers below hymenium initially clearly differentiated into hyaline subhymenium and deep reddish brown hypothecium, hypothecium pigmentation later extending and differentiation less visible ..... *Buellia lacteoidea*
1. Young spores without distinct median thickening (*Beltraminea*-type); layers below hymenium not differentiated, hyaline or pigmented throughout 2
   2. Thallus without atranorin; apothecia remaining immersed, disc irregular 3
   2. Thallus with atranorin; apothecia emergent, disc circular 4
3. Thallus thin, pale gray to dark gray, K+ orange to red (with norstictic acid); apothecia predominantly forming in center of areoles; exciple and epihymenium aeruginose (*cinereorufa*-green, HNO_3+ violet) ..... *Buellia aethalea*
3. Thallus thick, pale gray to pale beige, K−, KC+ pink and C+ pink (with lecanoric acid); apothecia predominantly forming along margins of areoles; exciple and epihymenium brown, not aeruginose (HNO_3−) ..... *Buellia eganii*
   4. Apothecia with aeruginose, HNO_3+ violet pigment (present at least in outer exciple) 5
   4. Apothecia without aeruginose pigment; with distinct eastern North American distribution ..... *Buellia maculata*
5. Thallus granular areolate to verrucose; hypothallus usually faint or absent; apothecia without thalline veil; aeruginose pigmentation usually confined to outermost exciple; species present only in North American Northeast (not in Sonoran Region) ..... *Buellia lepidastra*
5. Thallus areolate, not granular or verrucose; hypothallus usually distinct, rarely faint or absent; apothecia often with thalline veil; aeruginose pigment extending from exciple across epihymenium 6

6. Thallus with norstictic and/or stictic acid (K+ yellow or K+ orange to red, forming orange needles in the compound microscope); medulla I+ blue; inland, usually montane *Buellia spuria*

6. Thallus without norstictic acid (K−, not forming crystals), instead with 2′-*O*-methylperlatolic acid and/or confluentic acid; coastal but not necessarily maritime ... *Buellia stellulata*

Discussion

Species of the *Buellia aethalea*-group can be recognized by a distinctly areolate thallus, often delimited by an extensive black hypothallus, evenly thin-walled *Buellia* (= *Beltraminea*)-type ascospores, *Bacidia*-type asci, and lecideine apothecia sometimes remaining immersed in the thallus. These apothecia are characterized by a thin, and often reduced, exciple colored by the aeruginose HNO_3+ violet pigment *cinereorufa*-green and frequently have a thalline veil.

Thallus.—All species discussed here have a distinctly areolate thallus i.e., with segregated areoles derived from an independent, individual development. *Buellia lepidastra* is the only species with a ± granular areolate to verrucose thallus.

Thalli of all species usually establish on a distinct, black hypothallus that frequently not only surrounds the entire thallus as a distinct outline, but can also delimit separate areoles from one another. The development of this hypothallus varies considerably among specimens of all species and cannot be used to distinguish different species. In a few specimens the black hypothallus is even absent or only poorly developed, but in most specimens it is quite distinct. Thallus color of all species varies from an almost pure white to a dark gray. *Buellia eganii* often has a slight brownish tinge or may even appear distinctly brown. *Buellia lacteoidea* most typically has a creamy white or ivory thallus.

Because of its aeruginose outer exciple and the thin-walled ascospores without median thickening, *B. lepidastra* may belong to the *Buellia aethalea*-group. However, the thallus of *B. lepidastra* is distinctly granular areolate to verrucose and only rarely delimited by an indistinct hypothallus. Too little material has so far been examined to assess its affinities to the *Buellia aethalea*-group.

Apothecia.—All species have similar apothecia that remain immersed for much of their development. In *B. aethalea* and *B. eganii*, apothecia do not emerge from the thallus (Figs. 1A–B, 2A–B). This is also the case for most specimens of *B. lacteoidea* (Fig. 3A–B), but a few specimens of this species have been found with considerably swollen discs that surmount the thallus surface. In all other species, apothecia eventually become adnate to sessile with age.

The outline of the apothecial disc is initially circular in most species. In *B. aethalea*, *B. eganii*, and *B. lacteoidea* (Figs. 1A–B, 2A–B, 3A–B), the discs can become quite irregular and only rarely remain circular in outline. In *B. eganii*, the apothecial disc often becomes moderately convex, whereas it remains plane to concave in *B. aethalea*. Apothecia of *B. aethalea* are typically formed in the center of the areoles; those of *B. eganii* and *B. lacteoidea* develop along the edges of the areoles.

All species have lecideine apothecia. Species with immersed apothecia have been referred to as cryptolecanorine by Scheidegger (1993), even though these species do not have a thalline exciple. In species where the apothecia emerge from the thallus, necrotic thalline material often remains attached to the margin as a thalline veil (Figs. 4B, 5B). This can be very conspicuous in *B. spuria* and *B. stellulata*, but is rarely observed in other species with emerging apothecia. The proper exciple of all species is fairly thin and considerably reduced. The inner excipular hyphae are similar to the paraphyses and have swollen end cells that form the outer exciple. These outer cells are usually strongly carbonized with a brown pigment cap (cf. *elachista*-brown) and are often considerably darkened by a diffuse aeruginose pigment (*cinereorufa*-green). Scheidegger (1993) referred to this thin, considerably reduced exciple as the *aethalea*-type. He emphasized that this type is characterized by the presence of pigment A (= *cinereorufa*-green), but nevertheless assigns some species to this particular exciple type that lack the pigment. *cinereorufa*-green is absent from *B. eganii* and *B. maculata*, even though these species have structurally similar exciples as do all other species discussed here. It is difficult to assess if only the absence of that particular pigment is enough justification to exclude *B. maculata* and *B. eganii* from the *Buellia aethalea*-group.

The amount of *cinereorufa*-green can vary considerably among specimens or even species. In most species the aeruginose diffuse pigmentation extends far into the exciple and across the epihymenium. However, Imshaug (1951) noticed that the pigment is usually confined to the outermost part of the exciple of *B. lepidastra*.

Among these species, both *B. aethalea* and *B. eganii* have a hyaline hypothecium (Figs. 1C, 2C), that is quite unusual within the genus. A hyaline hypothecium is more typical for the genus *Rinodina*, and *Buellia* is usually characterized by a dark, pigmented hypothecium (Helms et al. 2003). Giralt and Matzer (1994) argue convincingly; however, that no single character can be used to distinguish the two genera, and some variation of hypothecium pigmentation has previously been reported in *Buel-*

lia. According to Scheidegger (1993), specimens of *B. aethalea* may have either a hyaline or a pigmented hypothecium. We have not observed strong pigmentation, but some of the specimens show a faint brownish tinge.

Imshaug (1951) emphasized that the hypothecium of *B. lacteoidea* is also unpigmented. This assessment has lead to many misidentifications of specimens of *B. lacteoidea* as *B. spuria* or *B. stellulata*. *Buellia lacteoidea* indeed has a large unpigmented layer of hyphae directly below the hymenium. This colorless subhymenium (Fig. 3C, F) can be distinguished from a pigmented layer below, the hypothecium (Fig. 3F). With age, the pigmentation of the hypothecium becomes more pronounced and may extend partially into the subhymenium. In contrast, *B. spuria* and *B. stellulata* both have layers of hyphae below the hymenium that are strongly pigmented throughout. Thus, a colorless subhymenium cannot be distinguished in these species.

Asci and ascospores.—All species have *Bacidia*-type asci with a conic, non-amyloid central tholus and amyloid flanks that merge at the ascus tip (Figs. 4E, H, 5D). This ascus type is the most diagnostic difference in distinguishing *Buellia* from *Rinodina*. Ascospores of all species are not pigmented at very early stages, very soon become olive, and are distinctly brown at maturity. Apart from *B. lacteoidea*, all ascospores are thin-walled with no septum thickening (*Beltraminea*- or *Buellia*-type). *Buellia lacteoidea* has a distinct septum thickening (*Physconia*-type) at least during some stage of the spore ontogeny. Spore ornamentation of all species is microrugulate, but sometimes appears smooth (not ornamented) in specimens of *B. spuria* and *B. stellulata*. Spore ornamentation is a direct result of fractures in the perispore wall layer (Nordin 2000). These fractures can reliably only be observed in the TEM. More material of both *B. spuria* and *B. stellulata* needs to be examined with the TEM to assess whether the ornamentation is a result of the spore ontogeny. It is possible that the observed variation corresponds to distinct taxonomic groups i.e., subspecies or even cryptic species within the two taxa. Differences in spore ornamentation could, however, also be related to the ontogeny of the perispore i.e., fracturing may occur at a later stage of spore development only.

Coniodiomata.—All species have bacilliform conidia formed on similar conidiophores in structurally identical pycnidia. Measurements of the conidia are not sufficiently different to segregate the species.

Chemistry.—The chemistry of all species is not complex. *Buellia aethalea* and *B. eganii* are the only species that consistently lack the depside atranorin. *Buellia aethalea* is characterized by the depsidone norstictic acid, and the thallus reacts K+ yellow becoming deep red (forming needle-shaped orange crystals). In contrast, thalli of *B. eganii* react K− (or indistinctly yellow) and C+ pink, KC+ pink. Egan (1971) already observed these fleeting reactions and suggested that gyrophoric or lecanoric acid should be present in the species. HPLC analysis confirms the presence of lecanoric acid. In addition, the depside 5-*O*-methylhiascic acid was also detected. Some specimens of *B. lacteoidea* contain gyrophoric acid and also react C+ pink, KC+ pink.

It was first assumed that thalli of *B. spuria* and *B. stellulata* might not consistently be different in their chemistry, and possibly belong to the same species. Thalli of *B. spuria*, however, consistently have atranorin and norstictic acid, whereas *B. stellulata* is characterized by atranorin and 2′-*O*-methylperlatolic and/or confluentic acid. These differences in secondary metabolites correlate with differences in distribution and iodine reactions of the thallus.

As previously reported by Scheidegger (1993), the iodine reaction of the thallus varies in specimens of *B. aethalea* and can therefore not be used as a distinct character to distinguish this species from any of the others. In all other species, the iodine reaction of the thallus is, however, very consistent. Thus, the two similar species, *B. stellulata* (medulla I−) and *B. spuria* (medulla I+ blue) are clearly distinguished by their different reaction.

Distribution.—Imshaug (1951) did not include *Buellia aethalea* in his monograph of North American species, but suggested that reports might be misidentifications. Although the North American Checklist (Esslinger 1997) has listed *Buellia aethalea*, it is not certain which particular specimens these records are based on. Among the Sonoran specimens only very little material can be assigned to *Buellia aethalea s.str.* Several herbarium specimens identified as *B. aethalea* from outside the Sonoran Region also do not belong to *Buellia aethalea s.str.* Instead, most of the material has proven to be *Buellia spuria*. Thus, it is difficult to assess how common *B. aethalea* is in North America. In the Southwest, the species appears to be confined to higher elevations. It is probably more common at higher latitudes.

Like *B. aethalea*, *Buellia eganii* is currently known from only a few localities. All these localities are subalpine to alpine habitats, usually above the timberline. The species was initially considered a synonym of *B. aethalea*, but is described here as a distinct species based on the absence of *cinereorufa*-green from the apothecia, comparatively exuberant thalli with larger apothecia forming along the margin of thallus areoles, and the presence of lecanoric instead of norstictic acid.

In the Sonoran Desert Region, *Buellia spuria* is clearly the most widely distributed species of the group. *Buellia spuria* is most common throughout montane habitats, but in southern California and Baja California it is also quite frequently encountered at lower elevations. Nevertheless, it is not a typical desert species and is absent from the central Sonoran Desert. Along the coast it is regularly confused with *Buellia stellulata*, a similar species that maintains a distinctly different thallus chemistry and does not extend far inland. *Buellia stellulata*, although typical along the coast, is not strictly maritime. Imshaug (1951) reported that the species is restricted to the Pacific coast. The species, however, also occurs along the Atlantic coast, where it has often been confused with *B. maculata*. *Buellia maculata* differs from *B. stellulata* by its different thallus chemistry and the absence of any aeruginose exciple pigmentation. *Buellia maculata* has apparently the same chemistry as thalli of *Buellia spuria*, but again can be distinguished from *B. spuria* by the absence of *cinereorufa*-green in the exciple.

Although previously reported from the region, *Buellia lepidastra* does not extend into the North American Southwest. Among the material reported as *B. lepidastra* from the Sonoran Region no specimens matched material from the Northeast. As Imshaug (1951) suggested, the species indeed appears to be confined to eastern North America.

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